International Journal of Agriculture and Plant Science
www.agriculturejournal.in
Online ISSN: 2664-7664
Received: 30-07-2026, Accepted: 31-08-2026, Published: 15-09-2026
Volume 8, Issue 3, 2026, Page No. 458-464

Combining ability and heterosis studies in maize (*Zea mays L.*) using quadriallel cross analysis

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DOI: https://doi.org/10.66856/ijaps.2026.8.3.8262

Abstract
The present investigation entitled "Combining Ability and Heterosis Studies in Maize (*Zea mays* L.) Using Quadriallel Analysis" was carried out to evaluate average line main effects (g_i), two-line (sij), three-line (Sijk), and four-line interaction effects (Sijkl), along with heterotic responses for grain yield and quantitative traits in maize. Five inbred lines (HUZM-21, HUZM-22, HUZM-23, HUZM-24, and HUZM-25) were evaluated in a Randomized Block Design. Analysis of variance revealed significant variation among tested double-cross hybrids for all the traits. Main effects—including 1-line general, 2-line arrangement, and 3-line arrangement—were significant across all traits, whereas specific effects (2-line, 3-line, 4-line) and 4-line arrangements were non-significant. Due to using five parents, only 2-line specific variance could be estimated (3-line and 4-line specific variances require parents, per Rawlings and Cockerham, 1962b) [11]. Additive effects accounted for most genetic variance, while arrangement effects were driven by dominance and epistasis. Evaluation of Average Line Main Effects (gi) values identified HUZM-24 (gi = +6.13 for biological yield; +0.38 for cob weight) and HUZM-25 (gi = +5.86 for biological yield; +1.66 for plant height; +1.44 for grain yield) as the best general combiners for vegetative biomass, ear characteristics, and yield components. For maturity parameters, HUZM-25 manifested desirable negative main effects for days to 50% tasseling (gi = -0.33) and days to 50% silking (gi = -0.35) indicating its breeding utility for earliness. Specific combining interaction effects (Two-Line Interactions (sij) revealed significant positive values for grain yield and kernel rows per cob in specific parent combinations, notably involving parent line HUZM-24 and HUZM-23. Three-line arrangement 123 showed prominent positive interaction effects for plant height (Sijk = +5.51) and biological yield (Sijk = +2.99). Among four-line arrangements, interaction effect Sijkl for combination 1234 gave high positive contributions for plant height (+13.52) and biological yield (+3.02), showing strong non-additive gene action in double-cross hybrids. Outstanding heterosis over mid-parent (MPH) and standard variety (SH) for grain yield was registered in double-cross HUZM-(25×24)×(22×21) (103.12% MPH, 43.47% SH) and single-cross HUZM-25×24 (108.03% MPH). Overall, both additive (gi) and non-additive interaction components (sij, Sijk, Sijkl) govern yield determination, highlighting HUZM-25 and HUZM-24 as ideal parental candidates for commercial hybrid breeding.

Keywords: Maize (*Zea mays* L.), Quadriallel Analysis, General Combining Ability (gi), Line Interaction Effects (Sijkl), Heterosis, Grain Yield

Introduction
Maize (Zea mays L.) is the third most important cereal crop in India after rice and wheat. It serves as a vital source of food, feed, and industrial raw material, earning it the title "Queen of Cereals" due to its highest genetic yield potential. Central America and Mexico are considered its primary centers of origin, supported by fossil pollen and archaeological evidence. In India, although cultivated year-round, over 80% of maize is grown during the rainy (Kharif) season (July to October). Evaluation of parental inbred lines for combining ability is essential to identify effective parents for hybrid production. According to Allard (1960) [1], the expected performance of a cross based on parental lines represents the General Combining Ability (GCA), while deviation from this value represents the Specific Combining Ability (SCA). Variance due to GCA is an indicator of additive gene action, which is fixable and useful for selection in segregating populations (Bocanski *et al.*, 2009). Conversely, variance due to SCA reflects non-additive gene action, including dominance and epistasis, which is crucial for heterosis exploitation. Heterosis, or hybrid vigor, depends on the genetic divergence between parental lines and the underlying nature of gene action. Assessing heterosis over mid-parent, better parent, and standard check hybrids provides valuable insights into hybrid performance and commercial potential (Badu-Apraku *et al.*, 2015) [2]. To further analyse double cross hybrids, the concept of quadriallel analysis was introduced by Rawlings and Cokerham (1962b) [11]. A quadriallel cross involves the evaluation of first-generation progeny derived from two unrelated F_1 hybrids, represented as (AxB) x (CxD). This approach estimates additive (D), dominance (H), and epistatic variances, while measuring one, two, three, and four-line average effects. Consequently, quadriallel analysis aids in determining the exact mating order of parental lines to develop superior double-cross hybrids in cross-pollinated crops. Therefore, the present investigation was undertaken to estimate combining ability effects, evaluate heterosis over different bases, partition genetic variance components, and identify optimal parental mating orders for maize improvement.

Materials and method

The experiment was conducted at the Genetics and Plant Breeding Research Farm, Kamla Nehru Institute of Physical and Social Sciences, Faridipur, Sultanpur, Uttar Pradesh, India. The experimental material was developed using five inbred lines in a quadriallel mating design. The five parental lines were HUZM-21, HUZM-22, HUZM-23, HUZM-24, and HUZM-25. DKC-9144 was used as the standard check. The experimental material consisted of 31 entries comprising five parents, ten single crosses, fifteen double crosses, and one standard check.

Ten single crosses were produced using the five inbred lines during Kharif 2024. Subsequently, quadriallel crossing was followed to produce fifteen double crosses in Rabi 2024-25. The double crosses, single crosses, parental lines, and DKC-9144 were evaluated during Kharif 2025 in a Randomized Complete Block Design (RCBD) with three replications. The spacing was maintained at 60x20 cm, and twenty plants were maintained in each row. Recommended agronomic and plant-protection practices were followed throughout the experiment.

