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Exploitation of heterosis and examination of inbreeding depression in pearl millet (*Pennisetum glaucum* (L.) R. Br.)

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ABSTRACT

A comprehensive investigation entitled “Exploitation of heterosis and examination of inbreeding depression in pearl millet (*Pennisetum glaucum* (L.) R. Br.)” was conducted at the Instructional Farm, Junagadh Agricultural University, Junagadh, across two consecutive seasons, namely summer 2024 and kharif 2024. Primary objective of this study was to elucidate the nature and magnitude of heterosis and inbreeding depression along with key yield-contributing traits under varying seasonal conditions.

The experimental material comprised of six basic generations viz., P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 of four crosses of pearl millet i.e. ICMB-95444 × J-2627 (Cross 1), 86-SB-21 × J-2640 (Cross 2), J-2636 × J-2340 (Cross 3) and J-2635 × J-2614 (Cross 4) developed through the crossing program conducted during kharif season in 2022-23.

The observations recorded for days to first flowering, days to maturity, plant height (cm), number of nodes on main shoot, number of effective tillers per plant, earhead length (cm), earhead diameter (cm), grain yield per plant (g), fodder yield per plant (g), 1000-seed weight (g), harvest index (%), panicle index (%) and blast incidence were subjected to estimate heterosis and inbreeding depression.

The analysis of variance indicated that mean squares due to crosses were significant for all traits in both environments, except blast incidence. Significant differences among populations within all four crosses and non-significant Bartlett's test confirmed homogeneity of error variance, validating the suitability of the material for genetic analysis. Furthermore, significant variation among the six generations within each cross justified the use of generation mean analysis along with estimation of heterosis.

Highly significant and positive relative heterosis, heterobeltiosis and inbreeding depression were observed across all crosses for most traits. The expression of significant heterosis over the mid-parent and better parent coupled with positive inbreeding depression, suggests a major contribution from dominance (h) and additive × additive (i) gene interactions. This indicates that selection for these traits would be more effective in later generations. Grain yield per plant in pearl millet showed consistently high heterosis across both seasons, with Cross 4 being the most superior. Significant inbreeding depression was observed in Cross 1, Cross 3 and Cross 4. Stable performance across kharif and summer suggests good adaptability, while non-additive gene effects play a key role in yield expression.

Keywords: Relative heterosis, Heterobeltiosis, Inbreeding depression, Pearl millet

Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a major staple food and fodder crop. Commonly known as bajra, it is also referred to as cattail millet, spiked millet or bulrush millet in different parts of the world. It is a diploid ($2n = 2x = 14$), annual cereal characterized by profuse tillering, belonging to the family *Poaceae* and subfamily *Panicoideae*. Pearl millet is a major highly cross-pollinated crop due to protogynous habit of flowering. Being a C_4 plant, it has a very high photosynthetic efficiency and dry matter production capacity. Pearl millet originated in tropical western Africa. From there, it differentiated into two races, globosum race that moved to the western side and the typhoides race that reached eastern Africa and spread to India and south Africa (Satyavathi *et al.*, 2021) [1].

Compared with other cereals, the crop adapts well to the driest and marginal soils. It is grown under the marginal environments with frequent drought, high temperature, low and erratic rainfall and infertile soils with poor water holding capacity. In north, pearl millet is grown as rainy season crop, whereas in south and north-west India it may be grown in two or even three seasons in a year. Pearl millet has a unique place among rainy season (*kharif*) crops due to its high potential of drought tolerance. It also provides good quality fodder to cattle in arid and semi-arid tropical regions and is recognised as a valuable forage crop due to its robust and fast growth habit. The stalk is used for fuel and thatching, the leaves for fodder (Singh *et al.*, 2017) [2].

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Pearl millet is a major source of dietary energy for rural population and is the fourth most important cereal after rice, wheat and sorghum in India. The grain of pearl millet is a good source of thiamine, riboflavin and niacin. Pearl millet grain is also used for non-food purpose like poultry feed, cattle feed and alcohol extraction. (Basavaraj *et al.*, 2010) [3]. Nutritionally, pearl millet grains are superior to rice and wheat, being rich in energy (360-370 kcal/100 g), protein (8-15%), essential amino acids, dietary fiber and minerals, particularly iron (6-8 mg/100 g) and zinc (3-4 mg/100 g). The crop also contributes to fodder, silage and stover for livestock, playing a dual role in food and feed security. (Rao *et al.*, 1951) [4].

The gene action of each quantitative and qualitative trait can be assessed through generation mean analysis. Several models for generation mean analysis have been developed, as described by Hayman (1958) [5]. Procedures to estimate the mean and variance of quantitative traits were proposed using six basic generations, including parents (P_1 and P_2), F_1 , F_2 and two backcrosses (BC_1 and BC_2). Generation means analysis is used to dissect gene action controlling quantitative traits by analysing basic generations based on means and variances using standard statistical models (Kearsey *et al.*, 1968; Mather *et al.*, 2013) [6, 7]. These models provide information on the average gene effects (additive effects), dominance deviations, and epistatic effects, which can help quantify the genotypic value of individuals and, in turn, contribute to determining the average generation genotypic value (Hayman, 1958) [5]. In this context, understanding the magnitude of gene action and type of epistasis can inform the design of breeding strategies (Ranjan *et al.*, 2021) [8].

Pearl millet is predominantly cross-pollinated crop characterized by protogyny, which facilitates the creation of hybrids. The phenomenon of heterosis, or hybrid vigor, has been extensively documented in pearl millet, particularly for yield and resistance traits, making hybrids favoured approach to boost productivity (Rai *et al.*, 2008) [9]. Nonetheless, hybrid breeding programs encounter challenges such as inbreeding depression when parental lines undergo self-pollination, highlighting the necessity of comprehending the genetic foundations of heterosis and inbreeding effects on yield and blast resistance. This suggests that in genetic out-crossing, the interaction of diverse alleles in the F_1 generation results in superior performance compared to the homozygous genotypes of the inbred parental lines. Although the enhanced performance of F_1 heterozygous hybrids over inbred parental homozygous lines is well established, continuous self-pollination of these hybrids over several generations can lead to inbreeding depression. (Srivastava *et al.*, 2020) [10].

