



Genetic architecture of yield traits and oil content in Indian mustard (*Brassica juncea*)

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ABSTRACT

The generation mean analysis was carried out to estimate nature and magnitude of gene effect for yield traits and oil content in two crosses RH 0749 × RLC-3 and RH 0749 × PDZ-1 of Indian mustard [*Brassica juncea* (L.) Czern & Coss]. Significance of scaling test as well as χ^2 in joint scaling test showed the presence of digenic or higher order interactions for all characters except for days to maturity in cross RH 0749 × RLC-3. Additive gene effects (*d*) were important for days to maturity, number of secondary branches per plant, number of seeds per siliqua, 1000-seed weight and seed yield per plant. Both additive (*d*) and dominance (*h*) gene effect were important for plant height, number of primary branches per plant, main shoot length, number of siliquae on main shoot, siliqua length and oil content. The dominant × dominant (*l*) type of gene interaction and duplicate epistasis was observed for most of the character in two crosses except for seed yield per plant in cross RH0749 × PDZ-1 for which complementary epistasis was observed. These results suggested that substantial improvement in yield may be achieved through recurrent selection and heterosis breeding.

Keywords: Generation mean, Gene effect, Gene interaction, Indian mustard, Scaling test

Rapeseed-mustard group of crops are grown in diverse agro-climatic conditions and plays an important role in oilseed economy of our country. India stands third in terms of area and production after Canada and China (FAOSTAT 2019). While majority of countries grow rapeseed, Indian mustard [*Brassica juncea* (L.) Czern & Coss] accounts for 80% of the total cultivated area in India. In recent years, though there has been an increase in the area and production of Indian mustard. However, the productivity levels of oilseeds in the country are still very low compared to the world average. The edible oils are the single largest agricultural product being imported in the country with an estimated share of about 50% in total agricultural imports and drain significant quantum of revenue to the foreign countries (Jat *et al.* 2019). Despite this fact, limited efforts have been made in the past for the improvement of this crop. However, for achieving significant improvement in yield potential, it is essential to understand the inheritance and gene action of yield and its associated traits in Indian mustard. Methods such as diallel, line × tester, and partial diallel have been used mostly for estimation of gene effects

in Indian mustard. Hence, results obtained pertain to the relative importance of additive and/or non-additive gene effects. Robinson (1961) noted the worth of epistasis and suggested that more importance should be given to selection between families and line breeding when epistasis is present and high. The genetic cause of heterosis can be estimated with greater reliability with the use of epistasis interaction, further it also helps in understanding the cause of loss of heterosis in later generations. Generation mean analysis is one of the techniques which provide the estimates of gene effects including non-allelic interactions. Thus, precise estimation of epistasis would be useful in the development of mustard hybrids. In mustard, such information is meagre. Therefore, efforts were carried out to study the importance of epistasis in the inheritance of yield and its component traits.

MATERIALS AND METHODS

A field experiment was conducted using six basic generations, viz. P₁, P₂, F₁, F₂, B₁ and B₂ of the two crosses, i.e. RH 0749 × RLC-3 and RH 0749 × PDZ-1 at research farm of CCSHAU, Hisar during 2015–16 and 2016–17. F₁ generation of each cross was back crossed to P₁ and P₂ to produce the B₁ and B₂, respectively. F₁ hybrids were selfed to obtain F₂ seeds. The plot size for P₁, P₂, and F₁ were 2 rows, 20 rows for F₂ and 10 rows of B₁ and B₂ each of 4 m length having row to row distance 30 cm and plant to plant distance 10 cm. The recommended package of practices was followed to raise a healthy crop. The observations were

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recorded for days to maturity, plant height (cm), number of primary branches per plant, number of secondary branches per plant, main shoot length (cm), number of siliquae on the main shoot, number of seeds per siliqua, siliqua length (cm), seed yield per plant (g), 1000 seed wt. (g), oil content (%). For all the traits, mean of all the six generations of two crosses were subjected to scaling test; A, B, C and D (Mather 1949) and joint scaling test (Cavalli 1952) for testing the adequacy of additive-dominance model as well as three parameter model (Jinks and Jones 1958). In cases, where the additive-dominance model was inadequate and three parameter model did not fit, six parameter model or digenic interaction model based on Hayman's (1958) approach was used to separate the components of genetic variance to its main effects and to provide information on the inheritance of various traits.