Data were recorded for thirteen characters. Plant height, biological yield per plant (g), cob weight (g), cob length (cm), cob girth (cm), number of kernel rows per cob, 100-seed weight (g), grain yield per plant (g), and shelling percentage (%) were recorded from five randomly selected plants. Days to 50% tasseling, days to 50% silking, anthesis-silking interval, and days to 75% dry husk were recorded on a plot basis.

Analysis of variance (ANOVA) was performed to test the significance of differences among genotypes for all traits. Combining ability analysis for quadriallel crosses was carried out following the procedure suggested by Rawlings and Cockerham (1962) [11]. Heterosis was computed as per cent increase or decrease of the mean values of single cross and double crosses over the better parent (Heterobeltiosis) and standard check (Standard Heterosis). Heterobeltiosis and standard heterosis were estimated as per Fonseca and Patterson (1968) [4] and Meredith and Bridge (1972), respectively.

Results and discussion

Analysis of variance

Analysis of variance (Table 1) revealed significant variation among tested double-cross hybrids for all the traits. Main effects—including 1-line general, 2-line arrangement, and 3-line arrangement—were significant across all traits, whereas specific effects (2-line, 3-line, 4-line) and 4-line arrangements were non-significant. Due to using five parents, only 2-line specific variance could be estimated (3-line and 4-line specific variances require parents, per Rawlings and Cockerham, 1962b) [11]. Additive effects accounted for most genetic variance, while arrangement effects were driven by dominance and epistasis.

Table 1: Analysis of variance for quadriallel.

Source of Variation	D.F.	Days to 50% Tasseling	Days to 50% Silking	A-S Interval	Days to 75% dry husk	Plant Height	Biological Yield	Cob Weight	Cob Length	Cob girth	No. of Kernel Rows/Cob	100 Seed weight	Grain Yield	Shelling %
Replications	2	10.56	2.40	2.22	13.88	35.46	636.16	256.96	1.27	2.82	0.42	14.15	188.42	10.15
Hybrids	14	10.17**	7.85***	1.16**	3.54**	473.99***	8159.51***	529.31***	6.85**	1.18**	1.56**	15.06**	212.69**	103.36**
1-LINE (General)	4	10.61**	7.41**	1.91**	6.57**	170.85**	10258.56***	64.19**	7.36**	0.97*	2.05**	6.52**	219.27**	209.55**
2-LINE (Specific)	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3-LINE (Specific)	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4-LINE (Specific)	-5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2-LINE Arrangement	5	16.77**	13.67***	0.47	1.24**	831.05***	7279.62***	785.42***	9.86**	1.34**	1.022**	20.52**	288.27**	57.55**
3-LINE Arrangement	5	3.22**	2.36**	1.25**	3.42**	359.4***	7360.16***	645.29***	3.43**	1.18**	1.68**	16.45**	131.85**	64.22**
4-LINE Arrangement	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Error	28	1.38	1.73	0.86	4.17	36.01	515.13	98.31	0.74	0.68	0.37	3.25	48.06	15.39
C.V. (%)	—	**2.26%**	**2.40%**	**36.08%**	**2.13%**	**3.21%**	**7.71%**	**7.72%**	**6.22%**	**6.11%**	**4.92%**	**5.34%**	**8.07%**	**5.85%**

The findings of the quadriallel analysis evaluating combining ability and heterotic potential across five inbred parents (HUZM-21, HUZM-22, HUZM-23, HUZM-24, and HUZM-25) and their hybrid combinations are presented below

An evaluation of combining ability effects revealed significant contributions from single parental lines as well as multi-line interaction effects across the studied yield components and phenological traits. The average line main effects (gi) (Table 2) measure the additive gene action transmitted by each inbred parent across cross combinations. Inbred lines HUZM-24 (gi = +6.13) and HUZM-25 (gi = +5.86) exhibited the highest positive main effects for biological yield. HUZM-23 also showed a notable positive effect (gi = +4.55), whereas HUZM-21 (gi = -13.52) performed poorly. HUZM-25 contributed positively to plant height (gi = +1.66), while HUZM-24 contributed negatively (gi = -1.36). Negative values for days to 50% tasseling and silking are highly desirable for breeding early-maturing hybrids. HUZM-25 registered the most favorable negative main effects for silking (gi = -0.35) and tasseling (gi = -0.33), followed by HUZM-24 (gi = -0.05 and -0.19, respectively). HUZM-23 (gi = +0.80) and HUZM-24 (gi = +0.38) were the best general combiners for increasing cob weight. For phenological and maturity traits—such as days to 50% tasseling, days to 50% silking, and days to 75% dry husk—negative combining ability estimates are desirable for developing early-maturing hybrids. The parental line HUZM-21 exhibited the highest positive 1-line general effect for days to 50% tasseling ($g_i = 0.36$), days to 50% silking ($g_i = 0.25$), and days to 75% dry husk ($g_i = 0.27$). In contrast, the parental cross HUZM-24 × HUZM-25 (12) demonstrated the most favorable negative 2-line general effect irrespective of arrangement (s_{ij}) for days to 50% tasseling (-0.17), days to 50% silking (-0.13), and days to 75% dry husk (-0.14). The superior additive effects (gi) observed in HUZM-25 and HUZM-24 indicate that these parents possess a high concentration of favorable additive alleles. They serve as ideal donor parents in recurrent selection or population improvement programs aimed at enhancing biomass, ear size, and earliness simultaneously. Similar findings have also been reported by Patel *et al.* (2022) [8] and Dattatray *et al.* (2023) who observed significant additive gene action governing plant height, biomass, and maturity traits in multi-parent maize crosses.

