RESEARCH ARTICLE

Genetic analysis of yield and yield components in soybean [*Glycine max* (L.) Merrill]

■ **S.R. SHINDE, J.V. PATIL AND R.M. PAWAR**

SUMMARY

The present investigation including nine generations of four crosses was undertaken to study the genetics of yield and yield components through generation mean analysis. Additive, dominance and epistasis interactions were found operating in control of almost all characters. Dominance gene action was found predominant in inheritance of yield and yield contributing characters like number of primary branches, clusters per plant and 100 seed weight indicating conventional selection procedure may not be effective enough for improvement of these characters, therefore, selections should be postponed in later generations or intermating among the selected segregants followed by one or two generations of selfing could be useful to break the undesirable linkage and allow to accumulate favourable alleles. Both additive and non-additive gene effects were involved in the expression of plant height, number of pods, oil per cent, protein per cent, and days for maturity. Reciprocal recurrent selection or bi-parental mating design should be used to improve these characters.

Key Words : Soybean, Gene action, Additive, Non-additive gene effects, Epistasis

Soybean [*Glycine max* (L.) Merrill] is considered as a "golden bean" and "wonder crop of the 20th century" due to its dual qualities *viz.*, high protein (40%) and oil (18 to 20%) content. The protein and oil account for 60 per cent of the seed with about 30 per cent carbohydrates (Nagraj, 1995). Soybean cultivation is rapidly expanding due to its high nutritional value for both humans and livestock and as an important industrial crop. India is the fourth largest producer of soybean in the world. However, India's share in world production of soybean is only 4 per cent. The current level of soybean yield being around 1.21 ton/ha which is about half of the world average productivity. Madhya Pradesh and Maharashtra are the leading soybean producers of India with 51 and 33 per cent of total production, respectively.

In order to exploit the existing genetic variability present in the breeding material efficiently and to plan

━━━━● MEMBERS OF THE RESEARCH FORUM ●━━━━

Author to be contacted :
S. R. SHINDE, Department of Agricultural Botany, College of Agriculture, KOLHAPUR (M.S.) INDIA
Email: sshivaji87@yahoo.in

Address of the Co-authors:
J.V. PATIL, Department of Agricultural Botany, Post Graduate Institute, Mahatma Phule Krishi Vidyapeeth, Rahuri, AHAMEDNAGAR (M.S.) INDIA
Email: jvp@sorghum.res.in

R.M. PAWAR,, Department of Agricultural Botany, Bharati Vidyapeeth's Loknete Mohanrao Kadam College of Agriculture, Kadegaon, SANGLI (M.S.) INDIA
Email: ranveer_1972@rediffmail.com

efficient selection programme, the breeder would need the basic information regarding the inheritance of grain yield and its components. Adoption of suitable breeding method for the improvement of any crop mainly depends on the nature of gene action involved in the expression of quantitative traits. The presence or absence of epistasis can be detected by the analysis of generation means using the scaling test which measures epistasis accurately, whether it is complementary or duplicate at the digenic and/or trigenic level. Two genetic models *viz.*, Cavalli (1952) and Hayman (1958) were simultaneously used for determining the nature of gene action involved in the inheritance of yield and yield contributing characters.

To decide suitable breeding strategy for the improvement of yield and yield contributing characters, the information regarding gene action involved in control of inheritance of these characters through generation mean analysis is of immense use to the plant breeder.

MATERIAL AND METHODS

The present investigation was conducted at Seed Research Farm, Seed Research Project, Central Campus, Mahatma Phule Krishi Vidyapeeth, Rahuri and Agricultural Research Station, Kasabe Digraj, dist. Sangli during the period from 2004-2006.

Four crosses *viz.*, JS 335 x MACS 450, MACS 450 x EC 391160, EC 391160 x EC 241780 and JS 335 x EC 241780 were effected in early summer, *Kharif* and *Rabi* 2005 to produce the F_1 seeds. In *Kharif* and *Rabi* 2005 and early summer 2006 generation advancement were made. Simultaneously, backcrosses B_1F_1's and B_2F_1's of four crosses were also produced. The B_1F_1's and B_2F_1's were selfed to produce B_1F_2's and B_2F_2's in *Rabi* 2005 and F_2s were selfed to obtain F_3 in early summer 2006 within the stipulated period.

