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Detection of epistasis, additive and dominance components of variation for seed yield and its attributes in Indian mustard (*Brassica juncea*)

H S MEENA[1], ARUN KUMAR[2], SWARNIM KULSHRESTHA[3], BHAGIRATH RAM[4], V V SINGH[5], P D MEENA[6] and DHIRAJ SINGH[7]

ICAR-Directorate of Rapeseed-Mustard Research, Bharatpur, Rajasthan 321 303

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ABSTRACT

This study was conducted to detect epistasis and importance of additive and dominance variances for seed yield and contributing traits using 27 progenies produced by crossing nine lines with three testers, viz. NPJ 112, RRN 727 and their F_1 in triple test cross fashion. Analysis of variance revealed the existence of epistasis for all the traits except secondary branches/plant and oil content. Its partitioning showed higher magnitude of (i) type for days to flowering, days to maturity and primary branches and (j+l) type for siliqua length, seeds/siliqua, 1000/seed weight and seed yield. Significant MS due to sums ($L_{1i} + L_{2i}$) and differences ($L_{1i} - L_{2i}$) for days to flowering, maturity, plant height, seeds/siliqua, 1000-seed weight and seed yield indicated the role of both additive (D) and dominance (H) variance in their inheritance. Estimates of D and H components revealed predominance of D for days to flowering, maturity, plant height, primary and secondary branches and 1000-seed weight and H for remaining 6 traits, viz. number of siliquae on main shoot, main shoot length, siliqua length, seeds/siliqua, oil content and seed yield. Non-significant correlation coefficient for all the traits except 1000-seed weight indicated the scatter of dominant alleles between testers. Degree of dominance $(H/D)^{1/2}$ indicated over dominance for siliquae on main shoot, main shoot length, siliqua length and seeds/siliqua. Thus, epistasis was an integral component with conspicuous role of both additive and dominance variance for different characters. Therefore, the study will be helpful in deciding the breeding strategy that would enable to utilize maximum proportion of fixable as well as non-fixable genetic variation in Indian mustard.

Key words: Additive variance, Dominance, Epistasis, Indian mustard, Triple test cross

The average productivity of Indian mustard [*Brassica juncea* (L). Czern & Coss.] in India during last one and half decade, oscillated between 1.0 to 1.2 tonnes/ha, which is much below the world average of 1.98 tonnes/ha. Moreover, there is a wide yield gap when productivity of India is compared with countries like Germany (4.3 tonnes/ha), France (3.8 tonnes/ha) and UK (3.4 tonnes/ha) (Yadava *et al*. 2012). The enhancement in production and productivity of the crop assumes significance, not only for the farmer an urgent but also for the edible oil industry and other closely linked enterprises. Thus, there is need to increase and stabilize the productivity of Indian mustard (Meena *et al.* 2015) to meet the growing demands of national and international markets. This can be achieved through effective utilization of germplasm resources by integration of genomic tools to impart efficiency and pace to breeding processes (Banga 2012). The insufficient intra-specific variability can be addressed using untapped genetic diversity in relative species (Kumar *et al.* 2015).

Seed yield is a very complex trait that possesses many components which finally result in a highly plastic yield structure (Meena *et al.* 2014b). Since, the exploitation of genetic differences in contributing traits can be a means of improving the seed yield understanding of the genetic behaviour of various contributing traits is useful for efficient selection of desirable genotypes. It is essential to know the genetic architecture of traits related to seed yield and their mode of inheritance.

Numerous biometrical designs have been employed in different crops for estimating various types of gene effects. In most of the designs, it is assumed that non-allelic interactions are absent, the fact is often contrary to the assumption (Tripathi *et al.* 2005). The detection, estimation and interpretation of epistasis has progressed much faster at the level of first degree statistics (Mather and Jinks 1982) which has certain limitations due to the cancellation of genetic effects. Triple test cross is a powerful method of

[1]Senior Scientist (e mail: singh_hari2006@yahoo.co.in), [2]Senior Scientist (e mail: aruncyto@gmail.com), [3]Junior Research Fellow (e mail: kulshresthaswarnim156@gmail.com), [4]Senior Scientist (e mail: bhagirathram_icar@yahoo.com), [5]Principal Scientist (e mail: singhvijayvir71@gmail.com), [6]Principal Scientist (e mail: pdmeena@gmail.com), [7]Director (e mail: director.drmr@gmail.com)

genetic analysis, which provides unbiased estimates for epistasis. In addition, it also estimates the additive and dominance components of variation with high accuracy when epistasis is absent (Kearsey and Jinks 1968). Amount and type of epistasis can have a major consequence on reliability of predictions and the design of breeding programme.