Materials and methods

A comprehensive investigation entitled “Exploitation of heterosis and examination of inbreeding depression in pearl millet (*Pennisetum glaucum* (L.) R. Br.)” was conducted at the Instructional Farm, Junagadh Agricultural University, Junagadh, across two consecutive seasons, namely summer 2024 and *kharif* 2024. The experimental material comprised of six basic generations viz., P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 of four crosses of pearl millet i.e. ICMB 95444 × J-2627 (Cross 1), 86-SB-21 × J-2640 (Cross 2), J-2636 × J-2340 (Cross 3) and J-2635 × J-2614 (Cross 4) developed through the crossing program conducted during *kharif* season in 2022-23.

Results

The analysis of variance for the compact family block design, involving thirteen characters, was carried out separately for each of the four crosses under two comparative environments (summer and *kharif*). The results of the analysis of variance between the families (crosses) and among the progenies within the families (between generations) are presented in Tables 1 and Table 2. The analysis of variance between families revealed that the mean squares due to crosses were significant for all the traits in both environments except blast incidence in *kharif* season. All four crosses also exhibited highly significant differences between populations in the mean sum of squares for most of the characters in both environments. The Bartlett's test for

homogeneity of error variance for four crosses indicated that error variances were homogenous for all traits as revealed by non-significant chi-square values. Hence, the selected crosses were diverse enough to study the additive, dominance and epistatic variances that govern the inheritance of different traits under both environments.

For days to first flowering, negative heterosis is considered desirable for early maturity. During the summer season, the genetic expression followed a similar directional trend. Mid-parent heterosis remained non-significant for all crosses, with Cross 1, Cross 3, and Cross 4 maintaining negative observed values. Better-parent heterosis demonstrated significant positive deviations in Cross 1 (5% level), Cross 2 (1% level), and Cross 4 (1% level), while it became non-significant in Cross 3. Observed inbreeding depression was again non-significant for all four crosses. In the *kharif* season, non-significant differences between observed and expected mid-parent heterosis in all four crosses indicated a reliable genetic model fit. While Cross 1, Cross 3, and Cross 4 showed desired negative mid-parent heterosis, these values were statistically non-significant. Conversely, better-parent heterosis showed significant positive deviations for all four crosses, with Cross 1, Cross 2, and Cross 4 significant at the 1% level and Cross 3 at the 5% level. Observed inbreeding depression remained non-significant across all four populations.

For days to maturity, negative heterosis is preferred for identifying early-maturing genotypes. During the summer season, the genetic parameters for maturity displayed a more subdued statistical profile. Mid-parent heterosis remained non-significant across all four crosses, with Cross 1 again maintaining its negative observed value. Regarding better-parent heterosis, only Cross 4 retained its significant positive deviation (at the 1% level), while Cross 3 shifted from non-significant in summer to significant in the *kharif* environment. Observed inbreeding depression continued to be non-significant for all crosses. The persistence of non-significant results in most crosses during summer suggests that the maturity trait is less influenced by extreme heterotic effects under high-temperature conditions. In the *kharif* season, observed mid-parent heterosis was non-significant for all four crosses, with only Cross 1 showing a trend in the desired negative direction. For better-parent heterosis, significant positive deviations were recorded in Cross 3 (at the 5% level) and Cross 4 (at the 1% level), indicating a tendency toward delayed maturity in these specific combinations. Conversely, Cross 1 and Cross 2 remained non-significant. Observed inbreeding depression was non-significant across.

For plant height in the summer season, the expression of plant height remained remarkably consistent and robust. Mid-parent heterosis continued to be highly significant for Cross 1, Cross 3, and Cross 4, with Cross 2 again showing a non-significant results. Similarly, better-parent heterosis remained highly significant across all crosses, although the significance for Cross 4 was recorded at the 5% level. The observed inbreeding depression closely mirrored the *kharif* results, staying significant in Cross 1, Cross 3, and Cross 4. These results suggest that the genetic mechanisms governing plant height in these Pearl Millet crosses are highly stable and less susceptible to the heat stress typical of the summer environment. In the *kharif* season, plant height in pearl millet exhibited substantial positive heterosis, which is a key indicator of hybrid vigor for biomass and forage potential. Mid-parent heterosis was highly significant at the 1% level in Cross 1, Cross 3, and Cross 4, while Cross 2 remained non-significant. Regarding better-parent heterosis, all four crosses showed highly significant positive deviations (1% level), with Cross 4 recording the maximum observed value. Observed inbreeding depression was significant in Cross 1 (5% level), Cross 3 (1% level), and Cross 4 (1% level), whereas Cross 2 showed a non-significant response, indicating varying degrees of genetic load for height across the four populations.

For Number of nodes on main shoot in the summer season, the results remained statistically identical in terms of observed performance. Mid-parent heterosis continued to be highly significant for Cross 1, Cross 3, and Cross 4, with Cross 2 remaining non-significant. For better-parent heterosis Cross 2 and Cross 3 were highly significant with

Cross 3 showed positive deviation. Inbreeding depression was highly significant for Cross 1, Cross 3 and Cross 4 with all four crosses showed positive deviation. In the *kharif* season, the number of nodes on the main shoot exhibited significant positive heterosis. Mid-parent heterosis was highly significant (1% level) in Cross 1, Cross 3, and Cross 4, while Cross 2 remained non-significant. Regarding better-parent heterosis, Cross 2 and Cross 3 showed highly significant deviations (1% level) with positive deviation in Cross 3 indicating a strong over-dominance effect for node formation. Observed inbreeding depression was also significant at the 1% level in Cross 1, Cross 3, and Cross 4, highlighting a clear reduction in node number upon selfing, whereas Cross 2 showed a non-significant response.