The experiment was laid out in Randomized Block Design with three replications and 32 treatments at Seed Research Farm, Mahatma Phule Krishi Vidyapeeth, Rahuri in *Kharif* 2006. The experimental material consisted of 32 treatments consisting parents, F_1's, F_2's, B_1F_1's, B_2F_1's, F_3's, B_1F_2's and B_2F_2's of four crosses. The parents, F_1's, F_2's, F_3's, backcrosses and their self's of all the crosses were randomized separately in each of the three replications. Sowing was done in rows of 3m length and 45cm apart accommodating 60 plants at 5cm distance in a row. One row was assigned to F_1's, B_1F_1's, and B_2F_1's while two rows to each of the parents and

four rows to F_2's, F_3's, B_1F_2's, and B_2F_2's. This has permitted for raising of 60 plants in F_1's, B_1F_1's, and B_2F_1's 120 plants in each of the parent and 240 plants in F_2's, F_3's, B_1F_2's, and B_2F_2's in each of the three replication for each cross. Fertilizer dose of 50 kg N and 75 kg P_2O_5/ha for irrigated situation was applied at the time of sowing. All inter-culturing operations were carried out regularly as per need and stage of crop growth.

The observations were recorded for 10 quantitative characters on 10 randomly selected plants from P_1, P_2 and F_1, 15 from B_1F_1, and B_2F_1, 40 from F_2 of straight crosses and back crosses and 60 from F_3 generation in each replication. Data were first tested for non-allelic interaction by individual scaling test – A, B, C, and D given by Mather (1949). Further analysis of data was performed according to the method of "Joint Scaling Test" given by Cavalli (1952). Three parameter model suggested by Mather (1949) and six parameter model suggested by Hayman's (1958) were used for computation of gene effects for grain yield and its components with six basic generations. The presence of epistasis was further tested for adequacy of the nine parameter model that allows an estimation of trigenic interaction.

RESULTS AND DISCUSSION

The results of individual and joint scaling test obtained in this investigation are presented in Table 1. All scaling tests were non-significant for 100-seed weight in JS 335 x MACS 450 and for plant height and 100-seed weight in EC 391160 x EC 241780 indicating the absence of epistasis and a simple additive dominance model was adequate to explain the gene action involved in the inheritance of these characters. In rest of the characters for four crosses at least one or two scales were found to be significant indicating presence of digenic / trigenic interactions. The results of gene effects are presented in Table 2 and are discussed as below:

Days to maturity :

The additive genetic effect (d) was equally important as non-additive genetic effect (h) in the crosses JS 335 x MACS 450, MACS 450 x EC 391160,therefore, for efficient utilization of fixable and non-fixable components of genetic variation, reciprocal recurrent selection was suggested for these crosses (Cecon *et al.*, 1985; Halvankar and Patil, 1993; Khattab, 1998; Sayad

et al., 2005 and Bhor *et al*., 2014).

Additive genetic effect (d) was significant with additive x additive (i) and additive x dominance significant epistasis in cross EC 391160 x EC 241780 indicating the expression of character was under the influence of additive gene action. The additive effects could facilitate fixation of the combination of genes and therefore, selection for days to maturity in this cross would give better response (Zhang *et al.,* 1987; Mehetre *et al*., 1998; Agrawal *et al*., 1999; Rahangdale and Raut, 2002 and Sayad *et al*., 2005).

The significant additive x additive non-allelic interaction with duplicate epistasis was observed in cross JS 335 x EC 241780 for days to maturity suggest the possibilities of obtaining transgressive segregants in later generations (Talwar *et al*., 1986; Ma *et al*., 1987 and Sharma and Phul, 1994).

Plant height (cm) :

The significant values of additive (d) and absence of digenic non-allelic interaction in cross EC 391160 x EC 241780 for plant height revealed that the selection would be useful to start from the early segregating generation for this trait (Singh *et al.,* 1974; Kaw and Menon, 1983; Mehetre *et al*., 1998; Agrawal *et al*., 1999; Rahangdale and Raut, 2002). Whereas, in cross MACS 450 x EC 391160 the dominance x dominance (l) interaction was larger than additive x additive (i) and additive x dominance (j) effects put together with significant additive x additive x additive iabc/ and additive x additive x dominance (jab/c) trigenic interactions.

