Analysis of genetic architecture through generation mean analysis for yield and yield contributing traits in crosses of Indian mustard (*Brassica juncea*)

ABSTRACT

Generation mean analysis was deployed to study the inheritance of 12 yield and its component traits in two crosses *viz.* PR-2009-6 × ALBELI (Family A) and PR-2009-6 × RGN-73 (Family B) of Indian mustard [Brassica juncea (L.) Czern& Coss] for parents P1 and P2, F1 , F2 , BC1 and BC2 generations. Analysis of variance showed presence of significant variability among families and also within families (among progenies) for various traits under study except for days to maturity, seeds per siliquae and siliquae length. Family A showed considerable interaction effects for siliquae on main raceme, number of seeds per siliquae and oil content. Family B displayed epistatic interactions for characters such as plant height, length of main raceme, siliquae on main raceme, siliquae length, oil content seed yield per plant and glucosinolate content. Fixable effects [d] and [i] were found important in the inheritance of plant height, seed yield per plant and glucosinolate content. Among non fixable effects, dominance [h] gene action was significantly important for determining length of main raceme, number of siliquae on main raceme, siliquae length, oil content, seed yield per plant and glucosinolate content. Interaction gene effects were found significant in controlling plant height, length of main raceme, number of secondary branches per plant, siliquae on main raceme, siliqua length,1000-seed weight, oil content, seed yield per plant and glucosinolate content. Thus, both main effects and epistatic effects were found important in controlling the various traits under study.

Keywords: Genetic Architecture Analysis, Indian mustard, Brassica juncea occupies

INTRODUCTION

Indian mustard (*Brassica juncea*) is a natural amphidiploid between *Brassica rapa* (AA; 2n=20) and *Brassica nigra* (BB; 2n=16) which arose as a result of independent hybridization events in the sympatric areas of the diploid progenitor species. *Brassica juncea* occupies a prominent position among *rabi* oilseed crops in India, in terms of area and production. Out of the different Brassica oilseeds grown, *Brassica juncea* is the oilseed of choice in the Indian subcontinent for edible oil. It is grown in more than 80 *per cent* of the total area cultivated for rapeseed mustard, contributing about 27 *per cent* of edible oil pool in India and more than 13 *per cent* globally. The oil extracted from its seed finds use in cooking media and several industries as well. Although, India ranks second in area and production of rapeseed-mustard in the world, it is still far behind when compared with the world average. Thus, large amount of edible oil is imported annually to make up for the ever rising demand.

The widespread cultivation of this crop and numerous uses necessitate the identification of high yielding genotypes based on genetic parameters to devise promising breeding programmes. Yield being a complex polygenic character, is a result of multiple contributing traits. Further complications in improving yield are created as it is predisposed to environmental changes that cause unavoidable fluctuations in varietal performance. The dual bottlenecks of polyploidy and domestication restrict the genetic base in *Brassica juncea*, which stands further narrowed because of intensive plant breeding activities. An in depth knowledge of the association between yield and its components is of paramount importance for the best utilization of these relationships by breeders. In this regard, profiling of genetic architecture of quantitative characters becomes imperative to ensure the success of breeding programmes. The mating designs such as diallel and line × tester provide estimates of additive and dominance components of gene effects in reference to the whole population studied but the partitioning of genetic variance into all probable components can be done efficiently through generation mean analysis.

Generation mean analysis is a quantitative biometrical approach which derives information on various gene effects whose coaction influences the inheritance of various quantitative characters. It is a unique biometrical tool which is useful in estimating main gene effects (additive and dominance) and their digenic (additive × additive), (additive × dominance) and (dominance × dominance) interactions responsible for inheritance of important quantitative traits. It is one of the best methods available for measuring epistasis accurately, whether it is complementary (additive × additive) or duplicate (additive × dominance) and (dominance × dominance) at the digenic level. The analysis for this method is based on measurements of phenotypic performances of important quantitative traits on as many as possible plants in basic experimental breeding generations *viz.,* parents, filial, backcross and segregating generations. It is instrumental in evaluating the performance of the parents used in crosses and can reveal the potential of hybridized material to be used either for heterosis exploitation or pedigree selection. The study of gene effects highlights the relative importance of various kinds of gene effects in control of a quantitative trait and how their interplay can be used to decide a suitable breeding strategy for the improvement of yield contributing traits.