For Number of effective tillers per plant During the summer season, the observed values remained highly robust with increased statistical precision. Mid-parent heterosis and better-parent heterosis were highly significant (1% level) across all four crosses, except Cross 2 in better parent heterosis. Observed inbreeding depression mirrored the *kharif* season exactly, remaining highly significant for Cross 1, Cross 3, and Cross 4, and non-significant for Cross 2. In the *kharif* season, the number of effective tillers per plant exhibited significant positive heterosis, which is a vital yield-contributing trait in Pearl Millet. Mid-parent heterosis was highly significant (1% level) in Cross 1, Cross 3, and Cross 4, and significant (5% level) in Cross 2. Regarding better-parent heterosis, all four crosses showed highly significant positive deviations (1% level) except Cross 2, indicating strong over-dominance for tiller production. Observed inbreeding depression was significant at the 1% level in Cross 1, Cross 3, and Cross 4, while Cross 2 showed a non-significant response, suggesting that most populations carry a genetic load that reduces tillering vigor upon selfing.

For earhead length During the summer season, the results for earhead length remained remarkably consistent with those of the *kharif* season. Mid-parent heterosis continued to be highly significant for Cross 1, Cross 3, and Cross 4, while Cross 2 maintained its non-significant status. Similarly, better-parent heterosis and inbreeding depression retained their established significance patterns across all four crosses except Cross 2 for inbreeding depression. In the *kharif* season, earhead length exhibited significant positive heterosis, a vital component for increasing grain sink capacity in Pearl Millet. Mid-parent heterosis was highly significant (1% level) in Cross 1, Cross 3, and Cross 4, while Cross 2 remained non-significant. Regarding better-parent heterosis, all four crosses showed highly significant positive deviations (1% level), indicating strong over-dominance for head length. Observed inbreeding depression was significant in Cross 1 (5% level), Cross 3 (1% level), and Cross 4 (1% level), suggesting a reduction in head length upon selfing, whereas Cross 2 showed a non-significant response.

For Earhead diameter During the summer season, the observed values for earhead diameter remained highly stable. Mid-parent heterosis and better-parent heterosis continued to be highly significant for Cross 1, Cross 3, and Cross 4, with Cross 2 again showing a non-significant results. Interestingly, the observed inbreeding depression became non-significant across all four crosses in the summer, despite maintaining the same numerical values. This shift suggests that environmental heat may slightly increase the standard error or variance, reducing the statistical detectable levels of inbreeding effects. In the *kharif* season, earhead diameter exhibited significant positive heterosis, contributing to increased grain volume per head. Mid-parent heterosis better-parent heterosis was highly significant (1% level) in Cross 1, Cross 3, and Cross 4, while Cross 2 was non-significant. highly significant positive deviations for better-parent heterosis, indicating robust over-dominance for head thickness. Observed inbreeding depression was significant at the 5% level in Cross 3 and Cross 4, while Cross 1 and Cross 2 remained non-significant, suggesting that the reduction in head girth upon selfing is more pronounced in specific genetic combinations.

For Grain yield per plant (g) During the summer season, the observed values for grain yield remained highly robust and statistically differed to the *kharif* results. Mid-parent continued to be highly significant

(1% level) for all crosses except Cross 2. Better-parent heterosis was highly significant (1% level) for all crosses. Observed inbreeding depression was highly significant for all four crosses. These results indicate that the physiological and genetic mechanisms driving grain yield are consistently expressed in these Pearl Millet hybrids, showing high adaptability to the increased temperatures and light intensity of the summer environment. In the *kharif* season, grain yield per plant exhibited exceptionally high and significant positive heterosis, reflecting the cumulative effect of yield-contributing traits in Pearl Millet. Mid-parent heterosis was highly significant (1% level) across all four crosses, with Cross 4 recording the maximum observed value. Regarding better-parent heterosis, all four crosses showed highly significant positive deviations (1% level), indicating massive over-dominance for grain production. Observed inbreeding depression was also highly significant at the 1% level in Cross 1, Cross 3, and Cross 4, while Cross 2 showed a non-significant response. This suggests a strong genetic load for yield in most populations, resulting in a significant performance reduction upon selfing.

For Fodder yield per plant During the summer season, the results for fodder yield remained remarkably different. Mid-parent heterosis were significant for Cross 1, Cross 3 and Cross 4 while better-parent heterosis were highly significant (1% level) for Cross 2 and Cross 3. Observed inbreeding depression followed the exact same pattern as the *kharif* season, staying highly significant for Cross 1, Cross 2, Cross 3, and Cross 4. These results indicate that the genetic potential for high biomass production in these Pearl Millet hybrids is extremely stable and resilient to the high temperatures and evaporative demand of the summer environment. In the *kharif* season, fodder yield per plant demonstrated substantial positive heterosis, a critical trait for the dual-purpose utility of Pearl Millet. Mid-parent heterosis was highly significant (1% level) in Cross 1, Cross 3, and Cross 4, and significant (5% level) in Cross 2. For better-parent heterosis, all four crosses exhibited highly significant positive deviations (1% level), with Cross 4 showing the most dramatic observed gain. Observed inbreeding depression was highly significant at the 1% level in Cross 1, Cross 3, and Cross 4, while Cross 2 was non-significant, suggesting that high fodder biomass in these hybrids is largely maintained by non-additive genetic effects that dissipate upon selfing.

For 1000-seed weight During the summer season, observed values for 1000-seed weight remained remarkably stable with nearly identical results. Mid-parent heterosis was highly significant for Cross 1, Cross 3 and Cross 4, with Cross 2 again showing a non-significant results. Similarly, better-parent heterosis maintained highly significant positive deviations across all four crosses. Observed inbreeding depression continued to be highly significant for Cross 3 and Cross 4. These consistent patterns indicate that genetic control for grain density and development in these Pearl Millet hybrids is highly robust and largely unaffected by the seasonal transition. In the *kharif* season, 1000-seed weight exhibited significant positive heterosis, which is a critical indicator of grain size and quality. Mid-parent heterosis was highly significant (1% level) in Cross 1, Cross 3 and Cross 4, while Cross 2 was non-significant. Regarding better-parent heterosis, Cross 2, and Cross 3 showed highly significant deviations (1% level), indicating strong over-dominance for seed weight. Observed inbreeding depression was significant at the 1% level in Cross 3 and Cross 4, whereas Cross 1 and Cross 2 recorded non-significant results, suggesting that the genetic stability for seed size varies across these specific cross combinations.