RESULTS AND DISCUSSION

Scaling test and joint scaling test: The scaling test showed that A, B, C and D scale were significant for all the traits in two crosses except days to maturity in cross RH 0749 × RLC-3 (Table 1). The significant value of any one of the four scale is taken as measure to indicate the inadequacy of additive-dominance model, whereas, non-significant estimates of all the four scale in scaling test suggested the adequacy of additive-dominance model. Joint scaling test was also used to fit data into three parameter model and χ^2 test was conducted to evaluate the goodness of fit to additive-dominance model (Table 1). Non-significant value of χ^2 for days to maturity in cross RH0749 × RLC-3 clearly showed that nonallelic interaction effect (epistasis) is absent and generation means depends only on additive-dominance effect of the gene. For the remaining traits, significant values of χ^2 in joint scaling test confirmed the presence of non-allelic interaction. Hence the data was further subjected to six parameter model. Of the 11 traits, 10 in two crosses witnessed similar trends of significantly positive nonallelic interaction for one or more of the scaling tests. The results obtained here remain in close agreement with earlier published report by Kabdal and Singh (2010), Singh *et al.* (2012), Prajapati (2014), Akanksha *et al.* (2017) and Manjunath *et al.* (2017).

Estimates of gene effects and epistatic effects: In the present study, scaling test and joint scaling test were found to be significant for most of the traits. This indicates that nonallelic interaction played a major role in the expression of traits. Digenic nonallelic interaction model with six parameters, namely m, d, h, i, j and l (Hayman 1958) portrayed that the epistatic interaction model sufficiently explained the gene action in the most of the studied traits in two crosses. The results showed that F_2 mean (*m*) performance were highly significant for all the traits in two crosses (Table 2). The additive, dominance and non-allelic types of gene interactions in two crosses for different traits were found different from each other. Additive component (*d*) was greater than the dominance (*h*) component for seed yield, 1000-seed weight, number of seeds per siliqua. Among

Table 1 Scaling test and joint scaling test (χ^2) for yield traits and oil content in two crosses of Indian mustard

Scaling test	Days to maturity	Plant height (cm)	No. of primary branches/plant	No. of secondary branches/plant	Main shoot length (cm)	No. of siliquae on main shoot	Siliqua length (cm)	No. of seeds / siliqua	1000-seed wt. (g)	Seed yield/plant (g)	Oil content (%)	
First cross (RH 0749 × RLC-3)												
A	0.14 ± 0.97	-8.90** ± 2.72	-2.08** ± 0.43	-3.31** ± 1.10	-1.24 ± 2.10	-14.65** ± 2.07	-0.37 ± 0.27	-1.29 ± 0.65	-1.61** ± 0.28	-2.83** ± 0.79	-1.35** ± 0.41	
B	0.98 ± 0.84	-1.74 ± 2.63	-4.44** ± 0.61	-3.37** ± 0.80	-6.66** ± 1.83	-9.49** ± 2.36	-0.68* ± 0.30	-1.53* ± 0.63	-1.18** ± 0.24	-4.13** ± 0.62	-0.78* ± 0.35	
C	1.82 ± 1.53	9.49* ± 4.30	-0.92 ± 0.82	-0.51 ± 1.44	-5.20 ± 3.17	-8.80* ± 4.10	0.39 ± 0.54	-2.64* ± 1.05	-1.57** ± 0.42	-3.32** ± 1.23	-1.16 ± 0.61	
D	0.34 ± 0.48	10.06** ± 1.46	2.80** ± 0.39	3.08** ± 0.62	1.34 ± 1.12	7.67** ± 1.10	0.72** ± 0.14	0.09 ± 0.33	0.61** ± 0.17	1.81** ± 0.47	0.48* ± 0.21	
χ^2	2.43	65.51**	78.12**	33.90**	13.62**	89.57**	30.27**	10.08*	40.55**	52.81**	13.78**	
Second cross (RH 0749 × PDZ-1)												
A	-1.72 ± 1.38	16.73** ± 5.42	0.07 ± 0.48	2.99 ± 1.59	-9.39* ± 4.10	-9.98** ± 1.42	-0.34 ± 0.28	-5.40** ± 0.65	0.21 ± 0.21	-7.26** ± 0.82	-0.37 ± 0.39	
B	-4.26** ± 1.32	13.81* ± 5.54	-1.24* ± 0.49	-2.74* ± 1.26	0.38 ± 4.04	-5.68** ± 1.80	0.49* ± 0.18	-3.58** ± 0.87	-0.95** ± 0.21	-10.02** ± 0.89	-1.47** ± 0.54	
C	4.18 ± 2.82	-20.92** ± 6.96	4.61** ± 0.76	8.40** ± 2.10	-24.84** ± 5.90	-1.11 ± 2.77	-0.76 ± 0.41	-8.38** ± 1.20	-0.15 ± 0.39	-13.99** ± 1.72	0.05 ± 0.78	
D	5.08** ± 0.70	-25.73** ± 4.10	2.88** ± 0.31	4.08** ± 1.06	-7.92** ± 2.54	7.27** ± 0.85	-0.45** ± 0.14	0.30 ± 0.54	0.29 ± 0.21	1.64** ± 0.43	0.95** ± 0.26	
χ^2	63.99**	39.96**	101.85**	34.04**	29.10**	112.89**	18.83**	85.38**	20.22**	126.81**	16.44**	

