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Research Article

Inheritance of yield and yield components in soybean (*Glycine max* (L.) Merrill.)

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Abstract
The present investigation was undertaken to study the genetics of yield and yield components in soybean through generation mean analysis. Three crosses *viz.,* MACS-450 × Monetta, DS-9712 × Kalitur and MACS-450 × Kalitur were made involving four parents during *kharif* 2013 to study the gene action for ten characters in soybean. Six generations (P_1, P_2, F_1, F_2, B_1 and B_2) were obtained by intermating diverse parents. Dominant gene action was observed in the inheritance of yield and yield contributing characters *viz*., number of pod per plant, 100 seed weight and yield per plant. Both additive and non-additive gene effects were significantly involved in the expression of number of pods per plant (cross II), number of clusters per plant (cross II and III) and all three crosses expressed duplicate epistasis for yield per plant. Bi-parental mating design may be used to improve these characters. Complementary epistasis was observed for the cross Kalitur × DS-9712 for plant height (cm) and cross Kalitur × MACS 450 for number of pods per plant, which suggested that the selection will be practiced in F_3 generation onwards for improvement of these characters.

Key words
Additive gene effects, gene action, selection, inheritance, soybean

Introduction

Soybean [*Glycine max* (L.) Merrill] cultivation is rapidly expanding partly due to its high nutritional value as food for both humans and livestock and as an important industrial crop. It is considered as a “Golden bean” due to its dual qualities *viz.,* high protein (40%) and oil (18 to 20%) content. India is the fourth largest producer of soybean in the world. However, India’s share in world production of soybean is only five per cent. On an average Madhya Pradesh and Maharashtra produce 51 and 33 per cent of total production of soybean respectively.

The classical breeding systems that make use of additive genetic variance will be effective breeding procedures for improving the seed yield. To exploit the existing genetic variability present in breeding material for seed yield as efficiently as possible, the breeder would need the basic information regarding the inheritance of grain yield and its closely related components for devising an efficient selection programme.

For genetic improvement of the crop, the breeding method to be adopted depends mainly 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 complimentary or duplicate at the digenic 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.

Considering the present study the crosses differing in pod shattering was undertaken to study the information on gene action involved in the control of yield and yield contributing characters through generation mean analysis.

Materials and methods

The present investigation was conducted at Post Graduate Institute, Botany Research Farm, MPKV, Rahuri during the period from 2013-2014 and 2014-2015. Three crosses *viz.,* Monetta × MACS-450; Kalitur × DS-9712 and Kalitur × MACS-450 were effected in *Kharif* 2013 to produce the F_1 seeds. In early *summer* 2014, F_1s sown and F_2s seeds were made. Backcrosses, BC_1 and BC_2 of three crosses were also made in early *summer* 2014 within the stipulated period.

The experiment was laid out in randomized block design (RBD) with three replications during *Kharif* 2014. The experimental material consisted of 18 treatments consisting of 6 parents, $3F_1$s, $3F_2$s, $3BC_1$s and $3BC_2$s, of three crosses (Monetta × MACS-450, Kalitur × DS-9712 and Kalitur × MACS-450). The parents, F_1s, F_2s, and back crosses were randomized separately in each of the three replications. Sowing was done in rows of 3 m length and having 45 x 10 cm distance in a row to row and plant to plant respectively. One row was assigned to P_1s, P_2s, F_1s, while the two rows to each of the B_1s and B_2s and 10 rows to F_2s. This has permitted for raising of 30 plants in each of P_1s, P_2s, F_1s, 60 plants in B_1s and B_2s, and 300 plants in each of the F_2s, in all the three replications of 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. The experiment was sown on 7th of July 2013. All inter-culturing operations were carried out regularly as per need and stage of crop growth.

The observations were recorded on the ten quantitative characters on 10 random plants from parents and F_1s; 20 plants from backcrosses and 40 plants from F_2s generations of all the three crosses 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). To compute gene effects for grain yield and its components with six basic generations, Mather’s (1949) three parameter model and Hayman’s (1958) six parameter models were used.