For Harvest index During the summer season, the harvest index maintained a similar and robust genetic profile. Mid-parent heterosis remained highly significant for Cross 1, Cross 3, and Cross 4, with Cross 2 showing a non-significant trend. However, better-parent heterosis became highly significant across all four crosses, as Cross 2 reached the 1% significance level in this environment. Observed inbreeding depression mirrored the *kharif* results, staying highly significant for Cross 1, Cross 3, and Cross 4, and non-significant for Cross 2. These consistent observed values across seasons suggest that the genetic mechanisms for grain-filling efficiency in these hybrids are

highly stable under varying environmental conditions. In the *kharif* season, harvest index, reflecting the efficiency of dry matter partitioning into grain, showed significant positive heterosis. Mid-parent heterosis was highly significant (1% level) in all four crosses. For better-parent heterosis, Cross 1, Cross 3, and Cross 4 exhibited highly significant positive deviations, whereas Cross 2 remained non-significant. Observed inbreeding depression was highly significant at the 1% level in Cross 1, Cross 3, and Cross 4, while Cross 2 showed a non-significant response. This indicates that for most crosses, the physiological efficiency gained in the F_1 generation is substantially reduced upon selfing.

For Panicle index During the summer season, the observed values for the panicle index remained identical to the *kharif* season, but the statistical significance for the most promising genotypes was enhanced. Mid-parent heterosis for Cross 4 became significant at the 5% level, while it remained non-significant for the other three crosses. Similarly, better-parent heterosis for Cross 4 reached a higher significance level (1% level) compared to the *kharif* environment. Observed inbreeding depression continued to be non-significant across all four crosses. This suggests that the summer environment, likely due to higher light intensity, allows for a more precise expression and statistical detection of superior grain-packing traits in certain hybrids. In the *kharif* season, the panicle index, representing the ratio of grain weight to total panicle weight. Mid-parent heterosis was non-significant for all four crosses, though all maintained positive observed values. For better-parent heterosis, all four crosses showed a non-significant deviation. Observed inbreeding depression was non-significant across all four populations, indicating that the grain-filling efficiency relative to the panicle structure is fairly well-fixed in these specific genetic combinations during the *kharif* cycle.

For Blast incidence During the summer season, the trend for disease resistance remained remarkably different and low. Mid-parent heterosis continued to be highly significant and negative (1% level) for Cross 1, Cross 2 and Cross 4, with the magnitude of resistance ap-

pearing slightly stronger in Cross 1 and Cross 4 compared to the *kharif* season. Better-parent heterosis remained highly significant for Cross 3 and Cross 4, while it became non-significant for Cross 1 and Cross 2. Notably, observed inbreeding depression remained highly significant and negative for Cross 1 and Cross 4 while significant for Cross 2, confirming that the genetic basis for blast resistance is well-stabilized even under the higher temperatures of the summer environment. In the *kharif* season, the blast index showed highly significant negative mid-parent heterosis across all four crosses (at the 1% level). For disease resistance traits like blast, negative values are highly desirable as they indicate a reduction in disease severity compared to the parental average. Conversely, better-parent heterosis showed significant positive deviations for Cross 1, Cross 3, and Cross 4, suggesting that while the hybrids outperformed the mid-parent average, they remained slightly more susceptible than the most resistant parent. Observed inbreeding depression was highly significant and negative for all four crosses, a favourable result indicating that the progeny in the subsequent F_1 generation maintained or even enhanced their resistance levels compared to the hybrids.

Conclusion

Highly significant and positive relative heterosis, heterobeltiosis and inbreeding depression were observed across all crosses for most traits. The expression of significant heterosis over the mid-parent and better parent coupled with positive inbreeding depression, suggests a major contribution from dominance (*h*) and additive $\times$ additive (*i*) gene interactions. This indicates that selection for these traits would be more effective in later generations. Grain yield per plant in pearl millet showed consistently high heterosis across both seasons, with Cross 4 being the most superior. Significant inbreeding depression was observed in Cross 1, Cross 3 and Cross 4. Stable performance across *kharif* and summer suggests good adaptability, while non-additive gene effects play a key role in yield expression.

Table 1. Analysis of variances (mean squares) among families (crosses) and among progenies within family of six basic generations for different characters in pearl millet during summer 2024

Source	d.f.	Days to first flowering	Days to maturity	Plant height (cm)	Number of nodes on main shoot	Number of effective tillers per plant	Earhead length (cm)	Earhead diameter (cm)
Analysis of variance among families								
Replications	2	1.85	2.11	32.45	0.05	0.12	1.54	0.02
Crosses	3	14.23**	18.95**	412.33**	1.85**	2.12*	12.45**	0.22**
Error	6	0.95	1.24	15.65	0.09	0.35	0.85	0.02
Chi square @	5	NS	NS	NS	NS	NS	NS	NS
Analysis of variance among progenies within family								
Results and Discussion								
ICMB-95444 $\times$ J-2627 (Cross 1)								
Replications	2	1.25	4.88	15.6	0.05	0.11	1.45	0.01
Generations	5	45.22**	98.65**	1250.40**	4.85**	3.95**	22.45**	0.85**
Error	10	0.85	3.12	18.55	0.11	0.25	0.92	0.03
86-SB-21 $\times$ J-2640 (Cross 2)								
Replications	2	1.15	3.95	18.25	0.04	0.15	1.65	0.02
Generations	5	38.65**	85.40**	1120.50**	3.95**	3.10**	19.85**	0.72**
Error	10	0.92	2.85	20.15	0.1	0.28	0.88	0.04
J-2636 $\times$ J-2340 (Cross 3)								
Replications	2	1.45	4.1	14.8	0.06	0.1	1.55	0.01
Generations	5	41.20**	92.15**	1180.20**	4.25**	3.45**	21.10**	0.78**
Error	10	0.88	3.05	19.2	0.12	0.24	0.95	0.03
J-2635 $\times$ J-2614 (Cross 4)								
Replications	2	1.35	4.55	22.4	0.07	0.14	1.75	0.02

(continued on next page)

Source	d.f.	Days to first flowering	Days to maturity	Plant height (cm)	Number of nodes on main shoot	Number of effective tillers per plant	Earhead length (cm)	Earhead diameter (cm)
Generations	5	52.40**	105.80**	1350.60**	5.15**	4.25**	24.50**	0.92**
Error	10	0.95	3.25	21.5	0.13	0.29	1.05	0.04

*, ** Significant at 5 and 1 % levels, respectively

@ Chi-square for Bartlett's test of homogeneity of error variances, S = significant and NS = non-significant

Table 1. Cont.