Table 2: Estimates of average line effects (*gi*) across main characters

gi	Days to 50% Tasseling	Days to 50% Silking	A-S Interval	Days to 75% dry husk	Plant Height	Biological Yield	Cob Weight	Cob length	Cob girth	No. of Kernel Rows/Cob	100 Seed weight	Grain Yield	Shelling %
HUZM-25	-0.33	-0.35	-0.02	-0.25	1.66	5.86	0.10	0.61	-0.07	0.05	-0.03	1.44	1.08
HUZM-24	-0.19	-0.05	0.14	-0.17	-1.36	6.13	0.38	0.27	-0.07	-0.08	-0.14	-0.13	-0.25
HUZM-23	0.11	0.06	-0.07	0.10	-0.14	4.55	0.80	-0.06	0.12	0.08	0.21	-1.77	-1.94
HUZM-22	0.05	0.08	0.08	0.05	-0.28	-3.02	-0.92	-0.31	0.03	0.11	-0.25	-0.36	0.25
HUZM-21	0.36	0.25	-0.13	0.27	0.13	-13.52	-0.36	-0.06	-0.01	-0.16	0.21	0.83	0.86

Crucially, the evaluation of 2-line specific order effects (Table 3) highlights that the spatial arrangement of parental lines in a double-cross hybrid significantly influences performance. For instance, in days to 50% tasseling, placing the parental pair as 12] resulted in a positive effect ($t_{ij} = 0.92$), whereas shifting the order to $(1) \times (2)$ yielded a strong negative effect ($t_{i.j.} = -0.46$). Specific parental arrangement involving HUZM-22 and HUZM-21 (tij = 9.81) demonstrated significant positive interactions for high yield traits.

Table 3: Two line interaction effect of line iand j due to the particular arrangement (ij) (--), i.e. tij, (i-) (j-), i.e. ti.j. and Sij, i.e. effect of i and j irrespective of arrangements.

	Days to 50% Tasseling			Days to 50% Silking			A-S Interval			Days to 75% dry husk			Plant Height			Biological Yield/plant			Cob Weight		
	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.
12	-0.17	0.92	-0.46	-0.13	-0.42	-0.42	0.04	0.03	-0.01	-0.14	0.59	-0.29	0.09	-5.81	2.90	4.00	23.77	-11.88	0.16	5.59	-2.79
13	-0.07	0.07	-0.03	-0.09	0.20	0.20	-0.03	-0.33	0.16	-0.05	-0.22	0.11	0.50	-6.44	3.22	3.47	-31.33	15.66	0.30	4.59	-2.29
14	-0.09	-2.29	1.14	-0.08	0.94	0.94	0.02	0.33	-0.16	-0.06	-0.37	0.18	0.45	14.1	-7.09	0.94	-6.44	3.22	-0.27	0.44	-0.22
15	0.009	1.29	-0.64	-0.03	-0.72	-0.72	-0.05	-0.03	0.01	0.00	0.00	0.00	0.59	-1.92	0.96	-2.55	14.00	-7.00	-0.08	-10.6	5.31
23	-0.02	-0.55	0.27	0.00	0.12	0.12	0.02	0.11	-0.05	-0.02	0.00	0.00	-0.50	12.4	-6.24	3.56	31.74	-15.87	0.39	5.44	-2.72
24	-0.04	0.29	-0.14	0.01	-0.12	-0.12	0.07	-0.11	0.05	-0.04	-0.14	0.07	-0.55	-11.6	5.83	1.03	-32.25	16.12	-0.17	-8.59	4.29
25	0.05	-0.66	0.33	0.06	0.42	0.42	0.00	-0.03	0.01	0.03	-0.44	0.22	-0.41	5.00	-2.50	-2.46	-23.25	11.62	0.005	-2.44	1.22
34	0.05	1.55	-0.77	0.05	-0.72	-0.72	0.00	-0.03	0.01	0.05	0.14	-0.07	-0.14	-2.74	1.37	0.50	14.51	-7.25	-0.04	-7.48	3.74
35	0.15	-1.07	0.53	0.10	0.38	0.38	-0.07	0.25	-0.12	0.12	0.07	-0.03	-0.00	-3.29	1.64	-2.99	-14.92	7.46	0.144	-2.55	1.27
45	0.13	0.44	-0.22	0.11	-0.09	-0.09	-0.01	-0.18	0.00	0.10	0.37	-0.18	-0.05	0.22	-0.11	-5.51	24.18	-12.09	-0.429	15.62	-7.81

Table 3: Continue……

	Cob length			Cob girth			No. of Kernel Rows/Cob			100 Seed weight			Grain Yield/plant			Shelling %		
	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.	sij	tij	ti.j.
12	0.14	1.00	-0.50	-0.04	0.03	-0.01	-0.009	-0.29	0.14	-0.05	1.14	-0.57	0.43	1.03	-0.51	0.27	-2.77	1.38
13	0.03	-1.33	0.66	0.01	0.11	-0.05	0.04	0.03	-0.01	0.06	1.66	-0.83	-0.11	5.66	-2.83	-0.28	1.92	-0.96
14	-0.05	0.00	0.00	-0.01	0.33	-0.16	0.05	0.55	-0.27	-0.09	-1.37	0.68	0.36	-3.22	1.61	0.44	-2.33	1.16
15	0.03	0.33	-0.16	-0.02	-0.48	0.24	-0.03	-0.29	0.14	0.06	-1.44	0.72	0.75	-3.48	1.74	0.64	3.18	-1.59
23	0.07	0.18	-0.09	0.01	0.22	-0.11	0.00	0.22	-0.11	0.02	-0.40	0.20	-0.63	3.11	-1.55	-0.73	-0.07	0.03
24	-0.01	-1.37	0.68	-0.01	-0.55	0.27	0.009	-0.14	0.07	-0.13	0.22	0.11	-0.16	-3.22	1.61	0.00	2.22	-1.11
25	0.07	0.185	-0.09	-0.02	0.29	-0.14	-0.08	0.22	-0.11	0.02	-0.51	0.25	0.23	-0.92	0.46	0.20	0.62	-0.31
34	-0.12	0.51	-0.75	-0.05	-0.14	0.07	0.06	-0.37	0.18	-0.01	-0.81	0.40	-0.71	-3.37	1.68	-0.56	1.03	-0.51
35	-0.04	-0.37	0.18	0.03	-0.18	0.09	-0.02	0.11	-0.05	0.14	-0.44	0.22	-0.31	-5.40	2.70	-0.36	-2.88	1.44
45	-0.12	-0.14	0.07	0.007	0.37	-0.18	-0.01	-0.03	0.01	-0.01	2.40	-1.20	0.15	9.81	-4.90	0.37	-0.92	0.46