The possibility of epistasis accounting for a significant proportion of genetic variance of quantitative trait has been previously investigated by Bhajan *et al*. (1994), Verma and Singh (1998), Kumar and Singh (2004), Tripathi *et al.* (2005), Singh *et al.* (2008), Mall and Bhajan (2015) and many others in rapeseed mustard with different sets of material. Despite various studies, there is still debate on the type of gene action predominant for important traits. Some of the studies stressed upon the major role of additive (D) variance while others on dominance (H) component in genetic control of various characters. Combining ability studies emphasized the predominance effect of GCA on yield and most of the yield components (McGee and Brown 1995, Wos *et al.* 1999, Gupta *et al.* 2006) indicating the importance of additive gene action. Pandey *et al.* (1999) reviewed the evidences for presence of significant SCA effects for seed yield and its components indicating importance of non-additive gene action. Meena *et al.* (2015) emphasized on the role of both additive and non-additive gene action with predominance of non-additive gene action for most of the yield attributes.

Thus, the information on genetics, especially on epistatic gene effects for improvement of characters in Indian mustard is highlight imperative. The pertinent literatures the importance of epistasis in the expression of seed yield and component traits (Tak and Khan 2000, Singh and Sachan 2003, Mall and Bhajan 2015). The present investigation was undertaken to detect the epistasis and type of gene action involved in the inheritance of seed yield & different attributing traits in Indian mustard employing triple test cross technique.

MATERIALS AND METHODS

The present investigation was conducted at ICAR-Directorate of Rapeseed-Mustard Research, Bharatpur from 2013-14 to 2015-16. The experimental material consisted of 39 genotype of Indian mustard involving 3 testers (NPJ 112, RRN 727 and their F_1), 9 lines (RH 749, RH 406, Rohini, NRCDR 2, NRCHB 101, DRMRIJ-31, SEJ-2, DRMR 2019, and DRMR 2035), and 27 F_1 hybrids (crosses) including 18 single and 9 three-way crosses (Table 1). The experimental materials were generated following the Triple Test Cross Design. Two genetically diverse true breeding testers, NPJ 112 (L_1) and RRN 727 (L_2) were crossed to generate the F_1 hybrid, NPJ 112 × RRN 727 (L_3) during 2013-14. The three testers (P_1, P_2 and F_1) were crossed with 9 diverse true breeding genotypes (lines) during *rabi* 2014-15 to produce L_{1i}, L_{2i} and L_{3i} families (27 crosses) as per triple test cross fashion. The crosses along with parents (testers and lines) were planted in randomized complete block design with three replications during *rabi* 2015–2016. The

Table 1 List of genotypes (testers and lines) and their pedigree

Genotype	Pedigree
Testers (P_1 & P_2)	
NPJ-112[$]	SEJ-8 × Pusa Jagannath
RRN 727[#]	RW-01-02 × Patan 67
Lines	
RH-749[$]	RH-781 × RH-9617
RH-406[$]	RH-6908 × RH-8812
Rohini[$]	Pure line selection from varuna
NRCDR-2[$]	MDOC-43 × NBPGR-36
NRCHB 101[$]	BL-4 × Pusa Bold
SEJ-2[$]	Synthetic amphiloid (*B. campestris* × *B. nigra)*
DRMRIJ-31[$]	HB-9908 × HB-9916
DRMR 2019[#]	EC-399288 × BEC-107
DRMR 2035[#]	PHR-1 × BEC-107