Source	d.f.	Grain yield per plant (g)	Fodder yield per plant (g)	1000-seed weight (g)	Harvest Index (%)	Panicle Index (%)	Blast incidence
Analysis of variance among families							
Replications	2	0.42	0.54	0.15	1.25	5.45	0.01
Crosses	3	209.42**	226.04*	4.85**	22.45**	45.22**	1.87**
Error	6	1.02	26.77	0.25	2.15	4.85	0.007
Chi square @	5	NS	NS	NS	NS	NS	NS
Analysis of variance among progenies within family							
ICMB-95444 × J-2627 (Cross 1)							
Results and Discussion							
Replications	2	11.86*	115.85	0.12	1.85	4.12	0.14*
Generations	5	432.39**	937.69**	6.85**	35.40**	115.60**	6.11**
Error	10	2.4763	72.47	0.21	2.1	5.25	0.02
86-SB-21 × J-2640 (Cross 2)							
Replications	2	0.64	89.83	0.15	1.45	3.95	0.02
Generations	5	307.83**	1205.42**	5.95**	32.10**	98.45**	2.64**
Error	10	1.41	34.45	0.24	2.25	4.85	0.04
J-2636 × J-2340 (Cross 3)							
Replications	2	0.92	103.75	0.14	1.65	4.05	0.02
Generations	5	231.61**	249.28**	6.25**	34.25**	105.20**	1.47**
Error	10	2.36	43.31	0.22	2.15	5.1	0.01
J-2635 × J-2614 (Cross 4)							
Replications	2	7.52	175.82	0.18	2.05	5.2	0.005
Generations	5	897.42**	3780.76**	7.45**	42.15**	125.40**	6.71**
Error	10	6.77	82.20	0.26	2.45	5.85	0.003

*, ** Significant at 5 and 1 % levels, respectively

@ Chi-square for Bartlett's test of homogeneity of error variances, S = significant and NS = non-significant

Table 2. Analysis of variances (mean squares) among families (crosses) and among progenies within family of six basic generations for different characters in pearl millet during *kharif* 2024

Source	d.f.	Days to first flowering	Days to maturity	Plant height (cm)	Number of nodes on main shoot	Number of effective tillers per plant	Earhead length (cm)	Earhead diameter (cm)
Analysis of variance among families								
Replications	2	1.65	2.05	28.55	0.05	0.11	1.45	0.01
Crosses	3	12.85**	16.45**	385.20**	1.65**	1.95*	11.20**	0.20**
Error	6	0.88	1.15	14.2	0.08	0.31	0.75	0.02
Chi square @	5	1.95 NS	NS	NS	NS	NS	NS	NS
Analysis of variance among progenies within family								
ICMB-95444 × J-2627 (Cross 1)								
Replications	2	1.1	4.15	12.8	0.04	0.09	1.25	0.01
Generations	5	38.45**	88.20**	1150.30**	4.15**	3.25**	19.85**	0.75**

(continued on next page)

Source	d.f.	Days to first flowering	Days to maturity	Plant height (cm)	Number of nodes on main shoot	Number of effective tillers per plant	Earhead length (cm)	Earhead diameter (cm)
Error	10	0.78	2.85	16.4	0.09	0.21	0.82	0.02
86-SB-21 × J-2640 (Cross 2)								
Replications	2	1.05	3.65	14.5	0.03	0.11	1.35	0.01
Generations	5	35.10**	81.50**	1050.20**	3.65**	2.85**	18.40**	0.65**
Error	10	0.85	2.6	18.2	0.08	0.24	0.78	0.03
J-2636 × J-2340 (Cross 3)								
Replications	2	1.25	3.85	13.6	0.05	0.08	1.4	0.01
Generations	5	36.80**	84.60**	1090.50**	3.85**	3.05**	19.15**	0.69**
Error	10	0.82	2.75	17.5	0.1	0.2	0.85	0.03
J-2635 × J-2614 (Cross 4)								
Replications	2	1.15	4.05	18.5	0.06	0.12	1.55	0.02
Generations	5	48.50**	95.20**	1250.40**	4.65**	3.85**	22.10**	0.82**
Error	10	0.88	2.95	19.8	0.11	0.26	0.95	0.03

*, ** Significant at 5 and 1 % levels, respectively

@ Chi-square for Bartlett's test of homogeneity of error variances, S = significant and NS = non-significant

Results and Discussion

Table 2. Cont.

Source	d.f.	Grain yield per plant (g)	Fodder yield per plant (g)	1000-seed weight (g)	Harvest Index (%)	Panicle Index (%)	Blast incidence
Analysis of variance among families							
Replications	2	10.55	40.15	0.14	1.1	4.95	0.04
Crosses	3	310.20**	1080.50**	4.25**	20.15**	42.50**	0.75
Error	6	19.85	48.2	0.21	1.95	4.25	0.31
Chi square @	5	NS	NS	NS	NS	NS	NS
Analysis of variance among progenies within family							
ICMB-95444 × J-2627 (Cross 1)							
Replications	2	10.2	38.5	0.1	1.55	3.85	0.02
Generations	5	1620.40**	3150.60**	5.95**	31.20**	98.50**	38.40**
Error	10	13.5	42.1	0.18	1.85	4.55	0.12
86-SB-21 × J-2640 (Cross 2)							
Replications	2	9.4	35.2	0.12	1.25	3.45	0.02
Generations	5	1480.20**	2950.40**	5.25**	28.50**	88.20**	35.60**
Error	10	12.8	39.5	0.21	1.95	4.15	0.15
J-2636 × J-2340 (Cross 3)							
Replications	2	9.8	36.5	0.11	1.35	3.65	0.01
Generations	5	1540.60**	3050.20**	5.60**	29.80**	92.40**	37.10**
Error	10	13.2	40.8	0.19	1.88	4.3	0.14
J-2635 × J-2614 (Cross 4)							
Replications	2	12.5	48.6	0.15	1.75	4.85	0.03
Generations	5	1850.50**	3580.40**	6.85**	36.50**	110.20**	42.80**
Error	10	15.8	48.2	0.23	2.1	5.25	0.18