When analysing 3-line specific order interaction effects ($t_{(ij)(k.)}$), (Table 4 & 5) alternate arrangements of the same three parental lines produced opposing estimates whose sum across all three permutations balanced to zero. For example, in days to 50% tasseling, the arrangement [12, 4] gave -0.92, while $(14)(2)$ and $(24)(1)$ gave 0.74 and 0.18, respectively. The triplet arrangement 123 and 124 showed strong positive specific interaction effects for biological yield (Sijk = +5.51, +2.99 respectively).

Table 4: Three-line interaction effect of line i, j and k irrespective of the arrangement i.e. Sijk

Sijk	Days to 50% Tasselling	Days to 50% Silking	A-S Interval	Days to 75% dry husk	Plant Height	Biological Yield /plant	Cob Weight	Cob length	Cob girth	No. of Kernel Rows/Cob	100 Seed weight	Grain Yield/plant	Shelling %
123	-0.13	-0.11	0.01	-0.10	0.05	5.51	0.42	0.12	-0.007	0.01	0.01	-0.15	-0.37
124	-0.15	-0.10	0.07	-0.12	0.003	2.99	-0.14	0.04	-0.03	0.02	-0.14	0.31	0.36
125	-0.05	-0.05	-0.003	-0.05	0.14	-0.50	0.04	0.12	-0.05	-0.06	0.01	0.71	0.56
134	-0.05	-0.06	-0.003	-0.03	0.41	2.46	-0.00	-0.07	0.02	0.08	-0.02	-0.23	-0.20
135	0.04	-0.01	-0.07	0.04	0.55	-1.03	0.17	0.01	0.01	-0.009	0.133	0.16	0.00
145	0.02	-0.003	-0.02	0.02	0.50	-3.56	-0.39	-0.07	-0.01	0.00	-0.02	0.63	0.73
234	-0.009	0.03	0.05	-0.005	-0.59	2.55	0.08	-0.03	0.02	0.03	-0.06	-0.75	-0.64
235	0.09	0.08	-0.02	0.06	-0.45	-0.94	0.27	0.05	0.01	-0.05	0.09	-0.36	-0.44
245	0.07	0.09	0.03	0.05	-0.50	-3.47	-0.30	-0.03	-0.01	-0.04	-0.06	0.11	0.28
345	0.17	0.13	-0.04	0.14	-0.09	-4.00	-0.16	-0.14	0.04	0.009	0.05	-0.43	-0.27

Table 5: Three line interaction effect of line i, j and k in specific arrangement i.e. t(ij)(k.)

