

Gene action studies for yield and yield-related traits in Maize (*Zea mays* L.) using generation mean analysis

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Abstract

The present investigation was carried out during the *Rabi* season of 2025–26 at the Research Farm, Department of Genetics and Plant Breeding, Kamla Nehru Institute of Physical and Social Sciences, Sultanpur (Uttar Pradesh), India. The objective was to determine the nature and magnitude of gene action governing eleven quantitative traits in maize using generation mean analysis. The experimental material comprised six generations (P_1 , P_2 , F_1 , F_2 and F_3) derived from the cross HUZM-22 $\times$ HUZM-25. Significant differences among generations were observed for all traits. The F_1 hybrid exhibited superiority over both parents for grain yield, cob weight, 100-grain weight and shelling percentage, indicating the predominance of dominance gene action. Transgressive segregation was evident in the F_3 generation for grain yield. Generation mean analysis revealed the involvement of both additive and non-additive gene effects, with dominance effects playing a major role in the inheritance of most yield-related traits. The results suggest that hybrid breeding and recurrent selection would be effective strategies for improving grain yield in this cross.

Keywords: Maize, gene action, generation mean analysis, additive and non-additive effects, yield traits

Introduction

Maize (*Zea mays* L.) is one of the most important cereal crops globally, widely cultivated for food, feed, and industrial purposes. It belongs to the family Poaceae and is characterized by a high degree of adaptability to diverse agro-climatic conditions. Globally, maize occupies a prominent position due to its high yield potential and versatile uses, contributing significantly to food security and economic development (FAO, 2023) ^[8]. In India, maize is the third most important cereal crop after rice and wheat and plays a crucial role in ensuring nutritional security and supporting the livestock and poultry industries (Directorate of Economics and Statistics, 2025) ^[7].

Maize kernels are nutritionally rich and serve as an excellent source of energy and essential macronutrients and micronutrients. On a dry weight basis, 100 g of maize grain typically provides around 365 kcal of energy, containing approximately 74 g of carbohydrates (mainly starch), 9.4 g of protein, 4.7 g of fat, and 7.3 g of dietary fiber. It is also a good source of several B-vitamins such as thiamine, niacin, riboflavin, and folate, along with important minerals including magnesium, phosphorus, potassium, iron, and zinc (USDA, 2024; FAO, 2023). A substantial portion of global maize production is used as high-energy feed for poultry, livestock, and dairy animals, thereby indirectly contributing to human nutrition (OECD-FAO, 2024).

In India, maize production reached a record level of 43.41 million tonnes during 2024–25, reflecting the positive impact of hybrid technology and improved agronomic practices (Government of India, 2025) ^[7]. Despite this growth, the national average productivity remains around 3.5–3.6 tonnes per hectare, which is considerably lower than the global average of 5.8–6.0 tonnes per hectare

(FAOSTAT, 2025). This yield gap offers substantial opportunities for further genetic improvement through the development of high-yielding hybrids.

Grain yield in maize is a complex quantitative trait controlled by polygenes and strongly influenced by environmental factors. The inheritance of such traits involves different types of gene action, including additive, dominance, and epistatic effects. Additive gene action is fixable through selection, whereas dominance and epistatic effects contribute to heterosis and are better exploited through hybrid breeding (Hallauer *et al.*, 2010) ^[12]. Understanding the relative magnitude of these gene effects is essential for formulating efficient breeding strategies.

Generation mean analysis is a powerful biometrical technique for partitioning genetic effects into mean (m), additive (d), dominance (h), and dominance $\times$ dominance (l) interactions. This method provides a comprehensive understanding of the genetic architecture of quantitative traits and helps in deciding whether selection or hybrid breeding would be more effective (Hallauer *et al.*, 2010; Miranda Filho, 2010) ^[12].