The success of a breeding programme can be ensured, once a clear outline of gene actions accessible in a breeding material is available. The present investigation was thus carried out to get a detailed view of the gene interactions that interplay in the genetic expression of yield so that appropriate breeding strategies can be proposed for their further improvement.

MATERIAL AND METHODS

PLANT MATERIAL AND EXPERIMENTAL DESIGN

The field experiment was conducted at Oilseed breeding block of Norman E. Borlaug Crop Research Centre of Govind Ballabh Pant University of Agriculture and Technology, Pantnagar, Udham Singh Nagar, Uttarakhand, India. The experimental material comprised of six generations including parents (P_1 and P_2), F_1, F_2, BC_1 and BC_2 from two cross families PR-2009-6 × ALBELI (Family A) and PR-2009-6 × RGN-73 (Family B). The crosses to generate F_1s were made during *Rabi* 2013. The seeds of F_1 generation were sown to grow F_2 plants and back crosses were also made during *Rabi* 2014. The final trial for evaluation was sown in open field conditions in *Rabi* 2015 where the two families with their parents (P_1 and P_2) and generations (F_1, F_2, BC_1 and BC_2) were grown in compact family block design in three replications. Each generation was planted in 3m rows with row to row distance of 30cm and plant to plant distance of 10cm. In each cross family one row of parents and F1's was grown and three rows each of F_2, BC_1 and BC_2 were planted. The data generated was evaluated for 12 characters *viz.* days to maturity, plant height, length of main raceme, number of primary branches/plant, number of secondary branches/ plant, number of siliqua on main raceme, siliqua length, number of seeds per siliqua, 1000 seed weight, seed yield per plant, oil content and glucosinolate content. Data from five randomly selected plants was recorded from all the rows of P_1, P_2, F_1, while data on fifteen plants was collected in F_2, BC_1 and BC_2.

GENERATION MEAN ANALYSIS

Generation mean analysis was performed with the objectives of estimating gene effects, variances, presence or absence of epistasis and the type of epistasis involved in the inheritance of the traits studied. Scaling tests A, B, C, D were used to check the adequacy of simple additive- dominance model as proposed by Hayman and Mather (1955) and Mather and Jinks (1971). For this purpose first degree statistics i.e. means of different generations were used. The standard error of A,B,C and D was calculated by taking square root of respective variances of VA, VB,VC and VD and the significance of each scale was verified using student 't' test. The P values for respective calculated 't' values were examined for establishing the significance of scales. Each type of scaling test depends on certain combination of interactions for its departure from zero, thus each type of test is capable of detecting its own characteristic constellation of interactions. D tests (additive × additive) interaction whereas C test signifies (dominance × dominance) types of gene interaction. If C and D is found

significant it indicates (additive × additive) and (dominance × dominance) types of interaction. (additive × dominance) type of interaction has no effect on C and D but it affects the outcomes of A and B.

JOINT SCALING TEST

Many a times, Mather's scaling test may not be able to explain the additive-dominance model adequately **(Deb and Khaleque 2009).** Thus, joint scaling test **(Cavalli 1952)** was used to examine the competence of simple additive- dominance model or to evaluate epistasis for all the measured traits using χ^2 test. A significant χ^2 indicates inadequacy of the model, so non-allelic interactions are added in the model.

ESTIMATION OF GENE EFFECTS THROUGH SIX GENERATION MEANS

In cases where the simple additive dominance model was found inadequate, six parameter model or digenic interactions model given by **Hayman's (1958)** approach was used to split the components of genetic variance to its main effects and to extract information on inheritance pattern of various traits. For proper estimation of gene effects, the absence of both linkage and higher order gene interactions were assumed in this study. The six parameters in generation mean analysis are represented by mean effect (m), additive (d), dominance (h) and gene interaction effects comprising additive × additive (i), additive × dominance (j) and dominance × dominance. The 't' values were calculated using standard error values obtained after taking the square roots of respective variances.

