

Gene Action for Seed Yield and Quality Traits in Indian Mustard [*Brassica juncea* (L.) Czern. & Coss.] Through Generation Mean Analysis

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ABSTRACT

The present investigation was undertaken to elucidate the nature and magnitude of gene action governing seed yield and oil quality traits in Indian mustard (*Brassica juncea* (L.) Czern. & Coss.) using generation mean analysis. Four crosses, namely PR36 × Rohini, PRE11 × CS60, PRE15 × CS58, and PRL26 × Giriraj, were studied using six generations (P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2) during the *Rabi* seasons of 2022–2024 at Ajitmal, Uttar Pradesh, India. Analysis of variance revealed significant genetic variability for seed yield, oil content, protein content, and fatty acid composition. Significant scaling tests indicated the presence of epistatic interactions, and therefore, the

six-parameter model was employed. Both additive (d) and non-additive (h) gene effects were involved in the inheritance of most traits, with additive × additive (i) and dominance × dominance (l) interactions being predominant in several cases. The results suggest that a combined breeding strategy involving hybridization followed by selection in advanced segregating generations would be effective for improving seed yield and oil quality traits in Indian mustard.

Keywords Additive gene action, Dominance, Epistasis, Fatty acid composition, Oil quality, Generation mean analysis.

INTRODUCTION

Indian mustard [*Brassica juncea* (L.) Czern. & Coss.] is one of the most important oilseed crops of the family Brassicaceae and contributes substantially to edible oil production in India. It occupies a prominent position among rapeseed–mustard crops due to its wide adaptability, high yield potential and diverse uses. In addition to being a major source of edible oil, mustard is utilized as a condiment, a leafy vegetable and a medicinal plant. The seeds contain about 30–42% oil and 20–25% protein, and the residual oilseed cake is widely used as a protein-rich feed for livestock (Downey and Röbbelen 1989, Rakow and Woods 1987).

The nutritional and industrial value of mustard oil largely depends on its fatty acid composition. Mustard

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oil contains relatively low levels of saturated fatty acids and appreciable amounts of unsaturated fatty acids such as oleic, linoleic and linolenic acids, which are beneficial for human health (Shyam *et al.* 2021). However, traditional Indian mustard varieties possess high levels of erucic acid (C22:1) and glucosinolates. High erucic acid content is considered undesirable for human consumption due to potential health concerns, while glucosinolates reduce the nutritional quality and palatability of the seed meal (Snowdon *et al.* 2007). Consequently, the development of varieties with low erucic acid and low glucosinolate content, commonly referred to as “double-zero” quality, has become a major objective in mustard breeding programs.

Improving seed yield and quality traits in Indian mustard is often challenging because these traits are quantitatively inherited and influenced by multiple genes and environmental factors. The expression of such traits is governed by different types of gene action, including additive, dominant, and epistatic interactions (Mather and Jinks 1982). Knowledge of the relative importance of these genetic components is essential for designing effective breeding strategies. Traits predominantly governed by additive gene effects can be improved through selection, whereas dominance and epistatic effects may be better exploited through hybrid breeding or population improvement programmes (Hayman 1958, Jinks and Jones 1958).

Generation mean analysis is a useful biometrical approach for studying the genetic architecture of quantitative traits. By analyzing the means of six generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2), this method enables estimation of additive, dominance and epistatic gene effects and provides valuable insights into the inheritance of complex characters (Mather and Jinks 1982, Gamble 1962). Such information is particularly important in oilseed crops like mustard, where both yield and quality traits need to be simultaneously improved.

Several studies have reported considerable genetic variability for oil content, fatty acid composition and glucosinolate content in *Brassica juncea*, indicating the scope for improving oil quality traits through breeding programmes (Kumari *et al.* 2022, Gadpayale

et al. 2022, Kumar *et al.* 2023). Recent studies have also highlighted the importance of understanding the inheritance of erucic acid and other fatty acids for developing nutritionally superior mustard varieties (Chaudhary *et al.* 2021, Gain *et al.* 2024, Singh *et al.* 2025).

Therefore, the present investigation was undertaken to elucidate the nature of gene action governing seed yield and important oil quality traits in Indian mustard using generation mean analysis. The results are expected to provide valuable information for designing effective breeding strategies aimed at developing high-yielding varieties with improved oil quality and reduced erucic acid content.