t(ij)(k)	Days to 50% Tasseling	Days to 50% Silking	A-S Interval	Days to 75% dry husk	Plant Height	Biological Yield /plant	Cob Weight	Cob length	Cob girth	No. of Kernel Rows/Cob	100 Seed weight	Grain Yield/plant	Shelling %
(12)((3)	-0.11	-0.12	0.01	0.18	0.66	-22.57	-7.24	-0.35	-0.14	-0.12	-0.18	-3.25	1.81
(12)(4)	-0.92	-0.83	-0.09	-0.68	-1.99	7.37	2.11	-0.29	-0.09	-0.11	-0.50	1.12	-0.22
(12)(5)	0.11	0.11	0.03	-0.09	7.12	-8.57	-0.46	-0.35	0.20	0.53	-0.46	1.09	1.18
(13)(2)	0.33	0.25	-0.09	0.24	0.11	10.9	0.25	0.48	-0.09	0.03	-0.46	0.79	0.25
(13)(4)	-0.22	-0.03	0.09	-0.11	7.50	-5.96	-6.00	-0.01	0.14	0.11	-0.87	-3.26	0.53
(13)(5)	-0.18	0.18	0.33	0.09	-1.16	26.37	1.14	0.87	0.16	-0.18	-0.33	-3.16	-2.72
(14)(2)	0.74	0.94	0.29	0.42	-4.31	10.70	0.00	0.20	0.12	-0.05	-0.38	-1.14	-0.88
(14)(3)	0.83	0.51	-0.24	-0.05	-2.94	6.53	5.55	0.14	-0.18	0.00	1.68	4.03	0.09
(14)(5)	0.72	0.42	-0.38	0.00	-6.92	-10.79	-6.00	-0.35	0.27	-0.50	0.07	0.33	3.12
(15)(2)	-0.61	-0.77	-0.18	-0.37	1.29	-9.74	2.53	-0.18	-0.01	-0.12	1.42	0.87	-0.75
(15)(3)	-0.68	-0.59	0.05	-0.24	-0.94	0.37	3.98	-0.46	0.38	0.14	-0.66	2.05	-0.94
(15)(4)	0.00	-0.07	0.16	0.61	1.57	-4.62	4.11	-0.31	0.11	0.27	0.68	0.55	-1.48
(23)(1)	-0.22	-0.12	0.07	-0.42	-0.77	11.64	6.98	-0.12	0.24	0.09	0.64	2.46	-2.07
(23)(4)	0.92	0.77	0.09	0.61	-5.62	-13.50	-3.92	0.38	-0.24	0.01	0.16	-2.74	0.14
(23)(5)	-0.14	-0.38	-0.27	-0.18	-6.07	-29.88	-8.50	-0.44	-0.22	-0.33	-0.40	-2.83	2.00
(24)(1)	0.18	-0.11	-0.20	0.25	6.29	-18.07	-2.11	0.09	-0.03	0.16	0.88	0.01	1.11
(24)(3)	-0.18	0.00	0.09	-0.16	3.92	23.50	2.96	0.388	0.42	0.07	-1.27	1.92	-0.46
(24)(5)	-0.29	-0.14	0.22	0.05	1.44	26.83	7.74	0.88	0.16	-0.09	0.61	1.27	-2.87
(25)(1)	0.50	0.66	0.14	0.46	-8.42	18.31	-2.07	0.53	-0.18	-0.40	-0.96	-1.96	-0.42
(25)(3)	0.01	0.00	-0.05	-0.01	1.64	14.94	7.00	0.05	-0.16	0.16	1.25	2.88	-1.38
(25)(4)	0.14	0.18	-0.05	0.00	1.77	-10.00	-2.48	-0.77	0.05	0.01	0.22	0.00	1.18
(34)(1)	-0.61	-0.48	0.14	0.16	-4.55	-0.57	0.44	-0.12	0.03	-0.11	-0.81	-0.74	-0.62
(34)(2)	-0.74	-0.77	-0.18	-0.44	1.70	-10.00	0.96	-0.77	-0.18	-0.09	1.11	0.81	0.31
(34)(5)	-0.20	-0.18	0.07	0.12	5.59	-3.94	6.07	-0.61	0.29	0.57	0.51	3.29	-0.72
(35)(1)	0.87	0.40	-0.38	0.14	2.11	-26.74	-5.12	-0.40	-0.22	0.03	1.00	1.11	3.66
(35)(2)	0.12	0.38	0.33	0.20	4.42	14.94	1.50	0.38	0.38	0.16	-0.87	-0.05	-0.61
(35)(4)	0.07	-0.01	-0.20	-0.42	-3.24	26.72	6.08	0.38	0.01	-0.31	0.29	4.35	-0.16
(45)(1)	-0.72	-0.35	0.22	-0.61	5.35	15.42	1.88	0.03	0.16	0.22	-0.75	-0.88	-1.64
(45)(2)	0.41	-0.03	-0.166	-0.05	-3.22	-16.83	-5.25	-0.11	-0.22	0.07	-0.83	-1.27	1.68
(45)(3)	0.12	0.20	0.12	0.29	-2.35	-22.77	-12.25	0.22	-0.31	-0.25	-0.81	-7.64	0.88

The four-line interaction effect Sijkl (Table 6 & 7) represents the ultimate double-cross performance. The arrangement 1234 and 1235 exhibited the highest non-additive contribution for biological yield (+13.52 and +3.02 respectively). The presence of highly significant two-, three-, and four-line interaction components confirms that non-additive gene action (dominance and epistasis) plays a major role in governing multi-parent cross performance in maize. High Sijkl values in four-way hybrids imply that specific combinations of double-cross parent arrangements can yield strong epistatic interactions that cannot be predicted solely from single-cross performance.

The four-line interaction effects (tij,kl) for all the evaluated traits were estimated as zero (0.00) in Table 7 This is attributed to the lack of sufficient degrees of freedom for estimating higher-order epistatic components with five parental lines (p=5), as well as non-significant four-line interaction variance ($\sigma^{[2]}{}_{sijkl}$) in the ANOVA. This indicates that grain yield and component traits in the present material are predominantly governed by additive line main effects (gi) and lower-order (two-line and three-line) interaction components, rather than complex four-line epistatic interactions.

Similar findings have also been reported by Dattatray *et al.* (2023) and K. Vinay *et al.* (2025) [6] emphasizing that epistatic interaction effects significantly govern multi-parent cross performance in maize.

Table 6: Four line interaction effect of line i, j, k and l irrespective of the arrangement i.e. Sijkl.

Sijkl	Days to 50% Tasseling	Days to 50% Silking	A-S Interval	Days to 75% dry husk	Plant Height	Biological Yield/plant	Cob Weight	Cob length	Cob girth	No. of Kernel Rows/Cob	100 Seed weight	Grain Yield/plant	Shelling %
1234	-0.36	-0.25	-0.02	-0.27	1.66	13.52	0.36	0.06	-0.07	0.16	-0.21	-0.83	-0.86
1235	-0.05	-0.08	0.14	-0.05	-1.36	3.02	0.92	0.31	-0.07	-0.11	0.25	0.36	-0.25
1245	-0.11	-0.06	-0.07	-0.10	-0.14	-4.55	-0.80	0.06	0.12	-0.08	-0.21	1.77	1.94
1345	0.19	0.05	0.08	0.17	-0.28	-6.13	-0.38	-0.27	0.03	0.08	0.14	0.13	0.25
2345	0.33	0.35	-0.13	0.25	0.13	-5.86	-0.10	-0.16	-0.01	-0.05	0.03	-1.44	-1.08

Table 7: Four line interaction effects of lines i, j and k and l due to the particular arrangement (ij) (kl), i.e. tij.kl.

t(ij)(kl)	Days to 50% Tasseling	Days to 50% Silking	A-S Interval	Days to 75% dry husk	Plant Height	Biological Yield/plant	Cob Weight	Cob length	Cob girth	No. of Kernel Rows/Cob	100 Seed weight	Grain Yield/plant	Shelling %
12)(34)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12)(35)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(12)(45)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(13)(24)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(13)(25)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(13)(45)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(14)(23)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(14)(25)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(14)(35)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(15)(23)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(15)(24)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(15)(34)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(23)(45)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(24)(35)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(25)(34)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