RESULTS AND DISCUSSION

ADEQUACY OF THE GENETIC MODEL

The data presented in Table 1 shows that scale D differed significantly from zero in Family A and scales A and B in Family B for days to maturity. In case of plant height, scales A,C and D were found significant in Family A and scales A, B and D in Family B. The data for the trait length of the main raceme showed that in Family A, scales A and C were significant and all the four scales were found significant in Family B. For the trait primary branches per plant all the scales except scale D were found to differ significantly in Family A and B. The data recorded for the character secondary branches per plant revealed the significance of scales A and D in Family A. Scales A and D proved significant in Family A and all scales except scale D were found significant in Family B for number of siliqua on main raceme. Only scale D was found significant in Family B for siliqua length. For number of seeds per siliqua scales A, C and D were observed as significant while scale B and D differed significantly from zero in Family B. The analysis for oil content revealed that all the scales were significant in Family A and only scale A was significant in Family B. The scales A,C and D were significant in Family A and A, B and C in Family B for seed yield per plant. All the scales were found significant in both the families for glucosinolate content. These results indicated the presence of epistasis for all the traits except thousand seed weight as one or more scaling tests were found significant in most of the traits.

In family A, digenic three parameter model was found most adequate for days to maturity, plant height, number of primary branches per plant and siliqua length. The four parameter model fitted best for siliqua on main raceme, seeds per siliqua and thousand seed weight. In case of traits such as length of main raceme, secondary branches per plant and seed yield, the digenic five parameter model proved its adequacy. Six parameter model was judged as the best fit for oil content and glucosinolate content in this family with a non significant χ^2 value.

In family B, digenic two parameter model proved its adequacy for traits such as days to maturity and seeds per siliqua. The digenic three parameter model was found the best fit in case of primary branches per plant, secondary branches per plant, thousand seed weight and glucosinolate content.

The digenic four parameter model was the best fit for traits such as plant height, siliqua length and seed yield. The five parameter model was judged as the best fit for siliqua on main raceme and oil content while the six parameter model was found most adequate for length of main raceme in this family.

GENE ACTION AND EPISTASIS EFFECTS

The significance of results in scaling test (Mather 1949) and joint scaling test (Cavalli 1952) for most of the traits in this study, highlighted the importance of higher order interaction in the expression of traits **(Shahid 1996).** This also proves that additive- dominance model alone is not enough to explain the inheritance of the traits studied. Thus, digenic interaction model with six parameters, namely *m, d, h, i, j and l* **(Hayman 1958)** was adopted and found appropriate for explaining gene actions involved in most of the traits. The genotypic mean of any population is under the influence of epistatic effects apart from additive and dominance gene effects **(Viana, 2000).** Due to difficulties in the estimation of such components, their relative importance cannot be evaluated.

The mean values (m) for all the traits were found highly significant in the F_2 generation for all the twelve traits studied in Family A. Additive effect (d) was found positive and significant in Family A for plant height, length of main raceme and thousand seed weight. This indicated that selection in the early generations can be practised for the improvement of these traits in the segregating generations of this cross. The value of dominance effect (h) was found negatively significant for days to maturity which meant that the parents used for making this cross can be used for generating plants showing early maturity. The values for dominance effect (h) and additive × additive (i) interaction effect were found significant for seed yield per plant. This implied that selection in the later generations of this cross could yield suitable plants for the improvement of this trait. These results were in agreement with that reported by **Kaur *et al.* (1998) and Yadav *et al.* (2012).** The data obtained for this family showed opposite signs of (h) and (l) for the traits *viz.,* length of the main raceme, primary branches per plant, secondary branches per plant, number of siliqua on main raceme, number of seeds per siliqua, and oil content which established internal cancellation of gene effects.

The mean values for all the traits were found significant in Family B except for thousand seed weight. The value for additive gene effect (d), additive × dominance (j) and dominance × dominance (l) interaction effects were found significant for oil content in this cross which indicated that the parents in this cross can be used in further improvement of oil content. These results complied with the results obtained by **Sachan and Singh (1988)** who observed the role of additive [i] gene effect in the inheritance of this particular trait. The values for dominant effect (h) and additive × additive (i) were reported as significant for seed yield per plant. Thus, the parents of this cross can contribute in the improvement of this trait if selection is delayed to later generations so that heterozygosity gets reduced in the population. **Rishipal and Kumar (2013)** have also reported the same type of interaction effects for seed yield. The significant values of dominance (h), additive × additive (i) and dominance × dominance (l) interaction effects were found significant for siliqua length. The same sign of (h) and (l) established the presence of complementary epistasis for this trait. This implied that the parents selected for this cross were diverse and can be used for the further improvement of this trait. These results were akin to the findings of **Labana *et al*. (1975).**

The significance of additive gene effect (d) was proved for the traits *viz.,* plant height and oil content, where the positive sign of (d) indicated the positive contribution of alleles for aforementioned traits. **Prasad *et al.* (2011)** also confirmed the importance of additive gene effect in the inheritance of plant height. The significance of additive gene action for oil content has been reported by **Kant and Gulati (2012), Kumar and Thakral (2003) and Gami (2012).** In traits where there is no cancellation of additive gene action, selection can be practiced in the early generations because of the fixable nature of this gene effect and further improvement in characters can be done using pedigree method and progeny selection.