MATERIALS AND METHODS

Plant material and experimental design

The field experiment was conducted at the Agricultural Research Farm, Janta Mahavidyalaya, Ajitmal, Auraiya (UP.), India, during the *Rabi* seasons of 2022–2024. Geographically, the experimental site is located at 26°56' N, 79°32' E, with an elevation of 144.24 m above mean sea level. The region falls under the tropical climatic zone and is characterized by typical subtropical weather conditions during the *Rabi* season. The experimental material comprised six generations; parents (P_1 and P_2), first filial generation (F_1), second filial generation (F_2), and backcrosses (BC_1 and BC_2), developed from four crosses of Indian mustard (*Brassica juncea* L. Czern. & Coss.), namely: PR36 × Rohini (Family A), PRE11 × CS60 (Family B), PRE15 × CS58 (Family C) and PRL26 × Giriraj (Family D).

Crosses among diverse parental lines were made during the *Rabi* season of 2022 to develop four F_1 hybrids. The parents of the respective crosses were used as the male parent and the F_1 generation as the female parent, and backcrosses were effected to produce the BC_1 (F_1 backcrossed to P_1) and BC_2 (F_1 backcrossed to P_2) generations, and the F_1 hybrids were selfed to obtain F_2 seeds during the *Rabi* 2023. The six generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) of these four different crosses, viz. PR36 × Rohini, PRE11 × CS60, PRE15 × CS58, and PRL26 × Giriraj were grown

during the *Rabi* season of 2024 to generate data on various traits for generation mean analysis.

The final experiment was sown on 15 October 2023. All six generations for each of the four crosses were evaluated in a randomized complete block design with three replications. Each genotype was sown in 3 m long rows with a spacing of 30 cm between rows and 10 cm between plants. The number of rows per generation varied as follows: three rows for the non-segregating generations (P_1 , P_2 , and F_1), twenty rows for the segregating F_2 generation, and fifteen rows each for the BC_1 and BC_2 generations. Recommended agronomic practices were followed to maintain a healthy and uniform crop stand throughout the experiment.

Observations recorded

The observations were recorded on seven traits, including seed yield, namely: yield/plant (g), Oleic acid (%), Linoleic acid (%), Linolenic acid (%), Erucic acid (%), Glucosinolate (%), Protein content (%), and Oil content (%). For data analysis, ten plants were sampled from each of P_1 , P_2 , and F_1 ; forty plants from F_2 ; and thirty plants each from BC_1 and BC_2 generations. Oil content, protein content, and fatty acid composition (oleic, linoleic, linolenic, and erucic acids) were determined using a Near Infrared Spectrometer (Model: NIRFlex N-500, Büchi, Switzerland) at the Oilseeds Section of the Department of Genetics and Plant Breeding, Govind Ballabh Pant University of Agriculture and Technology, Pantnagar, Udham Singh Nagar, Uttarakhand, India. Approximately 5 g of ground seed sample was placed in a quartz sample cup for each scan. For glucosinolate estimation, NIR calibration equations were validated against standard wet-chemical methods (ISO 9167-1, 1992). Results were expressed as percentages on a seed dry-weight basis.

Statistical analysis

The recorded data were subjected to statistical analysis using R (R Core Team 2013). Descriptive statistics such as coefficient of variation (CV), standard error (SE), and critical difference (CD) were calculated following standard procedures.

The six-parameter model of the generation mean analysis was applied to estimate genetic parameters and determine epistatic interactions. Mean data were first tested to determine non-allelic interaction through individual scaling tests A, B, C and D proposed by Mather (1949).

$$\begin{aligned}\text{Scale A} &= 2BCP_1 - P_1 - F_1 \\ \text{Scale B} &= 2BCP_2 - P_2 - F_1 \\ \text{Scale C} &= 4F_2 - 2F_1 - P_1 - P_2 \\ \text{Scale D} &= 2F_2 - BC_1 - BC_2\end{aligned}$$

Where,

P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 = Means from distinct generations. The variances of the values A, B, C and D were determined using the corresponding variances of different populations, as given below:

$$\begin{aligned}VA &= 4V(BC_1) + V(P_1) + V(F_1) \\ VB &= 4V(BC_2) + V(P_2) + V(F_1) \\ VC &= 16V(F_2) + 4V(F_1) + V(P_1) + V(P_2) \\ VD &= 4V(F_2) + V(BC_1) + V(BC_2)\end{aligned}$$

Where,

VA, VB, VC and VD are the variances of respective scales A, B, C and D; VP_1 , VP_2 , VF_1 , VF_2 , VBC_1 and VBC_2 are the Variances of P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 populations, respectively. Standard errors for A, B, C and D scales were calculated by estimating the square root of the respective variances.