[$, #] : Released cultivars and unreleased strains, respectively

treatments were raised in rows of 5 m length with 30 cm distance between rows and 15 cm between plants, each treatment was represented by two rows. Standard agronomic practices were followed to raise good crop. Recommended doses of fertilizers, viz. 80:40:40:40 kg/ha of N:P:K:S, respectively, were applied and irrigated thrice including pre-sowing irrigation. Observations were recorded on twelve quantitative traits, viz. days to flowering, days to maturity, plant height (cm), number of primary branches/plant, number of secondary branches/plant, main shoot length (cm), number of siliquae on main shoot, siliqua length (cm), number of seeds/siliqua, 1000-seed weight (g), oil content (%) and seed yield/ha (kg). Observations on days to flowering and maturity were recorded on per plot basis, seed yield was expressed in kg/ha and the observations on remaining traits were recorded on randomly selected ten competitive plants in each replication.

The triple test cross analysis was carried out as per Kearsey and Jinks (1968) and Ketata *et al*. (1976) through a computer generated programme WINDOW STAT version 8.6 from INDOSTAT Services, Hyderabad, India to detect epistasis and estimate the additive (D) and dominance (H) component of genetic variation. Analyses of variance (ANOVA) for test of significance were performed according to the method of Singh and Chaudhary (2004) for each trait. Significance of additive (D) and dominance variance (H) were estimated as per Jinks and Perkins (1970).

RESULTS AND DISCUSSION

The analysis of variance (Table 2) for the triple test cross set revealed mean squares due to treatments, parents, lines and testers for all the traits except oil content in crosses and days to flowering, number of primary branches/plant, number of siliqua on main shoot and number of seeds/siliqua in testers indicating considerable genetic variation among genotypes for various traits. The variation between first (P_1) and second parent (P_2) were highly significant for seed yield/

Table 2 Mean sum of squares for different sources of variation in triple test cross analysis for 12 characters in Indian mustard

Source of variation	DF	Day of flowering	Day of maturity	Plant height (cm)	Number of primary branches / plant	Number of secondary branches/ plant	Number of siliquae on main shoot	Main shoot length (cm)	Siliqua length (cm)	Number of seeds /siliqua	1000-Seed weight (g)	Oil content (%)	Seed yield/ha (kg)
Replication	2	13.41	105.239	158.96	0.103	2.37	29.27	63.96	0.19	0.31	0.03	1.75	13513.94
Treatment	38	158.1**	295.86**	2817.9**	5.22**	43.12**	188.64**	283.69**	1.58**	7.31**	3.18**	2.07**	1064598.00**
Parents	11	309.8**	536.51**	4056.5**	4.50**	71.48**	211.31**	361.58**	2.95**	6.64**	3.34**	3.50**	1001685.00**
Lines	8	172.5**	299.89**	1294.2**	5.31**	81.51**	179.44**	180.84**	2.53**	7.56**	0.69**	2.41*	422007.00**
Testers	2	34.3	156.00*	3977.2**	1.95	56.70**	9.83	420.43**	2.03**	4.39	6.94**	6.02**	3657496.00**
Line vs Testers	1	1959.3**	3190.5**	26314.1**	3.14*	20.8	869.27**	1689.8**	8.19**	3.7	17.3**	7.21**	327489.30**
Parent vs Crosses	1	416.2**	205.78*	831.5**	2.41	0.79	24.43	260.36*	1.44**	15.66**	12.8**	5.85*	854234.30**
Crosses	26	83.9**	197.51**	2370.3**	5.64**	32.75**	185.37**	251.63**	1.01**	7.28**	2.74**	1.33	1099306.00**
P1+P2 vs. F1	1	0.167	13.5	46.85	0.031	9.04	0.36	3.18	0.01	0.29	0.069	0.75	318840.12**
P1 vs. P2	1	14.815	33.33	1642.7**	0.78	1.08	3.41	178.38*	0.91**	1.16	2.91**	0.67	775312.09**
Line effect	8	152.6**	361.76*	2715.3*	8.53**	72.10**	241.86	261.27	0.43	5.24	2.32	2.06	1523237.00*
Tester effect	2	308.01**	212.83	13137.8**	24.55**	13.42	190.56	899.52*	6.23**	10.22	14.7**	1.89	5025947.00**
Line×Tester effect	16	21.65	113.46**	851.83**	1.82**	15.49	156.48**	165.83**	0.64**	7.93**	1.46**	0.89	396510.90**
Error	76	17.07	40.96	113.001	0.712	9.84	40.25	45.05	0.07	1.52	0.12	0.93	13654.72
Total	116	63.2	125.57	999.88	2.179	20.61	88.67	123.55	0.57	3.4	1.12	1.32	357926.9