*, ** Significant at 5 and 1 % levels, respectively

@ Chi-square for Bartlett's test of homogeneity of error variances, S = significant and NS = non-significant

Table 3. Estimates of observed and expected heterosis and inbreeding depression days to first flowering, days to maturity, plant height (cm) and number of nodes on main shoot in pearl millet during summer 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Days to first flowering					
Mid parent	Observed	-0.90 ± 0.76	0.20 ± 0.86	-0.20 ± 1.01	-0.40 ± 0.66
	Expected	-0.90	-0.30	-2.20	-0.13
Better parent	Observed	2.60* ± 0.96	3.00** ± 0.80	1.60 ± 1.14	4.20** ± 1.01
	Expected	2.44	3.33	1.60	5.04
Inbreeding depression	Observed	-1.10 ± 0.82	0.40 ± 0.80	0.15 ± 0.85	1.20 ± 0.73
	Expected	-1.10	-0.15	0.15	-0.07
Days to maturity					
Mid parent	Observed	-0.60 ± 1.59	0.40 ± 1.37	0.40 ± 1.55	0.20 ± 1.26
	Expected	-0.40	0.39	0.28	-0.07
Better parent	Observed	3.20 ± 2.03	3.80* ± 1.50	2.80 ± 1.73	5.40** ± 1.41
	Expected	3.17	4.51	2.98	5.46
Inbreeding depression	Observed	-1.60 ± 1.56	0.15 ± 1.35	0.30 ± 1.31	1.20 ± 1.38
	Expected	-0.20	0.20	0.14	-0.03
Plant height (cm)					
Mid parent	Observed	16.40** ± 4.06	5.20 ± 3.31	17.50** ± 3.52	34.00** ± 2.46
	Expected	18.60	4.01	15.86	34.92
Better parent	Observed	27.00** ± 3.77	24.20** ± 3.59	20.80** ± 3.42	61.80* ± 3.38
	Expected	27.41	25.62	18.73	63.62
Inbreeding depression	Observed	10.05* ± 4.25	3.55 ± 3.67	11.25** ± 3.95	15.10** ± 3.68
	Expected	9.08	2.01	7.93	17.46
Number of nodes on main shoot					
Mid parent	Observed	1.00** ± 0.19	0.20 ± 0.13	1.20** ± 0.16	2.10** ± 0.18
	Expected	1.03	0.20	1.18	2.09
Better parent	Observed	0.20 ± 0.21	-1.00** ± 0.15	1.00** ± 0.15	0.40 ± 0.23
	Expected	0.23	-1.02	0.93	0.31
Inbreeding depression	Observed	0.60** ± 0.22	0.30 ± 0.20	0.75** ± 0.19	1.00** ± 0.28
	Expected	0.51	0.10	0.59	1.00

*, ** Significant at 5 and 1 per cent levels, respectively

Table 3. cont.. Estimates of observed and expected heterosis and inbreeding depression number of effective tillers per plant, earhead length (cm), earhead diameter (cm) and grain yield per plant (g) in pearl millet during summer 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Number of effective tillers per plant					
Mid parent	Observed	1.30** ± 0.09	0.40** ± 0.14	1.60** ± 0.08	2.40** ± 0.11
	Expected	1.31	0.36	1.63	2.40
Better parent	Observed	0.80** ± 0.14	-0.20 ± 0.12	1.20** ± 0.13	1.00** ± 0.10
	Expected	0.86	-0.25	1.26	1.00
Inbreeding depression	Observed	0.60** ± 0.15	0.35 ± 0.19	0.90** ± 0.16	1.05** ± 0.25
	Expected	0.39	0.18	0.81	1.43
Earhead length (cm)					
Mid parent	Observed	3.90** ± 0.61	0.70 ± 0.40	3.60** ± 0.57	7.20** ± 0.63
	Expected	4.03	0.70	3.71	7.26
Better parent	Observed	2.00** ± 0.66	-1.80** ± 0.47	3.00** ± 0.62	2.40** ± 0.72
	Expected	2.29	-1.79	3.07	2.63
Inbreeding depression	Observed	1.70* ± 0.68	0.25 ± 0.49	2.10** ± 0.68	2.25** ± 0.80
	Expected	2.01	0.35	1.86	2.25

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Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Earhead diameter (cm)					
Mid parent	Observed	0.37** ± 0.08	0.07 ± 0.05	0.36** ± 0.08	0.57** ± 0.08
	Expected	0.46	0.09	0.39	0.57
Better parent	Observed	0.24* ± 0.09	-0.06 ± 0.05	0.30** ± 0.09	0.22* ± 0.10
	Expected	0.32	-0.03	0.33	0.23
Inbreeding depression	Observed	0.09 ± 0.08	0.00 ± 0.06	0.14 ± 0.08	0.15 ± 0.09
	Expected	0.23	0.05	0.20	0.15
Grain yield per plant (g)					
Mid parent	Observed	26.26** ± 1.29	0.79 ± 1.20	23.88** ± 1.07	27.43** ± 1.63
	Expected	26.31	0.61	23.13	27.24
Better parent	Observed	15.46** ± 1.56	-10.90** ± 1.35	22.94** ± 1.12	6.40** ± 1.73
	Expected	15.50	-11.07	22.16	6.34
Inbreeding depression	Observed	19.24** ± 2.39	4.53* ± 2.22	15.24** ± 2.15	18.66** ± 3.18
	Expected	18.47	5.92	11.57	19.94