If any scaling tests were found to be significant, the genetic effects were estimated by fitting the data into a six-parameter model for generation mean analysis as suggested by Hayman, (1958) to estimate the genetic parameters, viz., mean (m), additive gene effects (d), dominance gene effects (h) and three types of non-allelic gene interactions viz., additive x additive (i), additive x dominance (j) and dominance x dominance (l).

$$(1) m = \text{Mean} = F_2$$

$$(2) d = \text{Additive effect} = BC_1 - BC_2$$

$$(3) h = \text{Dominance effect} = F_1 - 4F_2 - (1/2)P_1 - (1/2)$$

$$P_2 + 2BC_1 + 2BC_2$$

$$(4) i = \text{Additive} \times \text{Additive effect} = 2BC_1 + 2BC_2 - 4F_2$$

$$(5) j = \text{Additive} \times \text{Dominance effect} = BC_1 - (1/2) P_1 - BC_2 + (1/2) P_2$$

$$(6) l = \text{Dominance} \times \text{Dominance effect} = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2$$

$$(7) \sqrt{H/D} V_1 = V(P_1) + V(P_2) + 4V(F_1) + 16V(F_2) + 16V(BC_1) + 16V(BC_2)$$

Where,

$V(P_1)$, $V(P_2)$, $4V(F_1)$, $16V(F_2)$, $16V(BC_1)$ and $16V(BC_2)$ = Variances of P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 populations, respectively.

The estimation of (h) and (l), along with their signs, was used to understand the nature of epistasis according to Mather and Jinks (1971), that is, if (h) and (l) had the same sign, the gene action was described as complementary, whereas if (h) and (l) had opposite signs, it was described as duplicate.

The degree of dominance, expressed as the square root of the ratio of dominance variance (H) to additive variance (D), was determined according to Robinson *et al.* (1949).

$$\text{Degree of dominance} = \sqrt{H/D}$$

RESULTS AND DISCUSSION

Analysis of variance

The analysis of variance for oilseed quality and yield

traits is presented in Table 1. The results revealed highly significant differences among the families for seed yield and oil quality traits, demonstrating substantial genetic diversity in the base material. Significant differences ($P \leq 0.05$) were observed among progenies in oil content, protein content, and erucic acid content, as well as in yield per plant. Notably, oleic acid and linolenic acid exhibited highly significant differences ($P \leq 0.01$) among progenies, suggesting a high scope for selection in fatty acid profiles. However, variation in glucosinolate content among progenies was not significant. The family $\times$ progeny interaction was highly significant for nearly all traits, including protein content, oleic acid, linolenic acid, erucic acid, and yield per plant. This indicates that progeny performance was inconsistent across families and that the expression of these traits is strongly influenced by family genetic background. Yield per plant showed significant variation at both the progeny and interaction levels, highlighting the complexity of yield inheritance. For quality traits, the significant interaction for glucosinolates despite non-significant progeny effects suggests that specific family-progeny combinations are crucial for breeding low-glucosinolate lines.

Generation mean analysis

Generation mean analysis was conducted to estimate the nature and magnitude of gene effects governing seed yield and quality traits in Indian mustard. The adequacy of the additive–dominance model was tested using scaling tests (A, B, C and D) following the procedure proposed by Hayman (1958) and Jinks and Jones (1958). Significant values of scaling tests for most traits indicated the presence of non-allelic gene interactions, suggesting that the additive–dominance

Table 1. Analysis of variance for seven characters in a family compact block design in Indian Mustard.

Source of Variation	df	Oil content (%)	Protein Content (%)	Oleic Acid (%)	Linolenic Acid (%)	Erucic Acid (%)	Glucosinolate (%)	Yield/ Plant (g)
Replication	2	0.59	5.3	1.50	0.06	10.79	11.13	0.79
Family	3	4.98	1.67	3.35	1.06	21.07	102.99	30.07
Error (a)	10	0.98	0.56	0.61	0.19	6.89	5.52	2.93
Progeny	5	0.58*	7.55*	66.84**	0.67**	14.47*	6.9	41.13*
Family $\times$ Progeny	15	3.87*	5.40**	27.82**	4.02**	85.96**	60.06*	18.94**
Error (b)	48	1.63	1.17	8.93	1.07	18.89	18.46	10.08

Table 2. Estimates of the Simple Scaling Test and Gene Effects for Quality Traits and Seed Yield in four crosses of Indian mustard.

model was inadequate. Therefore, the six-parameter model was used to estimate gene effects (Table 2).