For vegetative and phenological parameters, early maturity was evidenced by negative standard heterosis for days to 50% tasselling, silking, and 75% dry husk. The single cross HUZM-25X24 exhibited the most favourable negative standard heterosis for 75% dry husk (-4.12%), while the double cross HUZM-(25X22)X(24X23) achieved the maximum significant negative standard heterosis for 50% tasseling (-6.41%). Conversely, HUZM-(25X22)X(24X23) recorded the highest positive mid-parent heterosis (36.02%), better-parent heterosis (27.86%), and standard heterosis (10.06%) for plant height. Regarding yield and structural components, double crosses generally demonstrated superior heterotic responses over single crosses. For total biological yield, the double cross HUZM-(25X22)X(24X23) registered the highest mid-parent (115.26%) and standard heterosis (29.72%), while HUZM-(25X24)X(22X21) showed the maximum better-parent heterosis (92.54%). In terms of ear morphology, HUZM-25X24 was the leading single cross, showing high mid-parent and better-parent heterosis for cob weight (113.91% MPH; 109.66% BPH) and cob girth (24.87% MPH; 17.95% BPH). Among double crosses, HUZM-(25X24)X(23X22) exhibited maximum mid-parent (39.73%), better-parent (20.80%), and standard heterosis (18.43%) for cob length, whereas HUZM-(25X22)X(24X23) excelled in kernel rows per cob, achieving 26.18% standard heterosis. For overall grain yield (GY) and shelling performance, the single cross HUZM-25X24 produced the highest mid-parent (108.03%) and better-parent heterosis (86.19%), though HUZM-23X21 showed the maximum positive standard heterosis (21.56%) among single crosses. Among double crosses, HUZM-(25X24)X(22X21) emerged as the most promising hybrid, recording the highest mid-parent heterosis (103.12%), better-parent heterosis (34.84%), and standard heterosis (43.47%) for grain yield. Additionally, HUZM-(25X21)X(24X22) demonstrated the highest positive standard heterosis for shelling percentage (16.72%). Similar findings of these characters had also reported by by Kancho *et al.* (2020), Dongdon *et al.* (2021) [7], Sumalini *et al.* (2022) [8], Fentie *et al.* (2023), Jadhav *et al.* (2025) [6].

Table 7: Estimate of heterosis over Mid-parent, Better parent and Standard Variety

	Days to 50% tasseling			Days to 50% silking			A-S Interval			Days to 75% dry husk		
	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH	MPH	BPH	SH
HUZM-25X24	2.07	2.07	-5.13**	-0.65	-0.65	-5.56**	-44.4	-44.4	-16.7	-3.13	-3.79*	-4.12*
HUZM-25X23	7.07**	4.61*	1.92	5.06*	2.47	2.47	-26.3	-30.0	16.7	1.06	0.35	-1.37
HUZM-25X22	7.43**	5.30**	1.92	7.35**	5.66**	3.7	5.9	0.0	50.0	0.35	-0.35	-2.06
HUZM-25X21	11.72**	11.72**	3.85*	11.48**	10.39**	4.94*	6.7	-11.1	33.3	2.31	0.7	-1.03
HUZM-24X23	5.72**	3.29	0.64	5.06*	2.47	2.47	-5.3	-10.0	50.0	-1.05	-2.41	-2.75

HUZM-24X22	4.73*	2.65	-0.64	3.51	1.89	0	-17.6	-22.2	16.7	-1.05	-2.41	-2.75
HUZM-24X21	7.59**	7.59**	0	6.89**	5.84**	0.62	-6.7	-22.2	16.7	-0.18	-2.41	-2.75
HUZM-23X22	9.57**	9.21**	6.41**	7.17**	6.17**	6.17**	-33.3	-40.0	0.0	3.19	3.19*	0
HUZM-23X21	11.78**	9.21**	6.41**	11.18**	7.41**	7.41**	0.0	-20.0	33.3	3.04	2.13	-1.03
HUZM-22X21	9.46**	7.28**	3.85*	10.32**	7.55**	5.56**	28.6	12.5	50.0	1.97	1.06	-2.06
HUZM-(25X24)X(23X22)	5.23**	2.63	0	4.93*	1.85	1.85	0	-10	50	0	-1.72	-2.06
HUZM-(25X24)X(23X21)	7.67**	3.95*	1.28	6.92**	2.47	2.47	-5.88	-20	33.33	2.56	0.34	0
HUZM-(25X24)X(22X21)	7.17**	3.97*	0.64	6.80**	3.77	1.85	0	-11.11	33.33	0.79	-1.38	-1.72
HUZM-(25X23)X(24x22)	3.88*	1.32	-1.28	2.38	-0.62	-0.62	-22.22**	-30	16.67	-0.7	-2.41	-2.75*
HUZM-(25X23)X(24x21)	5.62**	1.97	-0.64	3.7	-0.62	-0.62	-29.41**	-40	0	0.79	-1.38	-1.72
HUZM-(25X23)X(22X21)	6.58**	3.95*	1.28	4.79*	1.23	1.23	-27.27	-40	0	2.57	1.05	-0.69
HUZM-(25X22)X(24X23)	-1.52	-3.95*	-6.41**	0.48	-2.47	-2.47	33.33	20	100.00**	-0.35	-2.07	-2.41
HUZM-(25X22)X(24X21)	1.02	-1.99	-5.13**	2.27	-0.63	-2.47	25	11.11	66.67	0.44	-1.72	-2.06
HUZM-(25X22)X(23X21)	1.85	-0.66	-3.21	0.32	-3.09	-3.09	-39.39**	-50.00**	-16.67	1.86	0.35	-1.37
HUZM-(25X21)X(24X23)	4.94*	1.32	-1.28	4.99*	0.62	0.62	-29.41*	-40	0	-0.26	-2.41	-2.75*
HUZM-(25X21)X(24X22)	9.22**	5.96**	2.56	8.74**	5.66**	3.7	0	-11.11	33.33	1.15	-1.03	-1.37
HUZM-(25X21)X(23X22)	12.65**	9.87**	7.05**	11.18**	7.41**	7.41**	-15.15	-30	16.67	3.64	2.1*	0.34
HUZM-(24X23)X(22X21)	9.95**	7.24**	4.49*	8.63**	4.94*	4.94*	-15.15	-30	16.67	3.98*	1.38	1.03
HUZM-(24X22)X(23X21)	5.23**	2.63	0	6.71**	3.09	3.09	21.21	0	66.67	2.21	-0.34	-0.69
HUZM-(24X21)X(23X22)	9.27**	6.58**	3.85*	7.99**	4.32*	4.32*	-15.15	-30	16.67	1.86	-0.69	-1.03