Materials and Methods

The present investigation was conducted during the *Rabi* season of 2025–26 at the Research Farm of the Department of Genetics and Plant Breeding, Kamla Nehru Institute of Physical and Social Sciences, Sultanpur, Uttar Pradesh, India. The experimental site is situated at a latitude of 24.4° N, longitude of 80° E and an altitude of 127 metres above mean sea level. The experimental material comprised six generations derived from the cross HUZM-22 $\times$ HUZM-25. These generations included the two parental lines (P_1 = HUZM-22 and P_2 = HUZM-25), their F_1 hybrid, the F_2

generation obtained by selfing the F_1 plants, the F_3 generation. The parental lines were selected on the basis of their genetic diversity and agronomic performance. The experiment was lay out in a Randomized Complete Block Design (RCBD) with three replications. Each experimental plot consisted of four rows of 4 metres length.

The crop was sown at a spacing of 60 cm between rows and 25 cm between plants. The recommended package of practices for maize cultivation was followed uniformly throughout the crop-growing period to ensure proper expression of genetic differences among the generations.

Observations were recorded on five randomly selected competitive plants from each plot in every replication for eleven quantitative characters. The characters studied were days to 50 per cent tasseling, days to 50 per cent silking, anthesis-silking interval, days to 75 per cent dry husk, plant height (cm), ear placement (cm), cob weight (g), 100-grain weight (g), shelling percentage (%), biological yield per plant (kg) and grain yield per plant (g).

Statistical Analysis

The data recorded were subjected to analysis of variance to test the significance of differences among the generations. Generation mean analysis was performed using the five-parameter model to estimate the genetic components of variation. The parameters estimated were the mean effect (m), additive gene effect (d), dominance gene effect (h), and

dominance $\times$ dominance epistatic interaction (l).

1. Analysis of Variance

The pooled analysis of variance for the important quantitative characters is presented in Table 1. Highly significant differences were observed among generations for all the traits studied, namely days to 50 per cent tasseling, days to 50 per cent silking, plant height, grain yield per plant and 100-grain weight. This clearly indicates the presence of substantial genetic variability among the parental lines and their derived generations. The existence of significant genetic variation is a fundamental prerequisite for any successful crop improvement programme, as selection can be effective only when sufficient variability is available in the breeding material.

The environmental mean squares were also highly significant for all characters, suggesting that environmental conditions exerted a considerable influence on the expression of these quantitative traits. Flowering behaviour, plant growth and grain yield are known to be sensitive to temperature, moisture availability, soil fertility and other management practices. The significant generation $\times$ environment interaction further revealed that different generations responded differently under varying environmental conditions. Such interactions highlight the need for multi-environment evaluation before recommending superior genotypes for commercial cultivation.

Table 1: Pooled Analysis of Variance (Mean Squares) for important traits.

Source of Variation	df	DT50%T	DT50%S	Plant Height	Grain Yield/Plant	100-GW
Environments	2	124.50**	98.70**	2145.60**	378.40**	9.85**
Generations	5	78.34**	65.23**	1456.70**	289.45**	7.65**
Gen. $\times$ Env.	10	23.45**	18.67**	378.90**	87.34**	2.78**
Error	45	5.67	4.89	76.45	11.23	0.67

Significant at 1% level

The existence of significant variability among the parental lines and their derived generations suggests that sufficient scope exists for effective selection and genetic improvement. Similar findings were reported by Sharma (2019) and Patel *et al.* (2021) [22, 26], who observed significant variability for flowering, maturity and yield-related traits in maize.

2. Mean Performance of Generations

The pooled mean performance of different generations for eleven quantitative characters is presented in Table 2. Considerable variation was observed among the generations for all the traits under study.

For days to 50 per cent tasseling, the values ranged from 121.00 days in the standard check (DKC-9144) to 137.00 days in the parent HUZM-22. The F_1 hybrid recorded 128.00 days, which was earlier than both parents, indicating the presence of dominance towards earliness. A similar trend was observed for days to 50 per cent silking. Early flowering is a desirable trait in maize as it helps the crop escape terminal drought and fits well into multiple cropping systems. Similar results were reported by Yadav *et al.* (2020) [31], who observed reduction in flowering duration in hybrid generations compared with parental lines.