*P < 0.05 and **P < 0.01

Table 2 Estimates of generation mean for yield traits and oil content in two crosses of Indian mustard

Characters	Crosses	m	D	h	i	j	l	Epistasis
Days to maturity	RH0749 × RLC-3	149.07** ± 0.16	0.88** ± 0.36	-1.26 ± 1.19				
	RH0749 × PDZ-1	147.19** ± 0.32	5.10** ± 0.29	-11.93** ± 1.88	-10.17** ± 1.40	1.27 ± 0.40	16.16** ± 3.05	D
Plant height (cm)	RH0749 × RLC-3	203.87** ± 0.52	-9.48** ± 1.02	-18.73** ± 3.47	-20.13** ± 2.92	-3.58 ± 1.60	30.77** ± 5.94	D
	RH0749 × PDZ-1	193.29** ± 1.17	7.56* ± 3.36	66.15** ± 8.59	51.46** ± 8.20	1.46 ± 3.48	-82.01 ± 15.14	D
No. of primary branches/plant	RH0749 × RLC-3	7.42** ± 0.14	0.08 ± 0.28	-4.90** ± 0.85	-5.60** ± 0.79	1.18 ± 0.33	12.12 ± 1.39	D
	RH0749 × PDZ-1	7.03** ± 0.10	0.70** ± 0.22	-5.53** ± 0.69	-5.77** ± 0.62	0.65 ± 0.30	6.93** ± 1.17	D
No. of secondary branches/plant	RH0749 × RLC-3	14.71** ± 0.20	0.98** ± 0.46	-4.39** ± 1.37	-6.17** ± 1.24	0.03 ± 0.60	12.86** ± 2.34	D
	RH0749 × PDZ-1	14.48** ± 0.35	2.96** ± 0.79	-6.38** ± 2.27	-8.16** ± 2.13	2.87 ± 0.91	7.91* ± 3.82	D
Main shoot length (cm)	RH0749 × RLC-3	73.57** ± 0.42	3.96** ± 0.73	2.35 ± 2.61	-2.69 ± 2.24	2.71 ± 1.24	10.59* ± 4.33	
	RH0749 × PDZ-1	68.74** ± 0.72	-0.52 ± 2.10	26.20** ± 5.70	15.84** ± 5.09	-4.89 ± 2.35	-6.83 ± 10.26	
No. of siliqua on main shoot	RH0749 × RLC-3	51.16** ± 0.43	-6.98** ± 0.68	-7.01* ± 2.88	-15.34** ± 2.21	-2.58 ± 1.00	39.49** ± 4.93	D
	RH0749 × PDZ-1	49.66** ± 0.31	-3.54** ± 0.57	-8.03** ± 2.10	-14.54** ± 1.70	-2.15 ± 0.88	30.20** ± 3.59	D
Siliqua length (cm)	RH0749 × RLC-3	4.40** ± 0.05	0.55** ± 0.08	-1.08** ± 0.37	-1.45** ± 0.28	0.15 ± 0.13	2.51** ± 0.64	D
	RH0749 × PDZ-1	4.55** ± 0.05	-0.15* ± 0.07	1.28** ± 0.33	0.91** ± 0.28	-0.41 ± 0.14	-1.06* ± 0.53	D
No. of seeds/siliqua	RH0749 × RLC-3	14.29** ± 0.11	0.90** ± 0.25	1.03 ± 0.82	-0.18 ± 0.67	0.12 ± 0.35	3.01* ± 1.46	
	RH0749 × PDZ-1	12.84** ± 0.20	0.37 ± 0.37	0.96 ± 1.18	-0.60 ± 1.09	-0.90 ± 0.50	9.59** ± 1.92	
1000-seed wt. (g)	RH0749 × RLC-3	5.52** ± 0.05	0.64** ± 0.13	-1.12** ± 0.39	-1.22** ± 0.34	-0.21 ± 0.14	4.03** ± 0.67	D
	RH0749 × PDZ-1	5.59** ± 0.08	1.88** ± 0.12	0.12 ± 0.43	-0.58 ± 0.42	0.58 ± 0.15	1.33** ± 0.62	
Seed yield/plant (g)	RH0749 × RLC-3	19.91** ± 0.17	2.18** ± 0.31	-2.25* ± 1.07	-3.63** ± 0.94	0.64 ± 0.38	10.60** ± 1.77	D
	RH0749 × PDZ-1	20.33** ± 0.17	4.10** ± 0.24	2.70** ± 1.16	-3.29** ± 0.86	1.37 ± 0.26	20.57** ± 1.98	C
Oil content (%)	RH0749 × RLC-3	38.69** ± 0.07	0.46** ± 0.15	-0.33 ± 0.50	-0.97* ± 0.43	-0.28 ± 0.23	3.11** ± 0.86	
	RH0749 × PDZ-1	38.90** ± 0.08	0.15 ± 0.19	-1.76** ± 0.63	-1.90** ± 0.53	0.55 ± 0.25	3.76** ± 1.11	D