*, ** Significant at 5% and 1% probability levels, respectively

ha (kg), plant height (cm), main shoot length (cm), siliqua length (cm) and 1000-seed weight (g) clearly indicating that P_1 and P_2 testers were genetically diverse with respect to major yield attributes. Thus, it would provide an estimate of additive and dominance variances with equal precision. The first tester (NPJ 112) is a high yielding variety developed at IARI, New Delhi for early sowing conditions and has high temperature tolerance at juvenile stage, while the second tester (RRN 727) strain developed at ARS, Navgaon (Alwar) has specific traits of extra early maturity, extremely dwarf, appressed siliqua orientation and smaller seeds. Hence, two tester parents represent diverse origin whose high genetic divergence was culminated into high amount of heterosis in their F_1 (L_3) for most of the desirable traits including seed yield/ha (kg). Significant mean sum of squares due to line v/s testers, parents v/s crosses and the effects due to lines, testers and line × tester again strengthened the validity substantial variation in the experimental set for further genetic analysis following the triple test cross method of Kearsey and Jinks (1968) to detect epistasis and determine the additive (D) and dominance (H) variances.

The analysis of variance (Table 3) for detection of epistasis revealed significant mean squares due to epistasis ($L_{1i} + L_{2i} - 2L_{3i}$) for all the characters except number of secondary branches / plant and oil content (%) indicating the importance of epistasis in the inheritance of various traits. Significance of epistatic gene action in expression of yield and several yield components has also been reported earlier (Bhajan *et al.* 1994, Verma and Singh 1998, Khulbe *et al*. 1998, Lalta *et al*. 2002, Kumar and Singh 2004, Singh *et al*. 2008, Mall and Bhajan 2015) in rapeseed-mustard. Two traits, number of secondary branches/plant and oil content could not reveal epistasis indicating that only additive gene action (D) might be involved in their inheritance. Therefore, improvement in number of secondary branches and oil content could be achieved through standard selection procedures (Verma and Singh 1998).

Further partitioning of total epistasis revealed that j + l type (additive × dominance and dominance × dominance) of epistasis was significant for all the characters exhibiting epistasis except number of primary branches, whereas i type (additive × additive) of epistasis was detected for days to flowering, days to maturity, number of primary branches and seed yield /ha. Furthermore, the involvement of both i type as well as j + l type of epistasis was observed for days to flowering, days to maturity and seed yield/ha (kg). Moreover, additive × additive (i) type of epistasis was found to be much larger in magnitude for days to flowering, days to maturity and number of primary branches/plant, while (j+l) type of epistasis was higher in magnitude for siliqua length (cm), number of seeds / siliqua, 1000 seed weight (g) and seed yield/ha (kg). It is thus, evident that epistasis was an integral component with conspicuous role of non-fixable (j+1) genetic interactions for most of the characters. Therefore, the detection and consideration of epistasis seems to be vital in breeding to determine the genetic cause of heterosis with greater reliance.

Table 3 Detection of epistasis for seed yield and contributing traits in Indian mustard

Source of variation	DF	Day of flowering	Day of maturity	Plant height (cm)	Number of primary branches/ plant	Number of secondary branches/ plant	Number of siliquae on main shoot	Main shoot length (cm)	Siliqua length (cm)	Number of seeds/ siliqua	1000-Seed weight (g)	Oil content (%)	Seed yield/ ha (kg)
i type Epistasis	1	293.37**	1032.93*	1365.33	98.61*	7.26	1317.4	4146.56	0.76	1.61	1.47	1.86	1268276.4*
j+I type Epistasis	8	127.04**	801.34**	2984.05*	11.62	128.09	749.6*	1152.18*	2.40**	29.64*	3.03**	3.31	2925430.7**
Total Epistasis	9	145.52**	827.07**	2804.20*	21.29**	114.67	812.69*	1484.89**	2.22**	26.53*	2.86**	3.15	2741302.4**
i type Epistasis × blocks	2	1.37	50.7	1184.78	2.08	140.48	134.3	384.45	3.42	7.12	0.20*	7.9	56283.18
j+I type Epistasis × blocks	16	1.41	154.62	853.77	4.66	80.79	275.93	371.57	0.21	10.001	0.04	3.95	45144.37
Total Epistasis × blocks	18	1.41	143.07	890.55	4.38	87.42	260.2	373.004	0.57	9.68	0.05	4.39	46382.01