The main effects of dominance component (h) was greater than the additive component (d). The dominance (h) and dominance x dominance (l) effects were in

Table 1: Estimation of individual and joint scaling test t^2 for yield and yield contributing characters in soybean

Cross	Scales									
	A	B	C	D	t^2	A	B	C	D	t^2
	Days to maturity					**Plant height (cm)**				
JS 335 x MACS 450	-6.83**	-5.93**	-9.38**	1.69**	21.53**	-18.8**	-3.77	-9.54*	6.51*	39.63**
MACS 450 x EC 391160	1.7**	-21.4**	-22.1**	-1.19*	34.45**	-41.9**	-81.5**	-99.0**	12.2**	3.41
EC 391160 x EC 241780	-0.03	-3.53**	-3.21*	0.18	6.09*	-11.87	-1.53	-4.49	4.45	6.97
JS 335 x EC 241780	-4.07**	-16.8**	-11.5**	4.68**	1.18	-4.67	-42.1**	-16.1**	15.3**	12.88**
	No. of primary branches/plant					**No. of clusters/plant**				
JS 335 x MACS 450	0.63	1.87**	-1.89	-1.69**	4.56	-3.00	7.57**	-21.4**	-13.0**	21.22**
MACS 450 x EC 391160	1.47*	2.77**	-9.25**	-6.74**	0.73	-42.9**	-23.1**	-109**	-21.7**	2.63
EC 391160 x EC 241780	1.93**	2.67**	-1.04	-2.82**	5.24*	32.4**	49.6**	-14.19	-48.1**	95.38**
JS 335 x EC 241780	2.37**	2.57**	-4.8**	-4.87**	0.12	-2.83	1.87	-71.2**	-35.1**	1.59
	No. of pods/plant					**100 seed weight**				
JS 335 x MACS 450	0.7	17.97*	-44.1**	-31.4**	11.29**	0.92	-0.43	-1.87	-1.18	9.26
MACS 450 x EC 391160	-53.4**	0.06	-231**	-88.7**	4.73*	-0.09	1.46**	4.53**	1.58**	33.83**
EC 391160 x EC 241780	104.0**	91.8**	-31.91	-114**	23.67**	-0.91	-0.76	0.74	1.21	6.68
JS 335 x EC 241780	-23.8**	-25.2*	-186**	-68.3**	13.72**	-2.28**	-2.08**	-1.72	1.32*	5.53*
	Seed yield/plant					**Oil %**				
JS 335 x MACS 450	2.05	5.22*	-15.7**	-11.5**	0.075	0.25	-0.93**	0.84	0.76**	1.35
MACS 450 x EC 391160	-17.7**	3.01	-74.6**	-29.9**	8.82**	-1.79**	-59.72	-61.45	0.03	2.84
EC 391160 x EC 241780	13.16*	10.0**	-18.8**	-21.0**	22.27**	-59.98	1.41**	-57.94	0.32	4.4
JS 335 x EC 241780	8.83**	25.5**	-17.7**	-26.1**	20.19**	1.14**	0.24	2.97**	0.79*	0.4
	Protein %					**No. of trichomes/cm²**				
JS 335 x MACS 450	0.53	-2.19**	-1.73**	-0.03	3.19	-1.07**	-0.9*	-3.59*	-0.81**	9.82**
MACS 450 x EC 391160	-2.83**	-0.35	-4.74**	-0.78	24.75**	-2.07**	1.03	-3.39**	-1.18**	8.15**
EC 391160 x EC 241780	2.65**	0.73**	1.05	-1.16**	17.41**	1.63*	1.57**	-1.45*	-0.76	39.63**
JS 335 x EC 241780	1.09*	-0.81*	-2.05**	-1.16*	12.67**	-0.6	-1.6**	-0.72	0.74**	17.27**