m, mean; d, additive; h, dominance; i, additive × additive; j, additive × dominance; l, dominance × dominance; D, duplicate; C, complementary. *P<0.05 and **P<0.01

interactions, dominance \times dominance (*l*) interaction was more important than the additive \times additive (*i*) and additive \times dominance (*j*) for most of the traits. The opposite sign of dominance (*h*) and dominance \times dominance (*l*) suggested that duplicate-type epistasis occurred in most cases except days to maturity in RH 0749 \times RLC-3, main shoot length in both the crosses, number of seeds per siliqua in both the crosses, 1000-seed weight in cross RH 0749 \times PDZ-1 and oil content in cross RH 0749 \times RLC-3, indicating predominantly dispersed alleles at the interacting loci. Complementary epistasis was evident for seed yield per plant in cross RH 0749 \times PDZ-1.

For days to maturity, only additive (*d*) gene effect was found significant in cross RH 0749 \times RLC-3 suggesting that improvement could be achieved through simple progeny selection. Manjunath *et al.* (2017) also reported significance of additive gene effect for days to maturity. However, in cross RH 0749 \times PDZ-1, both additive (*d*) and dominance (*h*) effects were important. Significant negative value of dominant (*h*) gene effects in cross RH 0749 \times PDZ-1 showed that crop duration could be decreased by exploiting these effects. The results are in agreement with Yadav *et al.* (2011) and Prajapati *et al.* (2014). In the case of plant height, dominance (*h*) gene effects coupled with additive \times additive (*i*) and dominance \times dominance (*l*) were important in RH 0749 \times RLC-3 and RH 0749 \times PDZ-1. Negative sign of significant effects in two crosses showed the genes for reduced plant height were dominant over the gene for tallness. Akanksha *et al.* (2017) also obtained significant negative estimates of dominance (*h*) effect and dominance \times dominance (*l*) type of interaction for plant height in Indian mustard.

Considering the magnitude and direction, dominance gene effect along with dominance \times dominance (*l*) interaction was important for the number of primary branches per plant in RH 0749 \times RLC-3 and RH 0749 \times PDZ-1. Significant negative value of dominance (*h*) gene effect in both the crosses suggests that the dominance effect was contributed by the parent having lesser number of primary branches per plant. Goswami (2005) and Singh *et al.* (2012) also reported significant negative estimates of the dominant gene effect for this trait. In regard to secondary branches per plant, additive (*d*) gene effect was important in two crosses. Among non-allelic interactions, dominance \times dominance (*l*) was important. Negative value of additive component in both the crosses coupled with duplicate epistasis suggested the possibility of exploitation of heterosis. Significant negative estimate of dominance (*h*) gene effect suggested that dominance was contributed by the parent having lesser number of secondary branches per plant in both the crosses. Thus, selection should be delayed to later generation when desirable segregants become available. Yadav *et al.* (2011) also reported the importance of additive gene effect for this trait.

For main shoot length, additive (*d*) gene effect along with dominance \times dominance (*l*) were most important in RH 0749 \times RLC-3, while dominance effect (*l*) and fixable

component additive \times additive (*i*) found to be most important in RH 0749 \times PDZ-1. This suggested that selection would be fruitful if the selection is delayed till the dominance component is reduced. Goswami (2005) as well as Kabdal and Singh (2010) also reported the importance of additive, dominance gene effect and dominance \times dominance (*l*) type of interaction for this trait in Indian mustard.

