Original Research Article

Gene Action for Quantitative Traits through Generation Mean Analysis in Indian Mustard (*Brassica juncea* L.)

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**A B S T R A C T**

The adequacy of different genetic models and nature and magnitude of gene effects responsible for the expression of seed yield and important yield contributing characters were studied in mustard. 6 generations of two crosses viz; MRNJ 88-1 X JMWR 9081-1 (Family A), MRNJ 131 X JMWR 9081-2 (Family B) sown in Compact Family Block Design were investigated. Data recorded showed the predominance of both Main effect (additive-dominance) and interaction effect for most of the yield and component traits except in number of primary branches per plant and number of secondary branches per plant where the role of main gene effect was distinct. Presence of interaction effects and duplicate epistasis suggested the possibilities of obtaining transgressive segregants in later generations. The role of fixable and non-fixable gene action in controlling different yield and component traits was also apparent. The present findings will help in deciding effective selection and breeding strategies to get desired improvement in seed yield and related traits.

**Keywords**
Gene action,
Generation mean analysis,
Quantitative traits,
Indian mustard,
Seed yield,
Epistasis

**Article Info**
Accepted: 04 July 2019
Available Online: 10 August 2019

**Introduction**

Brassica group of oilseeds are commonly known as “rapeseed and mustard” and are widely grown throughout the world as oilseed crop for edible, industrial purposes, vegetable crops, spices for human consumption and as fodder crops for livestock feeding. However, these crops are largely cultivated for production of oil and oil cakes. In terms of area under oilseeds, India holds premier position in the world, but the yield of most of the oilseed crops is less than the world average. On the other hand, the demand for edible oils is increasing very rapidly with increasing population and has been estimated at 10 million tonnes for the year 2015 and 11.2 million tonnes for 2030 (Paroda, 2000). In India, rapeseed-mustard are important oilseed crops and occupy second place only after
Despite all the efforts there is a huge gap between the demand and supply of oils. This situation indicates that there is a vast scope of improvement in this crop. Determination of suitable breeding method and selection strategy for improvement of a trait would depend on knowledge of gene effect controlling different yield and component traits. Generation mean analysis is an efficient tool to understand the nature of gene effect involved in expression of a character.

Therefore, information on the presence of type of epistatic genetic effect in the inheritance of various quantitative traits is important for adopting suitable breeding procedure to improve the trait. Generation mean analysis gives a comprehensive picture of gene action controlling the trait. It is relatively a simple first degree statistical technique to know the predominant genetic effects that are responsible in affecting the variation of character (Gupta et al., 2006; Kemparaju et al., 2009; Singh et al., 2012; Khodambashi et al., 2012 and Peerasak and Supapan, 2014).

Though the generation mean analysis has been extensively used to understand the gene effect in different crop, very less reports are available on the use of this technique for understanding the gene effect in Indian mustard.

In the view of above fact, present study was undertaken to estimate different kind of gene effect playing significant role in controlling the expression of seed yield and its contributing characters.

**Materials and Methods**

**Experimental material**

The experiment was carried out at oilseed breeding block of N.E Borlaug Crop Research Centre of G. B. Pant University of Agriculture and Technology, Pantnagar, District U. S. Nagar, Uttarakhand during Rabi 2012-13 and 2013-14. Two crosses viz; MRNJ 88-1 X JMWR 9081-1 (Family A), MRNJ 131 X JMWR 9081-2 (Family B) and their generations (P₁, P₂, F₁, F₂, BC₁, and BC₂) were developed (2012-13) which were evaluated in compact Family Block design with three replications (2013-14).

Observations were recorded on thirteen important economic characters. The row length for each plot was of 3m with a spacing of 30 cm (R-R) x 10 cm (P-P). Competitive plants from different generations of each family were randomly selected and tagged at the time of vegetative stage for recording of observations.

**Statistical analysis**

The data collected from two families (six generations each) were subjected to analysis of variance as prescribed for the compact family block design (Panse and Sukhatme 1962) to determine the significance of difference among various genotype means. The families showing significant differences among the progenies for the characters was subjected to simple scaling test (Mather 1949, Hayman and Mather 1955) to test the adequacy of additive dominance model for different characters, non-adequacy of which indicates the presence or absence of non-allelic interactions.

Joint scaling test given by Cavalli (1952) was then subjected to the two families to estimate the different genetic parameters. Adequacy of a model was judged by non-significance of \( \chi^2 \) value and significance of all genetic parameters. Type of epistatic interaction based on direction of [h] and [l] was also determined according to Hayman and Mather (1955) for each character.
Results and Discussion

The adequacies of different models are given in the table 1 and 2 for Family A and Family B. The estimates of six generations for joint scaling tests and their interaction effects are presented in table 3.