* and ** indicate significance of values at P=0.05 and 0.01, respectively

Table 2 : Gene effects for different quantitative traits in soybean crosses

Characters	Genetic components								Epistasis
	m	d	h	i	j	l	i abc/	jab/c	
Days to maturity									
JS 335 x MACS 450	111.09**	1.93**	-12.8**	-0.75	-3.94*	11.96	-2.00**	-0.58	D
MACS 450 x EC 391160	110.97**	-1.92*	-8.34**	8.89**	11.52**	3.43*	7.55**	17.65**	D
EC 391160 x EC 241780	122.35**	-4.88*	7.92	4.48**	13.66**	-6.66	7.43**	-16.32**	--
JS 335 x EC 241780	106.85**	-0.87	11.12**	10.40**	3.36	-9.46**	-6.15**	-40.29**	D
Plant height (cm)									
JS 335 x MACS 450	36.20**	3.57	5.41	5.55*	-15.07	3.11	-1.92	-5.61	--
MACS 450 x EC 391160	55.16**	6.18	-53.1**	-14.7**	-15.04	69.82**	-36.3**	-77.4**	D
EC 391160 x EC 241780	90.57**	16.73*	8.50	--	--	--	--	--	--
JS 335 x EC 241780	58.21**	-21.4**	3.90	6.40	38.00**	6.95	-0.13	50.86**	--
No. of primary branches/plant									
JS 335 x MACS 450	2.09**	-0.06	6.64**	2.04**	-1.40*	-4.06**	--	--	D
MACS 450 x EC 391160	4.46**	1.35	-7.97**	0.34	3.19	10.02**	1.33	28.45**	D
EC 391160 x EC 241780	5.24**	5.42**	-3.40	-1.15*	-8.89**	3.11	5.42**	11.65**	--
JS 335 x EC 241780	4.42**	-1.58	5.88**	-0.34	2.09	5.32**	1.55	20.53**	C
No. of clusters/plant									
JS 335 x MACS 450	11.26**	4.83	15.50*	9.95**	-21.98**	-1.18	-4.32	7.86	--
MACS 450 x EC 391160	22.58**	7.30	-56.70**	2.71	-39.88	104.44**	-11.6**	91.44**	D
EC 391160 x EC 241780	43.87**	48.36**	-42.30**	-16.40**	-126.6**	50.95**	-46.5**	70.30**	D
JS 335 x EC 241780	37.53**	-3.35	-86.00**	-13.60**	-3.35	99.42**	1.62	176.84**	D
No. of pods/plant									
JS 335 x MACS 450	37.50**	6.48	29.13	19.11**	-35.30	2.09	-5.87	26.75	--
MACS 450 x EC 391160	106.32**	-15.37	-231.4**	-35.90**	-5.89	262.26**	2.83	419.48**	D
EC 391160 x EC 241780	78.36**	58.69**	-16.08	-5.91	-125.65*	47.24	-69.0**	300.42**	--
JS 335 x EC 241780	106.32**	-15.37	-231.4**	-35.90**	-5.89	262.26**	2.83	419.48**	D
100 seed weight									
JS 335 x MACS 450	14.67**	-0.19	1.35**	--	--	--	--	--	--
MACS 450 x EC 391160	13.13**	3.52**	9.25**	1.32**	-5.92**	-8.20**	-2.88**	-14.00**	D
EC 391160 x EC 241780	14.26**	0.51**	-1.33**	--	--	--	--	--	--
JS 335 x EC 241780	12.71**	-1.28	4.44	1.90**	1.61	1.64	1.08	6.72*	--
Seed yield/plant									
JS 335 x MACS 450	22.53**	5.96	-27.17**	-6.56**	-13.27**	31.71	-4.97	55.75**	D
MACS 450 x EC 391160	31.54**	-0.21	-52.20**	-15.13**	-9.69	50.19**	1.64	112.70**	D
EC 391160 x EC 241780	22.53**	5.96	-27.17**	-6.56**	-13.27**	31.71	-4.97	55.75**	D
JS 335 x EC 241780	31.54**	-0.21	-52.20**	-15.13**	-9.69	50.19**	1.64	112.70**	D
Oil %									
JS 335 x MACS 450	18.61**	-0.65**	-1.99**	-1.37**	1.25**	2.11**	--	--	D
MACS 450 x EC 391160	18.10**	-0.53**	-3.31**	0.32	0.42	3.54**	--	--	D
EC 391160 x EC 241780	17.02**	1.13**	0.6**	-0.02	-2.97**	--	--	--	--
JS 335 x EC 241780	18.02**	-6.42**	-0.94	-1.79**	11.07**	0.40	6.79**	--	--
Protein %									
JS 335 x MACS 450	48.19**	-1.13**	-2.01*	-0.78**	2.56**	2.82**	--	--	D
MACS 450 x EC 391160	46.23**	0.83	-0.51	-0.41	1.55	4.98**	0.18	-3.45	--
EC 391160 x EC 241780	44.77**	-3.85**	1.54	-0.55	6.78**	0.54	2.82**	8.59**	--
JS 335 x EC 241780	45.82**	-2.29**	0.51	-0.06	6.38**	2.76	2.80**	7.78**	--
No. of trichomes/cm²									
JS 335 x MACS 450	1.72**	1.33*	-1.66*	0.48	3.50**	2.33**	-2.16**	1.15	D
MACS 450 x EC 391160	3.05**	-0.26	-5.94**	0.70	-3.39*	2.41*	-0.16	5.45**	D
EC 391160 x EC 241780	2.84**	-0.11	0.75	0.59	1.79	-0.46	0.49	-5.89**	--
JS 335 x EC 241780	4.98**	-1.67**	-7.13**	-2.75**	2.18*	5.97**	0.82	1.06	D