	Plant Height			**Biological Yield/Plant**			**Cob Weight**			**Cob Length**		
	MPH	**BPH**	**SH**	**MPH**	**BPH**	**SH**	**MPH**	**BPH**	**SH**	**MPH**	**BPH**	**SH**
HUZM-25X24	28.19**	19.42**	0.86	45.64**	32.96**	-28.62**	113.91**	109.66**	12.23	4.27	-4.69	-17.15**
HUZM-25X23	12.53**	9.71**	-7.34**	7.05	-13.49*	-24.64**	9.82	-16.03*	-18.43**	-10.47*	-15.54**	-17.20**
HUZM-25X22	6.77*	5.76	-8.96**	31.63**	29.02**	-27.87**	49.22**	30.93**	-10.84	28.82**	25.21**	8.85
HUZM-25X21	20.61**	19.50**	2.83	33.73**	28.82**	-25.35**	42.80**	5.32	13.94*	-10.58*	-21.41**	-9.83*
HUZM-24X23	8.52*	3.57	-16.92**	43**	7.89	-6.01	-5.57	-26.76**	-28.86**	-4.13	-16.87**	-18.50**
HUZM-24X22	5.86	-2.24	-15.85**	60.27**	43.69**	-19.67**	35.34**	20.87*	-17.70*	22.49**	14.97**	-5.65
HUZM-24X21	10.79**	2.32	-11.96**	47.08**	29.81**	-24.77**	25.85**	-5.94	1.76	-10.21*	-26.94**	-16.17**
HUZM-23X22	21.59**	17.45**	1.1	14.44*	-6.05	-18.16**	6.28	-9.61	-12.2	2.32	-6.02	-7.86
HUZM-23X21	21.04**	16.94**	0.62	12.18	-6.6	-18.64**	26.27**	19.83**	29.63**	7.16	-0.64	14.00**
HUZM-22X21	17.64**	17.61**	1.24	43.64**	41.11**	-18.23**	18.45*	-3.5	4.4	13.61**	-2.57	11.79*
HUZM-(25X24)X(23X22)	8.30*	1.8	-12.37**	103.62**	40.86**	22.70**	63.67**	13.81*	10.55	39.73**	20.80**	18.43**
HUZM-(25X24)X(23X21)	20.88**	13.66**	-2.21	47.27**	2.74	-10.50*	41.33**	1.32	9.62	18.72**	-3.85	10.32*
HUZM-(25X24)X(22X21)	17.14**	12.09**	-3.51	110.63**	92.54**	11.58*	57.79**	2.54	10.93	24.33**	-3.64	10.57*
HUZM-(25X23)X(24x22)	13.15**	6.37*	-8.44**	41.05**	-2.42	-15.00**	103.65**	41.61**	37.55**	-5.49	-18.30**	-19.90**
HUZM-(25X23)X(24x21)	14.10**	7.29*	-7.68**	57.00**	9.54	-4.58	36.43**	-2.18	5.82	21.36**	-1.71	12.78**
HUZM-(25X23)X(22X21)	18.07**	15.49**	-0.59	38.21**	1.01	-12.01*	54.76**	16.17*	25.67**	-12.47*	-27.19**	-16.46**
HUZM-(25X22)X(24X23)	36.02**	27.86**	10.06**	115.26**	48.91**	29.72**	86.33**	29.56**	25.85**	29.58**	12.03*	9.83*
HUZM-(25X22)X(24X21)	24.79**	19.42**	2.79	46.27**	33.70**	-22.52**	85.73**	20.70**	30.58**	16.65**	-9.59*	3.73
HUZM-(25X22)X(23X21)	21.71**	19.06**	2.48	18.44*	-13.44*	-24.60**	21.76*	-8.6	-1.12	-8.61	-23.98**	-12.78**
HUZM-(25X21)X(24X23)	26.16**	18.62**	2.07	84.66**	28.83**	12.22*	42.14**	1.91	10.25	15.34**	-6.6	7.17
HUZM-(25X21)X(24X22)	11.78**	6.97*	-7.93**	48.52**	35.76**	-21.33**	62.79**	5.79	14.45*	13.00*	-12.42**	0.49
HUZM-(25X21)X(23X22)	14.79**	12.29**	-3.34	54.13**	12.65*	-1.87	18.42*	-11.11	-3.84	13.84**	-5.31	8.65
HUZM-(24X23)X(22X21)	16.04**	9.61**	-5.65*	43.02**	0.69	-12.29*	24.06**	-6.27	1.4	5.83	-15.42**	-2.95
HUZM-(24X22)X(23X21)	4.85	-0.96	-14.75**	53.87**	8.33	-5.64	40.38**	6.06	14.74*	1.27	-19.06**	-7.13
HUZM-(24X21)X(23X22)	23.88**	17.01**	0.72	31.16**	-7.66	-19.56**	40.74**	6.34	15.04*	9.58	-12.42**	0.49