Adequacy of model

Digenic interaction model was found adequate in most of the trait except plant height, number of primary branches and number of secondary branches in family A and number of primary branches and test weight in family B where 3 parameter models was found adequate. While the 6 parameter model was found most appropriate for days to maturity in both the families.

In Family A digenic model with 3 parameters were adequate for days to flower initiation and seeds per siliqua. Digenic model with 4 parameters was found adequate for siliquae on main raceme, test weight and oil content. 5 parameter digenic model was found adequate for length of main raceme, siliqua length, siliqua density and seed yield.

Digenic model with 4 and 5 parameters was found adequate for most of the yield and component traits except Primary branches, test weight and days to maturity in Family B.

Detection of gene effects and the nature of epistasis

The dominance x dominance [l] interaction was larger than the additive x additive [i] and additive x dominance [j] effect among the interaction effect while for the main effect the dominance effect [h] was more pronounced as compare to additive effect [d]. Peerasak and Supapan (2014) had also reported the role of main effects and interaction effects for the inheritance of different characters in soyabeans. The dominance and dominance x dominance effects were in opposite direction, suggesting the occurrence of duplicate-type epistasis in most of the cases and indicating predominantly dispersed alleles at the interacting loci.

Duplicate epistasis for different traits had also been reported by Kemparaju et al., (2009), and Singh et al., (2012). Dominance gene effects were found to be relatively more important, as indicated by the fact that in all cases the dominance effect [h] value was much higher than the additive values [d].

Non fixable effects (dominance [h] and dominance x dominance [l]) played predominant role in the inheritance of days to flower initiation. Duplicate epistasis was also found in case of family A. Duplicate epistasis for different traits had also been reported by Kemparaju et al., (2009). For days to maturity fixable and non-fixable both type of effects were involved but the magnitude of non-fixable gene effect [d] and [l] was predominantly found. Duplicate epistasis was also found in both the families. Kabdal and Singh (2011) and Singh et al., (2012) reported presence of duplicate epistasis.

In case of plant height in family A main effect [d] and [h] were the major contributor while in case of family B along with the main effect the interaction effects [i] and [l] were also present and their magnitude were at par. For length of main raceme among the main effect the additive component was the major contributor. Additive x additive [i], dominance x dominance [l] and additive x dominance [j] was found involved in the inheritance of character but the magnitude of [j] was highest among all and that may be due to the contribution of the additive component of gene effect. For primary and secondary branches for both the families the main effects were predominant significant contributors.
### Table 1 Adequacy of different models by $\chi^2$ test for different characters for Family A

| Characters    | Models          | AD          | DI          |
|---------------|-----------------|-------------|-------------|
|               |                 | 3 parameter | 4 parameter | 5 parameter | 6 parameter |
| DFI           |                 | ns[m],[h],[l] | ns[m],[h],[l] | ns[m],[h],[l] | ns[m],[h],[l] |
| DM            | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| PH            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| LMR           | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| PB            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SB            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SMR           | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SL            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SS            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SD            | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| TW            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| OC            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SY            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |

Where, ns: non-significant $\chi^2$ value
**+: models with significant estimates and $\chi^2$ value
[m]: mean effect
[d]: the sum of dominance effects of all loci
[i]: the sum of digenic interactions among the homozygous combinations taking into account the signs of interaction and distribution of genes between parental lines
[j]: the sum of digenic interactions among the homozygous and heterozygous combinations, taking sign and distribution into account
[l]: the sum of digenic interactions among the heterozygous combinations taking into account, the sum being independent of the distribution of genes in the parental lines
AD: additive dominance, DI: digenic interaction, DFI: days to flower initiation, DM: days to maturity, PH: plant height, LMR: length of main raceme, PB: number of primary branches per plant, SB: number of secondary branches per plant, SMR: siliqua on main raceme, SL: siliqua length, SS: seeds per siliqua, SD: siliqua density, TW: test weight, OC: oil content, SY: seed yield

### Table 2 Adequacy of different models by $\chi^2$ test for different characters for Family B

| Characters    | Models          | AD          | DI          |
|---------------|-----------------|-------------|-------------|
|               |                 | 3 parameter | 4 parameter | 5 parameter | 6 parameter |
| DFI           |                 | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| DM            | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| PH            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| LMR           | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| PB            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SB            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SMR           | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SL            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SS            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SD            | **              | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| TW            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| OC            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |
| SY            | ns[m],[d],[h]   | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] | ns[m],[d],[h] |