* and ** indicate significance of values at P=0.05 and 0.01, respectively,   D – Duplicate,   C – Complementary

opposite direction, suggesting duplicate type of epistasis and indicating predominantly dispersed alleles at the interacting loci (Jink and Jones, 1958). Dominance gene effects were found to be relatively more important as indicated by the fact that in all cases the dominance (h) values were higher than additive (d) values (Talwar *et al.*, 1986; Sharma and Phul, 1994 and Khattab, 1998). While significant dominant and dominant x dominant gene interaction was reported by Rahangdale and Raut (2002) for this trait.

However, in the crosses JS 335 x MACS 450 and JS 335 x EC 241780, χ^2 values were found to be significant when trait was analyzed with eight parameter model indicating involvement of still higher order interactions. In both the crosses trait was observed to be controlled by significant (i), (d), (j) and (jab/c) digenic and trigenic interactions, respectively (Ma *et al.*, 1987 and Maloo and Nair, 2005).

Importance of both additive and non-additive gene effects for controlling the trait was reported by Talwar and Singh (1983), Cecon *et al.* (1985), Harer and Deshmukh (1991), Khattab (1998) and Bhor *et al.* (2014).

Number of primary branches per plant :

Dominance and dominance x dominance gene actions were found to be predominant in controlling the inheritance of number of primary branches per plant in three crosses *viz.*, JS 335 x MACS 450, MACS 450 x EC 391160 and JS 335 x EC 241780, while in cross EC 391160 x EC 241780 the magnitude of additive gene effects were higher than dominance which indicates the dominance of additive gene action in controlling the expression of this trait (Rajput *et al.*, 1987 and Agrawal *et al.*, 1999). The effect of dominant gene action for the trait should be eliminated through bulk selection method through which homozygosity could be achieved prior to the initiation of selection. The opposite sign of (h) and (l) in JS 335 x MACS 450 and MACS 450 x EC 391160 suggested duplicate type of epistasis, which would limit the range of variability and thus slow down the pace of progress through selection, therefore heterosis breeding would be advantageous. The importance of dominant gene action with duplicate epistasis was reported by Kaw and Menon (1983), Halvankar and Patil (1993) and Khattab (1998), whereas duplicate epistasis was reported by Rahangdale and Raut (2002) for this trait.

Number of clusters per plant :

Significant non-additive (dominance and epistasis) gene actions in the inheritance of this trait, revealed predominance of non-additive genetic control in all the crosses. The high magnitude of dominance effect suggested that selection of high yielding genotypes would be postponed till when the dominant effect would have diminished in later generations.

In cross MACS 450 x EC 391160 significant dominance (h) and additive x dominance (j), dominance x dominance (l) digenic non-allelic interactions with significant additive x additive x additive iabc/ and additive x additive x dominance (jab/c) trigenic interactions were involved in the inheritance of the character, whereas in cross JS 335 x EC 241780 significant h, i, l, and iabc/ were observed to be predominant. Opposite sign of h and l indicated the presence of duplicate epistasis in both crosses (Rahangdale and Raut, 2002).