In the above mentioned crosses several traits such as days to maturity, primary branches per plant, number of siliqua on main raceme, number of seeds per siliqua, thousand seed weight and seed yield per plant, were reported to have a higher magnitude of dominance as compared to additive gene action. Similar observations have been reported by **Ashish *et al.* (2019)** who confirmed the involvement of dominant gene action in the inheritance of seeds per siliqua. Such traits can be improved through conventional breeding approaches whereby pedigree, bulk or single seed descent methods of selection are employed and selection is delayed till advanced generations. For the characters, which are controlled by non-additive gene action (dominance or epistasis) heterosis breeding would be the most effective, however, mode of reproduction of crop or lack of a workable CGMS system would restrict it, therefore selection in later generations would be remunerative as by that time dominance could be reduced by selfing and breeding **(Manjunath *et al.* 2017).**

Both additive and dominant gene action were found significant for traits such as length of main raceme, seed yield per plant, oil content and glucosinolate content. These results showed congruency with the results reported by **Singh and Srivastava (1999), Katiyar (2000), Sachan (2004), Prajapati *et al.* (2018) and Meena *et al.* (2013).** Preponderance of both additive and dominant gene action in the inheritance of seed yield per plant has also been reported by **Chaudhary *et al.* (2021).** The negative sign of (h) for days to maturity implied that the parents contributed alleles having dominance effects which lowered the value of the trait. Since lower values are favourable for attaining early maturity, parents in this cross can be used in breeding programmes for further improvement of this trait. The similar signs of (d) and (h) in case of traits such as plant height, length of main raceme, oil content, seed yield per plant and glucosinolate content underlined the predominance of additive and dominance effects in the inheritance of these traits. In traits where negative estimates of *h, i* and *l* were observed, selection in later generations is recommended and the negative effect of these alleles can be removed through recurrent selection procedure **(Singh and Narayan 2000).**

Complementary epistasis was observed for siliqua length which indicated the chances of obtaining heterosis for this trait in Family B. Moreover, the opposite signs of (h) and (l) in Family A stipulated a possibility of obtaining transgressive segregants for traits *viz.,* length of the main raceme, primary branches per plant, secondary branches per plant, number of siliqua on main raceme, number of seeds per siliqua, and oil content in the succeeding generations (**Singh *et al*., 2014**).

Duplicate epistasis in most of the traits established the prevalence of dominance effect which cannot be used in breeding programmes unless variability is reduced in the advanced generations. In both the crosses scaling tests were found significant for most of the characters but non-allelic interactions were not significant for traits like days to maturity, primary branches per plant, secondary branches per plant and siliqua length. This could arise due to several reasons such as higher order interactions, complex genetic control or large environmental variance **(Milus and Line 1986).** Such results are also observed when higher order epistasis is present among more than two genes while controlling genetic interactions **(Purcell *et al.*2007).** The genetic estimates did not show any significant values in case of some traits studied in the two crosses, such as days to maturity, oil content, siliqua length and number of secondary branches. These observations can be attributed to dispersion or internal cancellation of gene effects.

CONCLUSION

Based on the results obtained in the current study, it is evident that yield and its contributing characters exhibited all three types of gene actions *viz.,* additive, dominance and epistasis. The best way to improve yield in this scenario is to adapt recombination breeding followed by selection in advanced generations. Moreover, further improvement can be expected through exploring additive gene effect first, through standard selection procedures. Another important factor to be taken into account is the dominance gene action which should not be lost, rather should get concentrated during the breeding programme. The difference between homozygotes at a locus with positive and negative alleles being distributed between parents is reflected in the predominance of additive gene effect in

the inheritance of several traits. Therefore, reciprocal recurrent selection appears to be another strategy that can exploit all the types of interactions observed in this experiment. This procedure ensures efficient utilization of both additive and non-additive gene effects. Also, in case where non-additive effects proved their adequacy recurrent selection for specific combining ability can be used as an appropriate breeding procedure. Therefore, it is apt to state that recurrent selection that capitalizes all three types of gene effects would definitely help in recovering desirable recombinants in advanced generations of the crosses used in this study.