*, ** Significant at 5% and 1% probability levels, respectively

Upadhyay and Kumar (2014) reported the prevalence of additive × additive interaction coupled with additive effects for seven traits (days to flowering and maturity, plant height, primary and secondary branches, number of siliquae on main shoot and main shoot length). Likewise, Mall and Bhajan (2015) emphasized on the predominance of (j+l) type of epistasis in expression of 11 traits including seed yield in Indian mustard. Prevalence of additive genetic variance implies that selection for the characters would be effective in early segregating generations and offers the possibility of genetic improvement through standard hybridization and simple selection procedures (Verma and Singh 1998). In contrast, (j+l) type of epistatic gene action (additive × dominance and dominance × dominance) are not-fixable by selection and the development of hybrids may be useful (Ketata *et al.* 1976).

Although significant epistasis was detected for all the traits except number of secondary branches/plant and oil content (%), the additive (D) and dominance (H) components were nevertheless computed in order to assess their relative contribution in the inheritance of various characters. Analysis of variance (Table 4) revealed significant mean squares due to both sums ($L_{1i} + L_{2i}$) and differences (L_{1i}- L_{2i}) for days to flowering, days to maturity, plant height, number of seeds/ siliqua, 1000-seed weight and seed yield indicating the role of both additive (D) as well as dominance (H) component in their inheritance. Only additive variance (D) was present for 2 traits (number of primary and secondary branches), while only dominance (H) component was significant for number of siliqua on main shoot, main shoot length, siliqua length and oil content. Earlier findings in Indian mustard (Verma and Singh 1998, Singh *et al.* 2008, Meena *et al.* 2015, Chaurasia and Bhajan 2015) also stressed on the importance of both components in genetic control of different traits.

The relative magnitude of D and H components (Table 5) indicated the predominance of the D component for six characters namely days to flowering, days to maturity, plant height, number of primary branches, number of secondary branches and 1000-seed weight and H for remaining 6 traits, viz. number of siliquae on main shoot, main shoot length, siliqua length, number of seeds/siliqua, oil content and seed yield. Tripathi *et al.* (2005) reported high magnitude of D for 9 characters and H for harvest index and oil content in yellow sarson. Thakral *et al.* (2000) reported the existence of both additive and non-additive genetic components with higher magnitude of additive component for 1000-seed weight and length of main shoot. Similarly, the importance of both additive and non-additive genetic components for various traits was earlier reported by Shweta *et al.* (2007) and Mall and Bhajan (2015) supports the present findings.

The estimates on degree of dominance $(H/D)^{1/2}$ exhibited over dominance for number of siliquae on main shoot, main shoot length, siliqua length and number of seeds/siliqua and partial dominance for days to flowering and maturity, plant height, number of primary and secondary branches and seed yield. Two traits, *viz*. 1000-seed weight and oil content revealed values (0.99 and 0.98) very close

Table 4 Analysis of variance for sums and differences in triple test cross progenies of Indian mustard for different traits