The number of clusters per plant had significant values of additive (d), dominance (h) and non-allelic interactions *i.e.* additive x additive (i), additive x dominance (j) and dominance x dominance (l) with significant additive x additive x additive iabc/ and additive x additive x dominance (jab/c) in cross EC 391160 x EC 241780, whereas, only dominance (h), additive x additive (i) and additive x dominance (j) were significant for this trait in cross JS 335 x MACS 450. Both the additive and dominance gene actions for this trait have been reported by Singh *et al.* (1974).

Number of pods per plant :

The significant values of additive and the non-allelic gene interactions *i.e.* additive x dominance (j) with additive x additive x additive iabc/ and additive x additive x dominance (jab/c) for number of pods per plant in cross EC 391160 x EC 241780 showed less complexity in the inheritance of the trait while the estimates of all the genetic components *i.e.* d, h, j, l, iabc/ and jab/c except i were significant for this trait in cross MACS 450 x EC 391160. The positive and significant value of d with negative value of the additive x additive non-allelic gene interaction for the character indicated that negative alleles are dispersed in the parents involved in the cross (Malik and Singh, 1987; Rajput *et al.*, 1987; Mehetre *et al.*, 1998 and Agrawal *et al.*, 1999).

The significant estimates of additive x additive non-allelic gene interaction was found to be responsible for controlling the inheritance of the character in cross JS

335 x MACS 450, while significant dominance (h) and additive x additive (i), dominance x dominance (l) with additive x additive x dominance (jab/c) non-allelic interactions were observed in cross JS 335 x EC 241780. These results indicate that number of pods per plant was predominantly controlled by higher values of dominance and dominance x dominance non-allelic interactions than the additive gene effects with duplicate epistasis (Kaw and Menon, 1983; Cecon *et al.*, 1985; Harer and Deshmukh, 1991; Halvankar and Patil, 1993; Sharma and Phul, 1994; Khattab, 1998; Rahangdale and Raut, 2002 and Maloo and Nair, 2005).

100 seed weight (g) :

The magnitude of significant dominant component was greater than additive with absence of non-allelic interaction in cross JS 335 x MACS 450 (Singh *et al.*, 1974; Sharma and Phul, 1994 and Maloo and Nair, 2005).

In cross EC 391160 x EC 241780 the additive genetic effect (d) was equally important as non-additive for this trait. Therefore, the efficient utilization of fixable and non-fixable components of genetic variation for this trait, reciprocal recurrent selection was suggested because it will concentrate additive effect but will not allow dissipating non-additive effect (Kaw and Menon, 1983; Talwar and Singh, 1983; Talwar *et al.*, 1986; Harer and Deshmukh, 1991; Ganesamurthy and Seshadri, 2002 and Sayad *et al.*, 2005).

The estimates of all the genetic components *i.e.* d, h, i, j, l, iabc/ and jab/c were significant for 100 seed weight in cross MACS 450 x EC 391160. The positive and significant value of d and significant value of the additive x additive non-allelic gene interaction for this character indicated that the positive alleles are dispersed in the parents involved in the crosses. Thus, selection for 100 seed weight should be delayed to later generation till the desired recombinants become available in the population. The significant but opposite values of h and l for 100 seed weight indicated the involvement of duplicate type of non-allelic gene interaction in the inheritance.

This trait was found to be under the influence of significant additive x additive (i) and additive x additive x dominance (jab/c) non-allelic interaction in cross JS 335 x EC 241780 (Ma *et al.*, 1987; Harer and Deshmukh, 1991; Halvankar and Patil, 1993; Mehetre *et al.*, 1998 and Agrawal *et al.*, 1999).

Yield per plant (g) :

Presence of significant dominance component (h) revealed that yield of soybean was predominantly under non-additive genetic control in all the crosses except JS 335 x MACS 450 in which character was under the influence of significant additive x additive (i) and additive x additive x dominance non-allelic interactions. The high magnitude of dominance effect suggested that the selection of high yielding genotypes would be postponed to later generation till when the dominance effect would have reduced. Estimates of additive effects can be small due to a high degree of dispersion of increasing alleles between parents and dominance can be large due to its bi-directional nature. The presence of duplicate epistasis in three crosses for the trait can hinder progress and make it difficult to fix genotypes at a high level of manifestation. Duplicate epistasis may restrict the expression of a trait in early segregating generations. The selection in early generations would not be effective for want of fixable components of variation. Such gene effects may be exploited by intermating the selected segregants and delaying the selections to advanced generations. The predominance of non-additive gene action in the control of yield was also reported by Kaw and Menon (1983), Halvankar and Patil (1993), Sharma and Phul (1994), Khattab (1998) and Bhor *et al.* (2014). Duplicate epistasis involved in the inheritance of yield was reported by Rahangdale and Raut (2002).