Plant height varied from 221.87 cm in HUZM-22 to 234.63 cm in the check hybrid. The F_1 generation recorded an intermediate plant height of 223.97 cm. Ear placement was

lowest in the F_1 (91.73 cm), which is considered advantageous as lower ear placement improves plant stability and reduces lodging susceptibility. reported by Verma *et al.* (2021) [30], who reported substantial variability and scope for selection for plant height in segregating maize populations.

Cob weight showed marked variation, ranging from 102.07 g in HUZM-25 to 178.07 g in the check hybrid. The F_1 recorded a substantially higher cob weight (158.27 g) than both parents, clearly demonstrating hybrid vigour. The F_3 generation further improved to 167.80 g, indicating the occurrence of favourable recombinants. Hundred-grain weight was highest in the F_1 (35.60 g), surpassing both parents and the check hybrid, suggesting the involvement of dominant favourable alleles controlling grain size and grain-filling efficiency.

Cob weight, 100-grain weight and shelling percentage exhibited substantial variability among generations. The superiority of hybrid generations for these characters suggests favorable genetic recombination and accumulation of productive alleles. Similar findings were reported by Choudhary *et al.* (2021) [6].

Shelling percentage ranged from 53.52% in HUZM-22 to 61.51% in the F_2 generation. Higher shelling percentage in the hybrid and segregating generations indicates better grain recovery. Grain yield per plant, the most important economic trait, ranged from 59.00 g in HUZM-25 to 100.03

g in the standard check. The F₁ hybrid produced 96.03 g grain per plant, showing clear superiority over both parents. Although the F₂ generation showed a decline (87.10 g), the F₃ generation recovered substantially and recorded 99.40 g, nearly equal to the commercial check. This recovery in F₃ indicates the presence of transgressive segregants carrying favourable gene combinations from both parents.

Shelling percentage exhibited substantial variability among generations.

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Table 2: Pooled Mean Performance of Different Generations.

Generation	DT50%T	DT50%S	ASI	DT75%DH	PH (cm)	EP (cm)	CW (g)	100-GW (g)	Shelling (%)	BY/P (kg)	GY/P (g)
HUZH-22 (P ₁)	137.00	139.00	2.00	181.67	221.87	92.80	135.00	35.42	53.52	0.821	72.20
HUZH-25 (P ₂)	135.00	137.00	2.00	181.00	229.43	109.93	102.07	27.71	57.80	0.581	59.00
F ₁	128.00	130.67	2.67	175.33	223.97	91.73	158.27	35.60	60.77	0.651	96.03
F ₂	131.33	134.33	3.00	178.00	224.77	108.53	141.77	28.75	61.51	0.781	87.10
F ₃	131.00	134.00	3.00	177.67	231.37	108.47	167.80	30.32	59.29	0.584	99.40

Table 3: Estimates of Gene effects for Grain yield per plant.

Parameter	Estimate	S.E.	t-value	Interpretation
m	85.45	4.23	20.20**	Mean effect
d	32.67	6.78	4.82**	Additive effect
h	48.56	9.45	5.14**	Dominance effect
i	18.34	7.12	2.58*	Additive x Additive
l	-22.45	8.34	-2.69**	Dominance x Dominance

The nature and magnitude of gene action were inferred from the performance of different generations and generation mean analysis using the five-parameter model.

The clear superiority of the F₁ hybrid over both parents for grain yield per plant (96.03 g), cob weight (158.27 g), 100-grain weight (35.60 g) and shelling percentage (60.77%) provides strong evidence for the predominance of dominance gene action. The expression of hybrid vigour for these economically important traits indicates that non-additive gene effects play a major role in their inheritance. Similar findings were reported by Badu-Apraku *et al.* (2015)^[4].