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Table.1 Estimates of genetic parameters under adequate genetic model with respective χ2 value and type of epistasis involved for 12 characters studied in two crosses of Indian mustard

	Days to maturity		Plant height		Length of main raceme		No. of primary branches		No. of secondary branches		No. of siliqua on main raceme	
Gene action	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**
Mean (m)	130.17**	128.78**	225.40**	122.99**	67.91**	22.30**	6.06**	5.32**	11.86**	9.36**	31.89**	36.56**
Additive (d)	1.16	--	6.28*	7.77**	5.64**	4.36**	--	--	--	--	--	1.57
Dominance (h)	-2.84	--	--	240.63**	16.84**	149.59**	-4.09**	--	-9.79**	--	27.87*	54.02**
Add × add (i)	--	--	17.68**	61.86**	--	40.77*	--	1.58**	--	--	8.26*	--
Add × dom (j)	--	10.84**	34.54**	--	--	17.56	--	--	--	--	9.06*	36.96**
Dom × dom (l)	--	--	--	145.43**	-19.96**	-144.34**	4.69**	1.91*	5.56*	--	-16.86*	-56.28**
χ2	7.67	3.83	4.51	0.37	0.67	--	6.46	1.77	0.38	0.07	1.27	0.34
Epistasis	-	-	-	D	D	D	D	-	D	-	D	D

	Siliqua length		No. of seeds per siliqua		Thousand seed weight		Seed yeild per plant		Oil content		Glucosinolate content	
Gene action	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**
Mean (m)	4.67**	2.41**	3.41**	36.65**	4.29**	--	5.03**	8.22**	24.69**	35.36**	84.30*	-10.88*
Additive (d)	--	--	--	1.57	0.78**	--	0.66	0.49*	0.73	5.76**	35.17**	6.94**
Dominance (h)	--	4.91**	22.65**	54.02**	--	9.01**	6.38**	--	27.04	-7.85**	82.62**	463.90**
Add × add (i)	--	1.86**	9.04*	--	-0.76**	2.96**	5.16**	1.38**	14.47**	--	71.67*	158.52**
Add × dom (j)	--	--	--	36.98**	1.13**	--	2.88	--	15.07**	15.83**	-22.15**	25.16**
Dom × dom (l)	--	3.36**	-13.32**	-56.28**	--	-5.48**	--	2.77**	-12.34	9.31**	--	-325.9**
χ2	3.49	3.67	4.95	0.34	1.08	---	0.1	2.98	--	0.71	0.005	---
Epistasis	-	C	D	D	-	D	-	-	D	D	-	D

Table.2 Estimates of scaling tests for 12 characters studied in two crosses of Indian mustard

Scaling test factors	Days to maturity		Plant height		Length of main raceme		No. of primary branches		No. of secondary branches		No. of siliqua on main raceme	
	Family A	Family B	Family A	Family B	Family A	Family B	Family A	Family B	Family A	Family B	Family A	Family B
A	-1.9	5.26**	12.99**	44.97**	11.63**	36.71**	-2.06**	-1.29**	-1.5	-1.47	8.45**	9.58**
B	-5.28	-4.83**	-12.52	39.27**	7.93	36.71**	-1.68**	-2.45**	-0.9	-0.13	0.39	46.45**
C	7.94	-3.43	42.00**	19.37	18.37**	32.78**	-2.95**	-5.86**	0.56	-1.99	0.59	58.95**
D	7.56	-1.93	20.76**	-32.43**	-0.6	-20.79**	0.39	1.06	1.51	-0.24	-4.13	1.45

Scaling test factors	Siliqua length		No. of seeds per siliqua		Thousand seed weight		Seed yeild per plant		Oil content		Glucosinolate content	
	Family A	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**	**Family A**	**Family B**
A	0.41	0.39	1.33**	-2.37	0.66	0.96	-3.68*8	-2.75**	6.47*	-12.70**	47.23**	96.27**
B	-0.23	0.83	4.33	4.22**	-0.39	0.33	-0.97	-1.41*	-8.59**	3.03	-25.11**	71.11**
C	-0.55	-0.63	-5.53**	-2.44	1.77	-0.54	-10.46**	-5.69**	-16.60**	-3.36	-143.40**	8.86**
D	-0.36	-0.93	-5.59**	-2.14*	0.75	-0.92	-2.96**	-0.76	7.23**	3.09	-35.52	-79.26**

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