Oil (%) :

All the genetic components *i.e.* d, h, i, j and l were significant for oil per cent in cross JS 335 x MACS 450. The significant but opposite sign values of h and l indicated duplicate type of non-allelic gene interaction for this trait showing complex inheritance, particularly additive and dominance components could be successfully exploited in later generation (Raut *et al.*, 2000 and Rahangdale and Raut, 2002).

Significant additive (d), additive x additive (i) and additive x dominance (j) digenic non-allelic interaction along with significant additive x additive x additive iabc/ trigenic interactions were found responsible for controlling inheritance of oil per cent in JS 335 x EC 241780. Therefore, this cross may give response to selection.

Both additive and non-additive gene actions were equally important for this trait with duplicate epistasis in cross MACS 450 x EC 391160, however, in EC

391160 x EC 241780 significant additive x dominance non-allelic interaction was found. Reciprocal recurrent selection has been suggested to improve oil per cent as both additive and non-additive gene effects are involved in the expression. The presence of duplicate epistasis in cross MACS 450 x EC 391160 can hinder progress and make it difficult to fix genotypes at a high level of manifestation (Malik and Singh, 1987 and Singh *et al*., 1988). Significant additive and additive x additive gene action controlling this trait was reported by Brim and Cockerham (1961) and Weber *et al*. (1970).

Protein (%) :

All the genetic components *i.e.* d, h, i, j and l were significant for protein per cent in cross JS 335 x MACS 450 with duplicate epistasis, whereas, dominance x dominance component was found to be predominant in cross MACS 450 x EC 391160 for the control of protein percent (Sharma and Phul, 1994). Equal importance of both additive and non-additive gene actions in the inheritance of protein per cent was reported by Ganesamurthy and Seshadri (2002).

Predominant additive gene action was found in the crosses EC 391160 x EC 241780 and JS 335 x EC 241780 for protein per cent, which is fixable and could be utilized in selection programme (Zhang *et al*., 1987 and Malik and Singh, 1987).

Number of trichomes per cm^2:

Both additive and dominance gene effects played important role in the expression of this trait in crosses JS 335 x MACS 450 and JS 335 x EC 241780. However, higher magnitude of dominance effect than additive gene effect indicates the importance of dominance gene action in cross MACS 450 x EC 391160 with involvement of duplicate epistasis. Whereas, in cross EC 391160 x EC 241780, involvement of higher order trigenic interaction *i.e.* additive x additive x dominance was found to be responsible for controlling this character (Bernard and Singh, 1969).

Considering overall results, simple additive dominance model was found to be adequate for plant height and 100 seed weight indicating absence of non-allelic interactions and simple nature of inheritance in few crosses. In all four crosses χ^2 values were found to be non-significant for number of primary branches and oil per cent displaying separation of digenic and trigenic non-allelic interactions. Highly significant χ^2 values

were observed for seed yield per plant even the trait was analyzed by eight parameter model. The dominance and dominance x dominance gene actions were found to be predominant in control of seed yield with duplicate epistasis.

Predominant dominance gene effects were observed for number of primary branches, plant height, number of clusters, 100 seed weight and days to maturity, suggesting that the conventional selection procedure may not be effective enough for improvement of these traits. Therefore, postponed selection in later generations or inter mating among the selected segregants followed by one or two generations of selfing would be useful to break undesirable linkage and allow the accumulation of favourable alleles for the improvement of these traits. Both additive and non-additive gene effects were playing important role in governing oil, protein and pods per plant with duplicate epistasis. Reciprocal recurrent selection or bi-parental mating would be useful for improving these characters. Selections can be effectively applied for the improvement of days to maturity and number of primary branches due to the predominance of significant additive gene effects with additive x additive and additive x dominance epistatic gene interaction.

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