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Combining ability, gene action and heterosis studies in maize (*Zea mays* L.)

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Abstract
The present investigation was undertaken to assess combining ability, nature of gene action and heterotic potential for yield and yield-contributing traits in maize (*Zea mays* L.). GCA and SCA variances were significant for most traits, and SCA variance exceeded GCA variance for all the characters, indicating the predominance of non-additive genetic effects. For grain yield, GCA and SCA variances were 119.925 and 407.645, respectively, with a GCA/SCA ratio of 0.2942. HUZM-23 and HUZM-21 were identified as good general combiners for grain yield, with GCA effects of 10.517 and 10.026, respectively. The cross HUZM-25 × HUZM-24 recorded the highest SCA effect for grain yield (36.69), followed by HUZM-23 × HUZM-21 (32.30). HUZM-23 × HUZM-21 exhibited (44.88%) heterobeltiosis and (21.07%) standard heterosis for grain yield. The results indicated substantial genetic variability and a predominance of non-additive gene action for most traits. The superior parental lines and hybrid combinations identified in the study could be utilized in maize improvement programmes, particularly for exploiting heterosis and developing high-yielding hybrids.

Keywords: Maize, genetic variability, diallel analysis, general combining ability, specific combining ability, gene action, heterosis

Introduction
Maize (*Zea mays* L.) is one of the most important cereal crops of the world and belongs to the family Poaceae. It is a versatile crop cultivated for food, feed, fodder and a wide range of industrial applications. The crop possesses high yield potential and broad adaptability and is therefore often described as the “Queen of Cereals.” Its ability to perform under diverse environmental conditions has contributed to its extensive cultivation throughout tropical, subtropical and temperate regions. The importance of maize continues to increase because of growing requirements for food, livestock feed, poultry feed and industrial raw materials (Yadav *et al., 2014*) [23].

Al thongh maize has high genetic yield potential but to fulfill the diverse need of maize grain it is important to develop such maize hybrid that can perform better under diverse agro-climatic regions. Combining ability analysis is important approach for identifying superior parents and cross combinations. Sprague and Tatum (1942) [19] differentiated combining ability into general combining ability (GCA) and specific combining ability (SCA). GCA refers to the average performance of a parent in a series of hybrid combinations and is mainly associated with additive genetic effects, whereas SCA represents the performance of particular cross combinations arising from non-additive genetic interactions (Kage *et al., 2013* [9].).

Heterosis is particularly important in maize because hybrid vigour can result in substantial improvement in grain yield and its components. Estimation of heterosis over the better parent and standard check helps identify hybrids having potential for commercial utilization.

Diallel crossing provides an efficient method for estimating combining ability and understanding the genetic architecture of quantitative traits. Griffing (1956) [7] developed methods for analysing diallel mating systems, which have subsequently been widely used in crop breeding programmes. The relative magnitude of GCA and SCA variances provides useful information about the importance of additive and non-additive gene effects. Therefore, the present field experiment was undertakers to evaluate the maize genotypes for genetic variability, combining ability and heterosis for different quantitative traits.

Materials and Methods
The experiment was conducted at the Genetics and Plant Breeding Experimental Field of Kamla Nehru Institute of Physical and Social Sciences, Faridipur, Sultanpur, Uttar Pradesh, (228118) India. The experimental site is situated in the Eastern Plain Zone of Uttar Pradesh and has a semi-arid climate. The soil of the experimental field was sandy loam with a near-neutral pH of approximately 7.0–7.4. The field is located at approximately 26°30′ N latitude and 82°11′ E longitude.

Crossing in diallel fashion was undertaken during Kharif 2024, while evaluation of the parental lines (HUZM-25, HUZM-24, HUZM-23, HUZM-22, HUZM-21) collected from BHU Varanasi and hybrids was carried out during Rabi 2024–25.

The experimental material consisted of 16 entries, comprising five parents, ten F_1 hybrids and one standard check. The experiment was laid out in a randomized block design with three replications. Each row was 4.0 m long, with 60 cm spacing between rows and 20 cm spacing between plants. One seed was sown per hill. Recommended agronomic practices, including irrigation, fertilizer application and weed management, were followed throughout the experiment.

Observations were recorded on five randomly selected plants from each plot in each replication for twelve quantitative traits, Days to 50% tasseling, Days to 50% silking, Anthesis-silking interval, Days to 75% dry husk, Plant height (cm), Ear placement (cm), Cob weight (g), Cob girth (cm), Number of kernel rows per cob, Number of kernels per row, 100-grain weight (g), Grain yield per plant (g).