The significance of at least one of the scaling tests for almost all traits in all crosses (except for a few cases like protein content in Cross C and glucosinolate in Cross C and D for specific scales) indicated the presence of epistatic interactions (non-allelic interactions). The highly significant χ^2 values further

confirmed that the simple additive-dominance model was inadequate, necessitating the use of the six-parameter model to estimate the components of genetic variance, including interaction effects. The results of scaling tests and gene effect estimates indicated that most traits exhibited significant epistatic interactions, suggesting complex genetic control. Similar results have been reported in Indian mustard by researchers studying yield and quality traits (Prajapati *et al.* 2014

and Manjunath *et al.* 2017).

For seed yield per plant, significant scaling tests in several crosses indicated the involvement of epistatic interactions. Both additive (d) and dominance (h) effects were significant in different crosses, revealing the contribution of both gene actions. Significant epistatic components, particularly additive $\times$ additive (i) and dominance $\times$ dominance (l) interactions, suggested that seed yield is governed by a complex genetic system involving both additive and non-additive gene effects. These results were in agreement with those reported by Ashish *et al.* (2020), Chaudhary *et al.* (2021), Akanksha *et al.* (2024) and Pathak *et al.* (2024). The presence of non-additive gene action indicates the usefulness of heterosis breeding, whereas additive effects suggest that selection in later generations may also be effective.

For oil content, scaling tests were significant in most crosses, demonstrating the presence of epistasis. Significant additive gene effects across several crosses suggested the importance of additive gene action in improving oil content. However, dominance and epistatic interactions were also detected, indicating that both additive and non-additive gene effects contribute to the inheritance of oil content in Indian mustard (Kumar *et al.* 2016, Chaudhary *et al.* 2021). The predominance of additive effects suggests that selection in later segregating generations may effectively improve oil content.

In the case of protein content, both additive and dominance gene effects were observed, along with significant epistatic interactions in several crosses. The significant additive $\times$ additive interaction indicates the role of additive type epistasis, which may facilitate improvement through selection in later generations (Khan *et al.* 2023).

The scaling tests for oleic acid content, dominance gene effects were relatively larger than additive effects in several crosses, suggesting the predominance of non-additive gene action. Significant dominance $\times$ dominance (l) interactions indicated duplicate epistasis in several crosses. Such results suggest that heterosis breeding and recurrent selection may be useful strategies for improving oleic acid content. Similar observations were reported by Prajapati *et*

al. (2014) in Brassica species.

The results of scaling tests for linolenic acid showed significant additive gene effects in several crosses, revealing that additive genes play an important role in determining this trait. However, the presence of epistatic interactions suggests that both additive and non-additive gene effects contribute to its inheritance. Therefore, selection in segregating generations may be effective for modifying linolenic acid levels.

For erucic acid content, both additive and dominance gene effects were significant, along with epistatic interactions. Significant additive $\times$ additive interactions indicated the presence of additive-type epistasis, suggesting that selection combined with hybridization could help develop low-erucic acid genotypes. Kavita *et al.* (2025) reported that low erucic acid is governed by recessive inheritance and is digenically inherited with an additive gene effect.

Most scaling tests for glucosinolate content were significant, suggesting the presence of epistasis. Significant additive gene effects suggested that additive genes contribute to trait inheritance. However, the presence of dominance and epistatic interactions indicated that the genetic control of glucosinolate content is complex. The importance of both additive and dominance gene effects was reported by Khan *et al.* (2023). These findings suggest that selection in advanced generations may help develop low-glucosinolate genotypes suitable for improving mustard oil quality.

CONCLUSION

The results of the present investigation revealed that both additive and non-additive gene effects are involved in the inheritance of seed yield and quality traits in Indian mustard. The significant scaling tests and χ^2 values indicated the presence of epistatic interactions for most traits, suggesting complex genetic control.

Additive gene effects were important for several quality traits, including oil content, protein content, and fatty acid composition, suggesting that selection in later generations would be effective for improving

these traits. However, significant dominance and epistatic interactions for traits such as seed yield and oleic acid content indicated the importance of non-additive gene action

These results provide useful guidance for designing breeding strategies aimed at improving seed yield and oil quality traits in Indian mustard.

Breeding implications

The findings of the present study provide useful insights for designing effective breeding strategies in Indian mustard:

1. Traits governed largely by additive gene effects can be improved through selection in advanced segregating generations.
2. Traits showing dominance and epistatic interactions may benefit from heterosis breeding and hybrid development
3. Improvement of oil quality traits such as erucic acid and glucosinolate content may be achieved through recurrent selection and pedigree breeding approaches.
4. Since both additive and non-additive gene actions were observed for most traits, a combined breeding strategy involving hybridization followed by selection would be most effective for improving yield and quality traits in Indian mustard.

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