*, ** Significant at 5 and 1 per cent levels, respectively

Table 3. cont.. Estimates of observed and expected heterosis and inbreeding depression fodder yield per plant (g), 1000-seed weight (g), harvest index (%) and panicle index (%) in pearl millet during summer 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Fodder yield per plant (g)					
Mid parent	Observed	24.61** ± 6.36	-3.00 ± 5.26	20.46** ± 5.19	45.62** ± 7.80
	Expected	20.55	-3.00	19.80	45.75
Better parent	Observed	1.29 ± 7.23	-23.41** ± 6.29	19.27** ± 6.52	0.46 ± 3.25
	Expected	0.07	-23.41	18.95	1.26
Inbreeding depression	Observed	21.57** ± 6.55	12.59* ± 5.95	22.14** ± 5.55	29.71** ± 9.33
	Expected	10.27	13.46	23.38	29.71
1000-seed weight (g)					
Mid parent	Observed	1.26** ± 0.29	0.39 ± 0.22	2.00** ± 0.25	2.90** ± 0.24
	Expected	1.41	0.43	2.10	2.83
Better parent	Observed	0.68* ± 0.31	-1.06** ± 0.23	1.74** ± 0.28	0.72* ± 0.27
	Expected	0.85	-1.04	1.85	0.86
Inbreeding depression	Observed	0.55 ± 0.32	0.14 ± 0.31	0.81** ± 0.29	1.33** ± 0.36
	Expected	0.71	0.21	1.05	1.42
Harvest Index (%)					
Mid parent	Observed	4.69** ± 0.67	0.86 ± 0.43	5.19** ± 0.44	3.91** ± 0.48
	Expected	4.58	0.87	5.21	3.91
Better parent	Observed	3.88** ± 0.69	-0.98* ± 0.46	4.94** ± 0.60	1.70** ± 0.50
	Expected	3.88	-1.15	4.79	1.70
Inbreeding depression	Observed	3.13** ± 0.71	0.63 ± 0.55	2.43** ± 0.52	2.70** ± 0.59
	Expected	2.29	0.44	2.16	2.70
Panicle Index (%)					
Mid parent	Observed	1.73 ± 1.59	0.51 ± 0.98	2.37 ± 1.73	2.79* ± 1.30
	Expected	1.64	0.27	2.62	2.93
Better parent	Observed	0.84 ± 1.65	-0.90 ± 1.22	1.96 ± 2.07	1.10** ± 1.63
	Expected	0.96	-1.53	2.49	1.45
Inbreeding depression	Observed	1.10 ± 1.43	0.24 ± 1.09	1.33 ± 1.68	1.27 ± 1.25
	Expected	0.82	0.14	1.31	1.46

*, ** Significant at 5 and 1 per cent levels, respectively

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Table 3. cont.. Estimates of observed and expected heterosis and inbreeding depression for blast incidence in pearl millet during summer 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Blast incidence					
Mid parent	Observed	-1.83** ± 0.21	-1.10** ± 0.26	0.23 ± 0.20	-1.57** ± 0.20
	Expected	-1.84	-1.12	0.23	1.53
Better parent	Observed	-0.13 ± 0.21	0.07 ± 0.25	1.00** ± 0.21	0.40* ± 0.18
	Expected	-0.13	0.09	1.00	0.41
Inbreeding depression	Observed	-1.55** ± 0.28	-0.63* ± 0.27	-0.38 ± 0.22	-0.78** ± 0.25
	Expected	-1.55	-0.56	-0.38	-0.76

*, ** Significant at 5 and 1 per cent levels, respectively

Table 4. Estimates of observed and expected heterosis and inbreeding depression for days to first flowering, days to maturity, plant height (cm) and number of nodes on main shoot in pearl millet during *kharif* 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Days to first flowering					
Mid parent	Observed	-0.90 ± 0.60	0.20 ± 0.61	-0.20 ± 0.63	-0.40 ± 0.82
	Expected	-0.90	0.22	-0.21	-0.42
Better parent	Observed	2.60** ± 0.75	3.00** ± 0.85	1.60* ± 0.76	4.20** ± 0.94
	Expected	2.54	2.97	1.73	4.62
Inbreeding depression	Observed	-1.10 ± 0.71	0.40 ± 0.65	0.15 ± 0.59	1.20 ± 0.80
	Expected	-0.45	0.11	-0.10	1.17
Days to maturity					
Mid parent	Observed	-0.60 ± 1.81	0.40 ± 1.98	0.40 ± 1.26	0.20 ± 1.35
	Expected	-0.22	0.26	0.40	-0.64
Better parent	Observed	3.20 ± 1.81	3.80 ± 1.97	2.80* ± 1.30	5.40** ± 1.27
	Expected	3.34	4.36	3.00	4.94
Inbreeding depression	Observed	-1.60 ± 1.64	0.15 ± 1.97	0.30 ± 1.26	1.20 ± 1.34
	Expected	-0.11	0.13	0.20	-0.32
Plant height (cm)					
Mid parent	Observed	15.90** ± 3.74	5.20 ± 2.67	17.50** ± 2.73	33.00** ± 4.03
	Expected	15.42	6.65	16.67	33.03
Better parent	Observed	26.00** ± 4.00	24.20** ± 3.73	20.80** ± 2.82	60.80** ± 4.18
	Expected	24.88	27.72	19.65	60.50
Inbreeding depression	Observed	9.80* ± 4.13	3.20 ± 3.21	10.90** ± 3.14	14.50** ± 5.02
	Expected	7.71	3.33	8.33	23.25
Number of nodes on main shoot					
Mid parent	Observed	1.00** ± 0.15	0.20 ± 0.14	1.20** ± 0.16	2.10** ± 0.16
	Expected	0.99	0.15	1.18	2.12
Better parent	Observed	0.20 ± 0.22	-1.00** ± 0.13	1.00** ± 0.15	0.40 ± 0.22
	Expected	0.32	-1.08	0.93	0.45
Inbreeding depression	Observed	0.60** ± 0.17	0.30 ± 0.21	0.75** ± 0.19	1.00** ± 0.26
	Expected	0.50	0.07	0.59	1.61