	Cob girth			**No. of kernal row/cob**			**100 seed weight**			**Grain yield/plant**			**Shelling %**		
	MPH	**BPH**	**SH**	**MPH**	**BPH**	**SH**	**MPH**	**BPH**	**SH**	**MPH**	**BPH**	**SH**	**MPH**	**BPH**	**SH**
HUZM-25X24	24.87**	17.95**	10.8	3.36	-1.67	4.12	0.71	-1.26	-4.59	108.03**	86.19**	10.14	-2.87	-11.17*	-2.19
HUZM-25X23	8.3	-4.07	3.86	2.74	-3.26	4.71	2.4	-1.01	-4.34	33.66**	2.29	-9.9	21.57**	21.00**	10.46
HUZM-25X22	21.60**	12.29*	10.74	8.51	2.17	10.59*	-11.28**	-19.81**	-4.07	43.10**	19.15	-16.30*	-3.36	-8.84	-6.14
HUZM-25X21	9.98	-1.81	4.41	0.41	-9.00*	7.06	1.14	-1.77	-5.08	33.47**	-3.95	2.19	-5.36	-8.63	-10.39
HUZM-24X23	-1.91	-8.4	-0.83	7.42	6.25	15.00**	-0.27	-1.7	-8.73*	-10.27	-25.00**	-33.94**	-7.45	-15.72**	-7.2
HUZM-24X22	9.87	7.26	5.79	2.2	1.09	9.41	-12.56**	-22.35**	-7.1	10.94	2.18	-28.22**	-18.43**	-21.08**	-13.10*
HUZM-24X21	0	-5.83	0.14	-13.16**	-17.50**	-2.94	-0.24	-1.2	-8.27*	35.57**	5.48	12.23	5.75	-0.03	10.08
HUZM-23X22	12.65*	7.63	16.53**	0	0	8.24	17.73**	3.25	23.52**	21.67*	9.35	-3.68	13.02*	6.14	9.28
HUZM-23X21	7.32	6.36	15.15**	-3.65	-7.5	8.82	16.20**	15.64**	5.31	25.01**	14.25	21.56**	-0.71	-4.58	-6.42
HUZM-22X21	9.41	5.44	12.12*	-4.17	-8	8.24	-5.28	-16.59**	-0.21	17.09	-2.8	3.42	-1.72	-4.05	-1.21
HUZM-(25X24)X(23X22)	12.79*	0.1	8.37	-1.48	-4.89	2.94	-2.93	-19.00**	-3.1	53.35**	15	1.29	-6.68	-16.36**	-7.9
HUZM-(25X24)X(23X21)	11.86*	1.27	9.64	2.41	-7	9.41	10.91*	6.39	2.8	39.24**	-1.73	4.56	-3.16	-14.27**	-5.6
HUZM-(25X24)X(22X21)	19.00**	6.99	13.77*	3.51	-6	10.59*	4.15	-12.91**	4.19	103.12**	34.84**	43.47**	3.48	-5.45	4.11
HUZM-	15.45**	2.47	10.94	11.47*	7.61	16.47**	-2.59	-18.71**	-2.76	69.77**	27.31**	12.14	7.29	-3.83	5.9

(25X23)X(24x22)															
HUZM-(25X23)X(24x21)	11.78*	1.2	9.56	-2.27	-11.25**	4.41	13.21**	8.59*	4.93	63.13**	15.14*	22.50**	-0.26	-11.70*	-2.77
HUZM-(25X23)X(22X21)	20.26**	10.18*	19.28**	4.04	-5	11.76*	9.65*	-8.91**	8.97*	59.55**	16.76*	24.23**	3.17	-4.11	-1.28
HUZM-(25X22)X(24X23)	23.77**	9.85*	18.93**	20.76**	16.58**	26.18**	-5.75	-21.35**	-5.92	68.31**	26.22**	11.17	-14.08*	-22.99**	-15.20**
HUZM-(25X22)X(24X21)	15.60**	3.94	10.52	-0.07	-9.25*	6.76	-15.73**	-29.53**	-15.69**	56.18**	3.68	10.32	11.05*	1.47	11.73*
HUZM-(25X22)X(23X21)	11.37*	2.04	10.47	7.32	-2	15.29**	1	-16.10**	0.37	40.36**	2.72	9.29	3.63	-3.69	-0.84
HUZM-(25X21)X(24X23)	13.83*	3.05	11.57*	-2.55	-11.50**	4.12	4.56	0.29	-3.09	56.10**	10.17	17.22*	4.84	-7.19	2.2
HUZM-(25X21)X(24X22)	1.43	-8.81	-3.03	-2.55	-11.50**	4.12	-0.42	-16.72**	-0.38	59.32**	5.77	12.53	16.01**	6.00*	16.72**
HUZM-(25X21)X(23X22)	13.37*	3.87	12.45*	4.04	-5	11.76*	-10.34**	-25.51**	-10.89**	37.04**	0.29	6.7	9.96	2.2	5.22
HUZM-(24X23)X(22X21)	9.07	2.54	11.02	-6.15	-12.25**	3.24	3.82	-14.57**	2.2	38.66**	5.52	12.27	-2.71	-11.29*	-2.32
HUZM-(24X22)X(23X21)	8.53	2.04	10.47	-2.14	-8.50*	7.65	-6.48	-23.05**	-7.95*	21.55*	-7.5	-1.58	-14.98**	-22.48**	-14.64**
HUZM-(24X21)X(23X22)	12.04*	5.34	14.05*	0.8	-5.75	10.88*	3.52	-14.82**	1.89	30.83**	-0.43	5.94	-4.62	-13.04*	-4.25

Conclusion

Grain yield and biomass accumulation in quadriallel maize crosses are governed by both additive (gi) and non-additive (Sijkl) gene actions. Parents HUZM-25 and HUZM-24 are identified as prime candidates for population improvement, while HUZM-(25×24)×(22×21) stands out as a promising commercial double-cross hybrid candidate

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