Where, ns: non-significant $\chi^2$ value
**+: models with significant estimates and $\chi^2$ value
[m]: mean effect
[d]: the sum of dominance effects of all loci
[i]: the sum of digenic interactions among the homozygous combinations taking into account the signs of interaction and distribution of genes between parental lines
[j]: the sum of digenic interactions among the homozygous and heterozygous combinations, taking sign and distribution into account
[l]: the sum of digenic interactions among the heterozygous combinations taking into account, the sum being independent of the distribution of genes in the parental lines
AD: additive dominance, DI: digenic interaction, DFI: days to flower initiation, DM: days to maturity, PH: plant height, LMR: length of main raceme, PB: number of primary branches per plant, SB: number of secondary branches per plant, SMR: siliqua on main raceme, SL: siliqua length, SS: seeds per siliqua, SD: siliqua density, TW: test weight, OC: oil content, SY: seed yield
Table 3: Estimates of genetic parameter under the adequate genetic model with respective $\chi^2$ value and type of epistasis

| Character | Family | M      | D      | H      | I      | J      | L      | $\chi^2$ | Epistasis |
|-----------|--------|--------|--------|--------|--------|--------|--------|---------|-----------|
| DFI       | A      | 69.28±0.43** | -10.08±1.71** | -0.00±0.00** | -4.84±3.32 | 9.13±1.52** | 1.62   | Duplicate |
|           | B      | 72.89±3.43** | 0.22±0.60 | -9.01±8.42** | -6.84±3.32 | 5.12±5.21  | 0.28   | ---       |
| DM        | A      | 168.49±9.92** | -2.49±4.90** | -94.16±9.99** | -39.99±1.88** | 3.66±1.56 | 55.66±3.29** | --- | Duplicate |
|           | B      | 111.33±3.07** | 0.66±0.33 | 39.33±7.05** | 17.33±0.55** | 6.66±1.65 | -22.66±4.21** | --- | Duplicate |
| PH        | A      | 145.50±1.47** | -3.78±1.46* | 10.44±3.03** | 1.20   |       |       |         |           |
|           | B      | 166.71±3.13** | -10.17±0.75** | -45.35±9.36** | -29.32±2.80** | 30.55±6.70 | 0.73   | Duplicate |
| LMR       | A      | 52.91±0.55** | -3.67±0.33** | -10.65±0.65** | 25.00±5.93* | -11.16±0.58** | 0.24   | ---       |
|           | B      | 24.34±4.54** | -3.50±0.45* | 27.71±5.36** | 12.66±5.7*  | 0.24    |       |         |           |
| NP        | A      | 5.29±0.25**  | 0.05±0.25  | 2.94±0.30**  | 0.12   |       |       |         |           |
|           | B      | 4.78±0.19**  | -0.01±0.19** | 1.37±0.29*   | 0.58   |       |       |         |           |
| Num SB    | A      | 16.01±1.21** | 0.75±1.07  | 7.76±2.35*   | 0.49   |       |       |         |           |
|           | B      | 12.39±0.85** | 1.77±0.19** | 6.50±1.68*   | 2.39±0.87 | 0.50   |       |         |           |
| SMR       | A      | 18.58±0.50** | 10.80±2.09** | 4.65±1.03** | -13.63±2.48** | 0.34   | Duplicate |
|           | B      | 24.34±4.54** | -3.50±0.45* | 27.71±5.36** | 12.66±5.7*  | 0.24    |       |         |           |
| SL        | A      | 2.88±0.81*   | -0.009±0.14 | 1.42±1.85   | 0.58±0.78 | -0.55±1.09 | 0.41   | Duplicate |
|           | B      | 4.15±0.17**  | 0.17±0.05* | -0.75±0.20*  | 0.56±0.19** | 0.24   |       |         |           |
| SS        | A      | 12.85±0.17** | -0.70±0.21* | 1.60±0.39*   | 0.58   |       |       |         |           |
|           | B      | 21.15±1.14** | 1.56±0.27** | -22.53±3.28** | -6.61±1.07** | 13.91±2.47** | 0.11   | Duplicate |
| SD SD     | A      | 0.51±0.07**  | 0.01±0.01  | -0.24±0.20  | -0.80±0.76 | 0.10±0.13 | 0.24   | Duplicate |
|           | B      | 0.64±0.05**  | 0.04±0.04** | -0.29±0.06** | -0.20±0.05* | -0.24±0.07* | 0.58   | ---       |
| TW        | A      | 2.89±0.10**  | -0.22±0.09* | -1.41±0.47*  | 1.53±0.51*  | 0.41   |       |         |           |
|           | B      | 3.04±0.05**  | 0.17±0.06  | -0.34±0.10*  |       |       |       |         |           |
| OC OC     | A      | 34.16±0.65** | 12.06±1.68** | 4.75±0.50** | -7.37±1.29** | 0.34   |       |         |           |
|           | B      | 40.76±3.64** | -0.05±0.66 | 2.02±9.83   | -2.85±3.61 | -9.92±7.27 | 0.0001 | Duplicate |
| SY        | A      | 7.94±0.65**  | -0.86±0.13** | 29.54±1.78** | 10.15±0.66** | -18.76±1.17** | 0.13   | Duplicate |
|           | B      | 3.38±0.12**  | 0.28±0.22  |       |       |       | 0.41   |         |           |