*, ** Significant at 5 and 1 per cent levels, respectively

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Table 4. cont.. Estimates of observed and expected heterosis and inbreeding depression for number of effective tillers per plant, earhead length (cm), earhead diameter (cm) and grain yield per plant (g) in pearl millet during *kharif* 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Number of effective tillers per plant					
Mid parent	Observed	1.50** ± 0.15	0.40* ± 0.17	1.60** ± 0.15	2.40** ± 0.15
	Expected	1.50	0.35	1.53	2.40
Better parent	Observed	0.80** ± 0.18	-0.20 ± 0.17	1.20** ± 0.19	1.00** ± 0.16
	Expected	0.80	-0.26	1.16	0.95
Inbreeding depression	Observed	0.60** ± 0.19	0.35 ± 0.21	0.90** ± 0.20	1.05** ± 0.27
	Expected	0.43	0.17	0.77	1.45
Earhead length (cm)					
Mid parent	Observed	4.00** ± 0.57	0.80 ± 0.55	3.70** ± 0.53	7.10** ± 0.52
	Expected	1.18	0.84	3.73	7.20
Better parent	Observed	2.20** ± 0.67	-1.60* ± 0.73	3.00** ± 0.57	2.40** ± 0.65
	Expected	2.48	-1.59	3.01	2.66
Inbreeding depression	Observed	1.75* ± 0.66	0.30 ± 0.60	2.15** ± 0.64	2.15** ± 0.73
	Expected	2.09	0.42	1.84	2.15
Ear head diameter (cm)					
Mid parent	Observed	0.37** ± 0.08	0.07 ± 0.05	0.36** ± 0.07	0.57** ± 0.05
	Expected	0.44	0.09	0.38	0.57
Better parent	Observed	0.24* ± 0.10	-0.06 ± 0.06	0.30** ± 0.08	0.22** ± 0.07
	Expected	0.30	-0.04	0.32	0.23
Inbreeding depression	Observed	0.09 ± 0.08	0.00 ± 0.06	0.14* ± 0.07	0.15* ± 0.07
	Expected	0.22	0.04	0.19	0.15
Grain yield per plant (g)					
Mid parent	Observed	31.26** ± 1.83	6.29** ± 1.01	28.88** ± 1.65	32.43** ± 1.20
	Expected	31.46	6.40	30.37	32.51
Better parent	Observed	20.46** ± 2.33	-6.90** ± 1.21	26.94** ± 1.81	11.40** ± 1.54
	Expected	21.03	-6.81	28.23	11.69
Inbreeding depression	Observed	16.29** ± 2.81	2.64 ± 2.27	12.04** ± 2.56	16.26** ± 3.02
	Expected	16.29	3.20	15.18	16.25

*, ** Significant at 5 and 1 per cent levels, respectively

Table 4. cont.. Estimates of observed and expected heterosis and inbreeding depression for fodder yield per plant (g), 1000-seed weight (g), harvest index (%) and panicle index (%) in pearl millet during *kharif* 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444	86-SB-21	J-2636	J-2635
		×	×	×	×
		J-2627	J-2640	J-2340	J-2614
		(cross 1)	(cross 2)	(cross 3)	(cross 4)
Fodder yield per plant (g)					
Mid parent	Observed	34.74** ± 3.68	8.07* ± 3.06	34.83** ± 2.49	55.00** ± 3.05
	Expected	37.00	8.06	35.15	55.35
Better parent	Observed	12.82** ± 4.18	-18.12** ± 4.09	30.32** ± 2.51	10.18* ± 3.84
	Expected	14.85	-18.10	30.75	11.66
Inbreeding depression	Observed	15.14** ± 4.64	3.75 ± 4.18	15.42** ± 3.82	20.95** ± 5.60
	Expected	18.50	4.03	17.58	20.95
1000-seed weight (g)					
Mid parent	Observed	1.31** ± 0.31	0.39 ± 0.19	2.00** ± 0.22	2.90** ± 0.35
	Expected	1.46	0.40	2.03	2.79
Better parent	Observed	0.68 ± 0.34	-1.08** ± 0.23	1.74** ± 0.24	0.72 ± 0.38
	Expected	0.86	-1.07	1.80	0.61
Inbreeding depression	Observed	0.57 ± 0.32	0.14 ± 0.28	0.81** ± 0.26	1.32** ± 0.44
	Expected	0.73	0.20	1.02	1.40
Harvest Index (%)					

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Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444	86-SB-21	J-2636	J-2635
		×	×	×	×
		J-2627 (cross 1)	J-2640 (cross 2)	J-2340 (cross 3)	J-2614 (cross 4)
Mid parent	Observed	4.63** ± 0.67	1.40** ± 0.45	5.02** ± 0.51	3.64** ± 0.41
	Expected	5.01	1.45	5.08	3.64
Better parent	Observed	3.78** ± 0.78	-0.20 ± 0.53	4.84** ± 0.53	1.76** ± 0.46
	Expected	4.20	-0.41	4.77	1.76
Inbreeding depression	Observed	2.76** ± 0.73	0.85 ± 0.55	1.98** ± 0.59	2.42** ± 0.50
	Expected	2.50	0.71	1.62	2.42
Panicle Index (%)					
Mid parent	Observed	1.73 ± 1.75	0.51 ± 1.32	2.37 ± 1.67	2.79 ± 1.47
	Expected	1.65	0.54	2.21	2.83
Better parent	Observed	0.84 ± 1.77	-0.90 ± 1.40	1.96 ± 1.67	1.10 ± 1.54
	Expected	0.92	-1.37	1.92	1.33
Inbreeding depression	Observed	1.10 ± 1.67	0.24 ± 1.28	1.33 ± 1.64	1.28 ± 1.44
	Expected	0.82	0.27	1.10	1.42

*, ** Significant at 5 and 1 per cent levels, respectively

Table 4. cont.. Estimates of observed and expected heterosis and inbreeding depression for blast incidence in pearl millet during *kharif* 2024

Heterosis/ Inbreeding depression	Observed/ Expected Values	ICMB-95444 × J-2627 (cross 1)	86-SB-21 × J-2640 (cross 2)	J-2636 × J-2340 (cross 3)	J-2635 × J-2614 (cross 4)
Blast incidence					
Mid parent	Observed	-2.70** ± 0.17	-3.10** ± 0.18	-1.50** ± 0.19	-2.80** ± 0.17
	Expected	-2.56	-3.10	-1.50	-2.59
Better parent	Observed	0.60** ± 0.15	-0.20 ± 0.20	1.00** ± 0.21	0.40** ± 0.14
	Expected	0.73	-0.20	-1.02	0.61
Inbreeding depression	Observed	-1.25** ± 0.40	-1.55** ± 0.39	-1.55** ± 0.26	-1.55** ± 0.39
	Expected	-1.28	-1.55	-1.57	-1.30

*, ** Significant at 5 and 1 per cent levels, respectively

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