1. Statistical Analysis

Analysis of variance for the randomized block design was performed following Panse and Sukhatme (1978) [12]. Combining ability analysis was performed following the diallel approach of Griffing. GCA and SCA effects were estimated and tested for significance using the appropriate standard errors and t-tests. Heterosis was estimated over the better parent and standard check. Heterobeltiosis was calculated according to Fonseca and Patterson (1968) [6], while standard heterosis was estimated according to Meredith and Bridge (1972).

Results and Discussion

1. Analysis of Variance

The analysis of variance revealed significant differences among genotypes for 11 out of 12 characters**,** indicating substantial genetic variability in the experimental material. Significant genotypic variation was observed for days to 50% tasseling, days to 50% silking, anthesis-silking interval, plant height, ear placement, cob weight, cob girth, num ber of kernel rows per cob, number of kernels per row, 100-grain weight and grain yield. Days to 75% dry husk was the only trait for which genotypic differences were non-significant.

The significant differences among parents for nine characters further demonstrated divergence among the parental lines. Hybrids differed significantly for ten characters, while parent-versus-hybrid differences were significant for eight characters. Significant differences between hybrids and the standard check were recorded for anthesis-silking interval, ear placement, cob weight and grain yield Ram L *et al.* (2015) [15].

Table1: Summary of analysis of variance for 12 traits

Source of variation	D.F	D50%T	D50%S	A-S Interval	D75% DH	PH (cm)	EP (cm)
Replication	2	8.2708**	12.4375**	0.4375	17.0625	114.3515*	9.3652
Genotype	15	7.6764**	13.7722**	3.4889**	3.6222	729.4475**	315.9957**
Parents	4	4.9333*	5.2667*	0.2333	0.1000	925.4673**	380.0277**
Hybrids	9	9.8519**	12.4630**	0.6111	3.9111	516.1771**	218.0613**
Parent vs Hybrid	1	2.8444	72.9000**	44.1000**	0.0444	2362.3690**	1199.7551**
Check vs Hybrid	1	2.7273	0.6818	6.1364**	18.4364	42.6960	182.1910**
Error	30	1.4264	1.7931	0.4597	7.4181	30.5535	20.7023

Table1: Count….

Source of variation	D.F	CW	CG	KRPC	KPR	100SW (g)	GY (g)
Replication	2	55.5100	1.0340	0.2831	1.9352	0.9815	155.8340*
Genotype	15	2259.0080**	2.5913**	1.7294**	32.5224**	36.3097**	1719.5842**
Parents	4	2202.0307**	3.2693**	2.4993**	17.0907	39.1833**	1602.2440**
Hybrids	9	2501.3030**	1.8979**	1.5361**	44.535**	39.4194**	1681.6623**
Parent vs Hybrid	1	2487.9804**	8.7111**	0.4271	13.5334	24.0250*	1238.7690**
Check vs Hybrid	1	300.6818**	0.2793	1.3619	8.2255	14.6371	2295.2185**
Error	30	18.0364	0.5120	0.3640	8.7921	4.6977	32.4542

* and ** indicate significance at 5% and 1%, respectively.

The existence of significant genetic variation provides sufficient opportunity for selection of superior parents and hybrids. Similar importance of genetic variability for yield and yield-related traits has been reported in maize by Maruthi and Rani (2015), Tripathi *et al*. (2017), Bartaula *et al*. (2019) [4, 11, 21] and Thakur *et al.* (2023) [20].

2. Per Se Performance of Parents and Hybrids

Considerable variation was observed among both parents and hybrids for all major yield-related traits.