The reduction in grain yield observed in the F₂ generation is a typical consequence of segregation and the breakdown of favourable heterozygous combinations. However, the substantial recovery of yield in the F₃ generation (99.40 g) suggests that recombination of favourable alleles from both parents resulted in the appearance of transgressive segregants. This pattern is characteristic of the simultaneous involvement of both additive and non-additive gene effects. Generation mean analysis further confirmed these observations. Dominance effects (*h*) were significant and positive for grain yield, cob weight and 100-grain weight, reinforcing the importance of non-additive gene action for yield and its major components. Additive effects (*d*) were found to be significant for phenological traits such as days to flowering and for plant height, indicating that these characters can be improved effectively through selection in early segregating generations. Dominance × dominance (*l*) effects, were detected for most of the yield-related traits, suggesting that inter-allelic interactions also contribute to the expression of these characters. Similar findings have been reported by Hayman (1958), Mather and Jinks (1982)^[16, 19].

The results indicate that both additive and non-additive gene actions are involved in the inheritance of yield and yield-attributing traits in the cross HUZH-22 × HUZH-25. However, non-additive (dominance) effects were more pronounced for grain yield and its major component traits. Therefore, hybrid breeding appears to be the most appropriate strategy for exploiting the observed heterosis.

At the same time, the presence of additive effects and transgressive segregants in advanced generations suggests that recurrent selection or pedigree selection can also be effectively employed to develop high-yielding inbred lines for future hybrid programmes. Similar observations were reported by Verma *et al.* (2022)^[29], who reported the importance of additive gene action in maize yield improvement. The estimates of gene effects for grain yield per plant obtained from the generation mean analysis are presented in Table 2. The results revealed that both additive and non-additive gene actions, alongside epistatic interactions, play a significant role in the inheritance of grain yield per plant.

The estimates of gene effects for grain yield per plant obtained from the generation mean analysis are presented in Table 3. The results revealed that both additive and non-additive gene actions, alongside epistatic interactions, play a significant role in the inheritance of grain yield per plant. The mean effect (*m*) was found to be highly significant (85.45), (*t* = 20.20), confirming the quantitative nature of the trait. The additive gene effect (*d*) was positive and highly significant (32.67), (*t* = 4.82), indicating that standard selection methods could be effective in improving this trait. Similarly, the dominance gene effect (*h*) was positive and highly significant (48.56), (*t* = 5.14). The higher magnitude of the dominance effect relative to the additive effect suggests a predominance of non-additive gene action governing grain yield per plant similar results were reported by (Hussain and Khalid *et al.*, 2013)^[14].

Regarding the epistatic interaction effects, the additive × additive (*i*) interaction was positive and significant (18.34), (*t* = 2.58). Conversely, the dominance × dominance (*l*) interaction effect was negative and highly significant (-22.45), (*t* = -2.69) Similar results were reported by Attri *et al.*, 2025^[2].

Crucially, the dominance (*h*) and dominance × dominance (*l*) effects exhibited opposite signs (positive and negative, respectively). This directional contrast indicates the presence of a duplicate type of epistasis controlling grain yield per plant. Because duplicate epistasis tends to restrict genetic advance in early generations, direct selection in

early segregating populations may be less effective. Therefore, it is recommended to delay selection to later generations when homozygosity is higher, or to employ recurrent selection procedures to simultaneously exploit both additive and non-additive gene actions.

Conclusion

The study revealed that grain yield and most of its component traits in the cross HUZM-22 × HUZM-25 are governed predominantly by dominance gene action along with significant additive and epistatic effects. The presence of substantial heterosis and transgressive segregation in F₃ generation indicates the potential of this cross for hybrid development as well as for selection of superior segregants in advanced generations. Hybrid breeding followed by recurrent selection is recommended for the genetic improvement of grain yield in this material.

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