Source of variation	DF	Day of flowering	Day of maturity	Plant height (cm)	Number of primary branches / plant	Number of secondary branches/ plant	Number of siliquae on main shoot	Main shoot length (cm)	Siliqua length (cm)	Number of seeds/ siliqua	1000-Seed weight (g)	Oil content (%)	Seed yield/ha (kg)
Sums (L_1+L_2)													
Replication	2	23.15	113.81	631.25	0.11	21.54	40.36	24.97	0.01	0.83	0.1	3.98	11856
Lines(sums)	8	237.43**	402.56**	5690.75**	14.1**	112.41*	310.61	254.2	0.92	12.60*	4.91**	3.07	2129876.00**
Error	16	0.27	58.06	196.12	1.02	29.72	128.59	129.87	0.05	4.47	0.02	1.44	13752
Total	26	75.003	168.35	1920.25	4.98	54.53	177.81	160.06	0.31	6.69	1.53	2.14	664721.23
Differences (L_1-L_2)													
Replication	2	0.26	117.44*	359.15	1.33	20.43	14.43	42.85	0.04	3	0.06	0.3	4042
Lines (differences)	8	44.26**	186.75**	2412.65**	3.43	19.27	376.05**	279.26*	1.78**	21.85**	4.82**	2.46*	610899.50**
Error	16	0.38	23.69	105.27	2	23.28	55.13	87.91	0.12	2.97	0.02	0.9	16360.37
Total	26	13.88	81.08	834.76	2.39	21.83	150.75	143.32	0.62	8.78	1.5	1.33	198347

*, ** Significant at 5% and 1% probability levels, respectively

Table 5 Estimates of additive (D) and dominance (H) variance components, degree $(H/D)^{1/2}$ and direction(r) of dominance for various traits in Indian mustard

Source of variation	Day of flowering	Day of maturity	Plant height (cm)	Number of primary branches/ plant	Number of secondary branches /plant	Number of siliquae on main shoot	Main shoot length (cm)	Siliqua length (cm)	Number of seeds /siliqua	1000-Seed weight (g)	Oil content (%)	Seed yield/ha (kg)
D	316.2**	459.33**	7326.17**	17.43**	110.26*	242.69	165.78	1.15	10.84*	6.53**	2.18	2821498.67**
H	58.5**	217.41**	3076.5**	1.9	-5.34	427.89**	255.13*	2.22**	25.18**	6.4**	2.07*	792718.83**
Degree of dominance $(H/D)^{1/2}$	0.43	0.69	0.65	0.33	0.22	1.33	1.24	1.39	1.52	0.99	0.98	0.53
Correlation (r)	-0.46	0.57	-0.42	0.007	0.17	0.15	-0.08	-0.47	0.22	-0.78*	0.005	-0.2

*, ** Significant at 5% and 1% probability levels, respectively

to complete dominance. Partial to over-dominance was earlier reported (Rai *et al*. 2005, Mall and Bhajan 2015) for various traits in Indian mustard. The correlation coefficient between sums and differences was non-significant for all the traits except 1000 seed weight, indicating that dominant alleles were dispersed between the testers and alleles with increasing and decreasing effects were equally important in contributing towards dominance for most of the characters. Significantly negative correlation coefficient observed for 1000-seed weight (r=-0.78*) indicated the direction of dominance towards higher seed size. Similar findings were earlier reported by Bhajan *et al.* (1994), Tripathi *et al*. (2005) and Mall and Bhajan (2015).

It is thus, evident from present findings that epistasis plays an important role in the inheritance of different characters in Indian mustard. Therefore, the epistatic interaction effects cannot be ignored and the genetic model employed must account for the estimation of inter-allelic interactions. Otherwise, the estimates are liable to be biased and misleading. Besides detecting and estimating epistasis, triple test cross analysis also reveals the significant contribution of additive and dominance variation, direction of dominance and average degree of dominance for characters under study. Predominance of non-fixable genetic effects including epistatic effects indicated the perceptible advantage of heterozygosity for enhanced expression of siliquae on main shoot, length of main shoot and siliqua length, seeds/siliqua, oil content and seed yield.

In nutshell, the findings indicated the existence of epistasis & importance of both additive and non-additive gene action in the inheritance of various characters. In such cases a breeding strategy which would enable to utilize maximum proportion of fixable genetic variation (additive and additive × additive epistasis) as well as non-additive genetic components (dominance, additive × dominance and dominance × dominance) would be effective. In order to make an effective breeding programme, biparental mating among randomly selected plants in F_2 and subsequent generation would help in pooling the desired genes together to develop pure lines. Further crossing of these lines would help in exploiting non-additive genetic components of variation to develop hybrids, if commercially feasible. Also biparental mating, recurrent selection and selective diallele mating might be effective to exploit additive × additive type of epistasis.

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