Table 2: Range and superior performance of parents and hybrids

Trait	Parent range	Best parent	Hybrid range	Best hybrid
Days to 50% tasseling	52.00–55.66	HUZM-21	49.33–55.33	HUZM-25 × HUZM-24
Days to 50% silking	56.66–60.00	HUZM-21	51.00–58.00	HUZM-25 × HUZM-24
ASI	4.33–5.00	HUZM-24/23	1.66–3.00	HUZM-25 × HUZM-24
Plant height	140.46–184.60	HUZM-23	161.96–195.06	HUZM-25 × HUZM-24
Ear placement	42.20–73.40	HUZM-23	55.83–78.23	HUZM-25 × HUZM-21
Cob weight (g)	53.46–112.53	HUZM-21	65.66–152.66	HUZM-23 × HUZM-21
Cob girth (cm)	10.83–13.20	HUZM-23	11.46–13.93	HUZM-23 × HUZM-21
Kernel rows/cob	10.53–13.06	HUZM-21	10.40–12.53	HUZM-25 × HUZM-22
Kernels/row	16.60–22.06	HUZM-21	14.36–28.40	HUZM-24 × HUZM-21
100-grain weight (g)	32.33–40.63	HUZM-22	29.69–42.96	HUZM-23 × HUZM-22
Grain yield (g/plant)	32.13–79.83	HUZM-21	32.93–115.53	HUZM-23 × HUZM-21

The complete mean-performance show that HUZM-21 and HUZM-23 were the highest-yielding parents, with 79.83 and 78.00 g/plant, respectively. Among hybrids, HUZM-23 × HUZM-21 recorded the highest grain yield of 115.53

g/plant, followed by HUZM-22 × HUZM-21 (81.53 g/plant). The same hybrid also recorded the highest cob weight (152.66 g) and cob girth (13.93 cm).

The hybrid mean for grain yield (66.51 g/plant) was considerably higher than the parental mean (55.39 g/plant), indicating an overall advantage of hybrid combinations over parents similar results were reported by Patel *et al.* (2019) [14].

3. General and Specific Combining Ability

The combining ability analysis revealed significant GCA and SCA effects for most traits. The presence of significant GCA indicates the contribution of average parental genetic effects, while significant SCA reflects the importance of specific parental interactions Sprague and Tatum (1942) [19].

Table 3: GCA and SCA variance components

Trait	σ²GCA	σ²SCA	GCA/SCA ratio	Gene action
Days to 50% tasseling	0.4318	1.8153	0.2379	Non-additive
Days to 50% silking	0.4832	4.6603	0.1037	Non-additive
ASI	-4.5000	1.4683	-3.1000	Non-additive
Days to 75% dry husk	-2.0000	-1.8000	0.1115	Non-additive
Plant height	30.9597	257.1457	0.1204	Non-additive
Ear placement	15.5700	102.1350	0.1524	Non-additive
Cob weight	181.3925	613.3049	0.2958	Non-additive
Cob girth	0.2370	0.4150	0.5712	Non-additive
Kernel rows/cob	0.0858	0.3990	0.2150	Non-additive
Kernels/row	1.0949	8.6452	0.1266	Non-additive
100-grain weight	3.3820	6.9440	0.4870	Non-additive
Grain yield	119.9253	407.6450	0.2942	Non-additive

The SCA variance was greater than GCA variance for every trait. The GCA/SCA ratio remained below unity for all characters, indicating the predominance of non-additive genetic effects. This was particularly pronounced for days to 50% silking, plant height, ear placement, cob weight, number of kernels per row and grain yield.

For grain yield, SCA variance was 407.645, more than three times the GCA variance of 119.925, resulting in a GCA/SCA ratio of 0.2942. Such a result indicates that dominance and other non-additive interactions played a major role in determining grain yield similar results were reported by Waghmare, *et al.* (2025) [22].

The results conclusion that hybrid breeding and exploitation of heterosis would be more effective for improving traits predominantly governed by non-additive gene action.

4. GCA Effects of Parents

The GCA effects identified considerable differences among the five parental lines.

For grain yield, HUZM-23 (10.517) and HUZM-21 (10.026) recorded significant positive GCA effects and were identified as good general combiners. In contrast, HUZM-25 (-8.10) and HUZM-24 (-1.40) showed negative significant effects.

HUZM-23 was also a good general combiner for plant height, ear placement, cob weight, cob girth and 100-grain weight. HUZM-21 showed good combining ability for plant height, ear placement, cob weight, cob girth, kernel rows per cob, kernels per row and grain yield similar results were reported by Kumar, *et al.* (2018) and Chiuta, *et al.* (2020) [5, 10].

Table 4: Important parental GCA effects

Trait	Parent with desirable GCA	GCA effect
Plant height	HUZM-23, HUZM-21	(3.168**), (3.454**)
Ear placement	HUZM-23, HUZM-21	(4.809**), (2.371*)
Cob weight	HUZM-23, HUZM-21	(9.640**), (14.370**)
Cob girth	HUZM-23, HUZM-21	(0.554**), (0.373**)
Kernel rows/cob	HUZM-22, HUZM-21	(0.311*), (0.368**)
Kernels/row	HUZM-21	(2.210**)
100-grain weight	HUZM-23, HUZM-22	(1.500**), (2.400**)
Grain yield	HUZM-23, HUZM-21	(10.517), (10.026)

* and ** indicate significance at 5% and 1%, respectively.