For number of siliquae on the main shoot, estimates of dominance \times dominance (*l*) non-allelic interaction was higher and significant in two crosses. Significant but negative value of additive component as well as duplicate epistasis suggested the possibility of heterosis. Singh *et al.* (2012) also reported importance of dominance \times dominance interaction for this trait. In regard to the inheritance of siliqua length, additive (*d*) gene effect as well as dominance \times dominance (*l*) non-allelic interaction was important in cross RH 0749 \times RLC-3. In contrary, dominance (*h*) gene effect and additive \times additive (*i*) interaction were important in cross RH 0749 \times PDZ-1. Goswami (2005) reported preponderance of additive gene effect and additive \times additive (*i*) interaction for siliqua length.

Additive (*d*) gene effects were important for the inheritance of number of seeds per siliqua. Significance of additive gene effects were also reported by Yadav *et al.* (2011) for this trait. Among the interactions, dominance \times dominance (*l*) type was more important, owing to significant values and in the desirable direction. Significant dominance \times dominance (*l*) type interactions were also reported by Manjunatha *et al.* (2017). In regard to 1000-seed weight, additive (*d*) gene effect was more important in addition to dominance \times dominance (*l*) type of non-allelic interaction in the two crosses. Yadav *et al.* (2011) also observed the importance of additive gene effect. Significant negative estimates of dominance gene effect (*h*) suggest that the dominant effect was contributed by the parent having alleles responsible for a low value for 1000-seed weight. Thus, selection for this trait should be delayed till later generation when desirable segregants become available. The importance of dominance \times dominance interaction was also observed by Akanksha *et al.* (2017).

For seed yield per plant, preponderance of additive (*d*) gene effect were recorded. These results are in agreement with the findings of Yadav *et al.* (2011). Among the interactions, dominance \times dominance (*l*) was important in both the crosses. Duplicate type of epistasis was observed for cross RH 0749 \times RLC-3, while the complementary type of digenic epistasis was observed in RH 0749 \times PDZ-1 cross. Presence of complementary gene action for above mentioned traits indicates that parents selected for crossing are diverse. Therefore, it is possible to realize enhanced genetic gain in breeding programme. Akanksha *et al.* (2017) also reported a complementary type of epistasis for this trait.

For oil content, additive (*d*) gene effect and dominance \times dominance (*l*) non-allelic interaction played important role in cross RH 0749 \times RLC-3, while dominance gene effect and dominance \times dominance effects were significant in the cross RH 0749 \times PDZ-1. Negative sign of dominance (*h*)

gene effect suggest that dominance effects were contributed by the parents having alleles responsible for low value for oil content. Goswami (2005) also observed importance of additive and dominance effect in inheritance of this trait. Overall, the positive sign of additive effect for days to maturity, number of secondary branches per plant, number of seeds per siliqua, 1000-seed weight, seed yield per plant and oil content in two crosses indicated the important role of additive gene action for the inheritance of these traits. Among the non-allelic interactions, dominance \times dominance (l) type appears to contribute more towards the performance of most traits in two crosses compared to additive \times additive (i) and additive \times dominance (j) type of non-allelic interaction. The estimates of h , i and l were found significant with negative sign for most of the traits except main shoot length and number of seeds per siliqua, suggested that selection should be delayed to later generations, so that negative alleles are removed. Hence, improvement of these traits could be achieved through recurrent selection procedure (Singh and Narayanan 2000). These findings are in agreement with those reported by Goswami (2005), Kabdal and Singh (2010), Singh *et al.* (2012), Prajapati *et al.* (2014), Manjunatha *et al.* (2017) and Akanksha *et al.* (2017) in which significant (l) for most of the yield attributes in Indian mustard were observed.

From the on-going discussion, we can conclude that the nature and magnitude of gene action vary with breeding material used in different crosses for different traits. Thus, specific breeding strategy has to be followed for a particular cross to obtain better improvement in a particular trait. In general, pure lines could be developed through hybridization following pedigree method for the improvement of traits governed by additive gene action. For traits governed by non-additive gene action (dominance or epistasis) heterosis breeding would be most effective. Further, duplicate type of epistasis was also found in a majority of traits in two crosses. In such situation, the selection intensity should be mild in the earlier and intense in the later generations because it marks the progress through selection. Therefore, use of biparental mating followed by recurrent selection is suggested as the best strategy to meet the need of yield improvement.

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