Where, * Significant at 5% probability level; ** significant at 1% probability level; M: mean; D: additive effect; H: dominance main effect. I: additive x additive effect; J: additive x dominance effect; L: dominance x dominance effect.

Non fixable gene effect was predominant for the number of siliquae on main raceme where dominance [h], dominance x dominance [l] and additive x dominance [j] were involved in family A and in family B both the fixable gene effect i.e. [d] and [i] and dominance effect [h] were the key effects for the inheritance of character. Duplicate epistasis was detected in family A. Singh et al., (2007) and Singh et al., (2012) reported the presence of duplicate epistasis for this trait. Siliqua length was also inherited by the fixable and non-fixable gene effects but their magnitude were significant and low for family B and non-significant for Family A. Duplicate epistasis was found in family A. In seeds per siliqua the dominance x dominance [l] was in major role while the additive [d] effect played a minor role. In family B additive [d], dominance [h], additive x additive [i] and dominance x dominance [l] effects were significant but the magnitude of non-fixable gene effects were high. Duplicate epistasis was also detected. Results were in conformity with the findings of Singh et al., (2012).

For siliqua density in case of family B additive [d], dominance [h], additive x additive [i] and additive x dominance [j] effects was major contributor towards inheritance of character. For the test weight in family A duplicate epistasis was detected that showed involvement of dominance and dominance x dominance gene effect whereas in family B major role was played by the dominance main effect.
In case of seed yield the additive [d], additive x additive [i], dominance [h], additive x dominance [j] and dominance x dominance [l] gene effects were significantly involved for both the families. Duplicate type epistasis was detected for family A. Singh et al., (2012) has also reported the presence of duplicate epistasis for seed yield. The magnitude of non-fixable gene effect was higher than the fixable type of gene effect. In Family A the inheritance of oil content was controlled by the dominance [h], additive x additive [i] and dominance x dominance [l] effect. Duplicate epistasis was present. Singh et al., (2012) also reported the involvement of duplicate epistasis in the inheritance of oil content.

Considering the overall results, it is apparent that most of the characters in both the families were found under the control of both fixable (additive, additive x additive) and non-fixable (dominance and epistatic) gene effects coupled with duplicate type of epistasis except in number of primary branches per plant and number of secondary branches per plant. More predominant role of non-additive effects (Kumar et al., 2006; Tahir et al., 2007; Singh et al., 2007; Prajapati et al., 2008 and Yadav et al., 2011) suggest that selection could be delayed upto late segregating generations or inter mating among the selected segregants followed by one or two years of selfing could be suggested to break the undesirable linkage and allow accumulation of favourable alleles for improvement of trait. Also the more effective role of additive effect indicates that selection could be effective in early segregating generations. The magnitude of dominance and epistatic effects present in the material may be exploited through appropriate recurrent selection procedure. Therefore breeding strategies should be designed accordingly to get desired results. Thus, present investigation contributes significantly to acquiring knowledge about nature of gene action and its magnitude for quantitative characters that will be helpful in deciding effective breeding methods for improvement of seed yield and related traits. The different types of gene effects estimated provides a test for gene action and are useful for analysing the genetic makeup of a crop so as to further improve the trait. The estimates obtained from each cross may be unique to that cross and may not be applicable to parental population. Additive genetic variance formed the major part of genetic variance for important yield component traits. Therefore improvement in yield can be achieved through indirect selection of component trait rather than going for a direct selection of yield per se.

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