The strong GCA performance of HUZM-23 and HUZM-21 suggests that these lines possess favourable alleles for grain yield and associated characters and could be effectively utilized in future hybridization programmes.

5. SCA Effects of Hybrids

Significant SCA effects were recorded for several cross combinations. For grain yield, HUZM-25 × HUZM-24 recorded the highest SCA effect (36.69), followed by HUZM-23 × HUZM-21 (32.30). Five crosses showed positive significant SCA effects for grain yield. HUZM-23 × HUZM-21 was particularly important because it combined a high SCA effect with the highest per se grain yield. It also recorded high SCA for cob weight (35.04), demonstrating favourable genetic interaction for yield components similar results were reported by Yadav, *et al.* (2017 [24]) and Kumar, *et al.* (2018) [10].

Table 5: Selected superior SCA effects

Traits	Cross	SCA effects
HUZM-25 × HUZM-24	Plant height	30.91**
HUZM-25 × HUZM-24	Cob weight	31.88**
HUZM-25 × HUZM-24	Grain yield	36.69
HUZM-25 × HUZM-22	Cob weight	19.32**
HUZM-24 × HUZM-22	Kernels/row	4.74**
HUZM-24 × HUZM-21	Kernels/row	6.66**
HUZM-23 × HUZM-21	Cob weight	35.04
HUZM-23 × HUZM-21	Grain yield	32.30
HUZM-22 × HUZM-21	Cob weight	29.40**

The occurrence of high SCA effects in crosses involving parents with contrasting GCA status suggests that favourable non-additive interactions contributed to superior hybrid performance.

6. Nature and Magnitude of Gene Action

The comparison of GCA and SCA variances indicated that non-additive gene action predominated for all twelve traits according to the thesis variance-ratio analysis. The lowest GCA/SCA ratio was recorded for days to 50% silking (0.1037), followed by kernels per row (0.1266), plant height (0.1204), ear placement (0.1524) and kernel rows per cob (0.2150).

The relatively higher GCA/SCA ratio for cob girth (0.5712) suggests comparatively greater importance of additive effects for this trait than for most other characters. For grain yield, the low GCA/SCA ratio (0.2942) indicates that non-additive effects were considerably more important than additive effects. Such a genetic situation favours exploitation of heterosis rather than relying solely on pedigree selection similar results were reported by Saminu, *et al.* (2023) [17].

The higher SCA variance for most characters suggests favourable gene interactions and supports hybrid development as an appropriate strategy for improving yield and associated traits.

7. Heterosis

Heterosis was estimated over the better parent and standard check DKC-9144 for all twelve characters. The expression of heterosis varied considerably among crosses and traits, reflecting differences in parental genetic constitution and specific gene interactions. The flowering traits, several hybrids showed significant negative heterobeltiosis, which is desirable for earliness. HUZM-24 × HUZM-22 recorded −4.30% heterobeltiosis for days to 50% tasseling, while HUZM-24 × HUZM-22 recorded −8.50% for days to 50% silking. The anthesis-silking interval, significant negative heterosis was observed in several crosses. Reduced ASI is generally desirable because closer synchronization between pollen shedding and silk emergence can improve reproductive success under stress conditions. The plant height, HUZM-25 × HUZM-24 showed the highest positive heterobeltiosis (28.30%), followed by HUZM-22 × HUZM-21 (13.00%) and HUZM-25 × HUZM-21 (11.61%). The ear placement, HUZM-25 × HUZM-21 recorded the highest positive heterobeltiosis (34.34%), followed by HUZM-25 × HUZM-24 (31.06%) and HUZM-24 × HUZM-21 (29.82%). The cob weight, HUZM-25 × HUZM-24 recorded the highest positive heterobeltiosis (55.27%), followed by HUZM-25 × HUZM-22 (37.22%) and HUZM-24 × HUZM-22 (20.93%). The number of kernels per row, HUZM-24 × HUZM-22 recorded 38.86% heterobeltiosis and HUZM-24 × HUZM-21 recorded 28.70% similar results were reported by Reddy, *et al.* (2017), Bankole, *et al*. (2024 [3, 16]) and Jadhav, *et al.* (2025) [8]

8. Heterosis for Grain Yield

Grain yield was the most important trait in the present investigation. Three hybrids showed positive significant heterobeltiosis for grain yield.

Table 6: Superior hybrids for grain yield heterosis

Cross	Heterobeltiosis (%)	Standard heterosis (%)	Grain yield (g/plant)
HUZM-25 × HUZM-24	130.73	-1.90	77.06
HUZM-23 × HUZM-21	44.88	21.07	115.53
HUZM-25 × HUZM-22	18.78	-3.30	63.66
HUZM-24 × HUZM-23	-5.80	-6.60	32.93
HUZM-24 × HUZM-21	-4.50	-5.40	43.80

The cross HUZM-25 × HUZM-24 recorded the highest heterobeltiosis (130.73%) for grain yield, whereas HUZM-23 × HUZM-21 showed the highest positive standard heterosis (21.07%). The superiority of HUZM-23 × HUZM-21 becomes particularly important when all three criteria per se performance, SCA effect and heterosis are considered simultaneously. This cross recorded the highest grain yield (115.53 g/plant), high positive SCA (32.30) and positive heterobeltiosis (44.88%) and standard heterosis (21.07%). Therefore, HUZM-23 × HUZM-21 can be considered the most promising hybrid combination identified in the present investigation similar results were reported by Ali, *et al.* (2019) [1].

Table 7: Overall promising parents and hybrids

Category	Genotype	Evidence
Best general combiner for grain yield	HUZM-23	GCA = 10.517
Best general combiner for grain yield	HUZM-21	GCA = 10.026
Best SCA for grain yield	HUZM-25 × HUZM-24	SCA = 36.69
Promising SCA + high yield	HUZM-23 × HUZM-21	SCA = 32.30
Highest grain yield	HUZM-23 × HUZM-21	115.53 g/plant
Highest cob weight	HUZM-23 × HUZM-21	152.66 g
Highest cob girth	HUZM-23 × HUZM-21	13.93 cm
Highest grain-yield heterobeltiosis	HUZM-25 × HUZM-24	130.73%
Highest grain-yield standard heterosis	HUZM-23 × HUZM-21	21.07%

9. Integration of Combining Ability, Heterosis and Per Se Performance

One of the most important outcomes of the study was the identification of crosses that combined high mean performance with favourable combining ability and heterosis.

The cross HUZM-23 × HUZM-21 is especially valuable because HUZM-23 and HUZM-21 were themselves good general combiners for grain yield. The cross also recorded a high positive SCA effect, suggesting favourable interactions between parental alleles.

At the same time, HUZM-25 × HUZM-24 demonstrated the highest heterobeltiosis and SCA effect for grain yield, although its actual grain yield was lower than HUZM-23 × HUZM-21. Therefore, hybrid selection should not rely on heterosis alone, per se performance, SCA and standard heterosis should be considered together similar results were reported by Jadhav, *et al.* (2025) [8].

Conclusion

The parental lines differed substantially in their combining ability. HUZM-23 and HUZM-21 were identified as superior general combiners for grain yield, with positive GCA effects of (10.517) and (10.026), respectively. These parental lines also exhibited desirable combining ability for several yield-contributing characters and can therefore be considered valuable parents for future maize hybridization programmes.

The SCA variance exceeded GCA variance for all studied traits. In grain yield, the SCA variance was (407.645) compared with a GCA variance of (119.925), resulting in a GCA/SCA ratio of (0.2942). This demonstrated the predominant role of non-additive genetic effects and indicated that exploitation of heterosis would be an effective breeding strategy for improving grain yield and associated traits.

The cross HUZM-25 × HUZM-24 recorded the highest SCA effect for grain yield (36.69) and the highest heterobeltiosis (130.73%). However, HUZM-23 × HUZM-21 was the most promising overall hybrid because it recorded the highest grain yield (115.53 g/plant), highest cob weight (152.66 g), highest cob girth (13.93 cm), high positive SCA effect (32.30), (44.88%) heterobeltiosis and (21.07%) standard heterosis.

On the basis of the combined evidence of per se performance, GCA, SCA, heterobeltiosis, and standard heterosis, HUZM-23, HUZM-21 and the hybrid HUZM-23 × HUZM-21 were identified as particularly valuable genetic materials. HUZM-23 × HUZM-21 should be further evaluated under multi-location and multi-season trials before any recommendation for commercial exploitation.

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