Results and discussion

The results obtained in the present investigation for individual and joint scaling test are presented in table 1. Significant individual and joint scaling tests were observed in all characters for three crosses indicated presence of epistasis. The results of gene effects are presented in table 2 are discussed as below:

Days to 50% flowering: In Monetta × MACS 450 and Kalitur × MACS-450, cross combinations the predominance of additive gene effect (negatively significant and desirable direction) was observed for the trait, days to 50% flowering and hence it can be exploited effectively by selection, for the improvement of the character. These findings are in agreement with earlier reports of Agrawal *et al.* (1999), Rahangdale and Raut (2002), and Datt *et al.* (2011)

Additive gene effect (d) was positively significant in crosses Kalitur x DS-9712 indicating that expression of this trait was under the influence of additive gene action but for lateness. The additive effects could facilitate fixation of the combination of genes and therefore, selection for days to 50% flowering in these crosses would give better response. The results confirms the earlier reports of Mehetre *et al.* (1998) and Agrawal *et al.*(1999). The significant additive x dominance (j) non-allelic interaction was observed for all three crosses.

Days to maturity: In cross combination of Monetta × MACS 450, the predominance of additive gene effect (negatively significant but in desirable direction) with duplicate epistasis was observed for days to maturity and hence it can be exploited effectively by selection for the improvement of this trait. These findings are in agreement with earlier reports of Rahangdale and Raut (2002) and Datt *et al.* (2011). In Monetta × MACS 450 cross, the additive genetic effect (d) was equally important as non-additive (h) with duplicate epistasis, therefore, for efficient utilization of fixable and non-fixable components of genetic variation, reciprocal recurrent selection or biparental mating can be used in this cross. These findings are in agreement with earlier reports of Khattab (1998)

Additive genetic effect (d) with additive x additive (i) epistasis was negatively significant in desired direction (earliness in maturity) in cross Monetta × MACS 450 indicating that the expression of this character was under the influence of additive gene action for early maturity. The additive effects could facilitate fixation of the combination of genes and therefore, selection for days to maturity in that cross would give better response. The results confirms the earlier reports of Mehetre *et al.*(1998) and Rahangdale and Raut (2002). The significant additive x additive non-allelic interaction with duplicate epistasis was observed in cross Monetta × MACS 450 for days to maturity suggesting the possibilities of obtaining transgressive segregants in later generations. The results are in agreement with earlier reports of Sharma and Phul (1994).

Plant height (cm): Both additive (d) and dominance (h) gene effects were significant in all the three crosses Monetta × MACS 450, Kalitur × DS-9712 and Kalitur × MACS-450. The results were in agreement with earlier reports of Harer and Deshmukh (1991), Khattab (1998). Additive gene effect was significant in negative direction in the cross Monetta × MACS 450, while it was positive in cross Kalitur × DS-9712 and Kalitur × MACS-450. It revealed that selection for this trait would be useful to start from the early segregating generation. The above findings confirm earlier finding of Mehetre *et al.* (1998), Agrawal *et al.* (1999) and Rahangdale and Raut (2002).

Among interaction components, an estimate of additive x additive (i) component was positively significant in cross Kalitur × MACS-450. The cross, Monetta × MACS 450 recorded significant duplicate epistasis, however positively significant complimentary epistasis was observed for cross Kalitur x DS9712. Similar results were earlier reported by Maloo and Nair (2005).

All the three crosses observed significant as additive and additive x additive gene effects for this character were reported by Datt *et al.* (2011). Significant dominant and dominant x dominant gene interaction was reported for crosses II and III for plant height. Rahangdale and Raut (2002) reported similar results for this character. Cross I, Monetta × MACS 450 showed that the dominance (h) and dominance x dominance (l) effects were in the opposite direction, suggesting duplicate type epitasis and indicating predominantly dispersed alleles at the interacting loci.

Number of primary branches per plant: An additive gene action were found in the crosses, Monetta × MACS 450 and Kalitur × MACS-450 controlling the inheritance of number of primary branches per plant in all the crosses. Dominance gene action was observed in cross Monetta × MACS 450. 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 for the character.

Number of pods per plant: Predominance of additive (d) gene effect was found for the crosses, Kalitur × DS-9712 and Kalitur × MACS-450. These results are in reported by Malik and Singh (1987), Mehetre *et al.* (1998) and Agrawal *et al.* (1999). Dominance (h) gene effect was found for the crosses Kalitur × DS-9712 and Kalitur × MACS-450. These results are in agreement with reports of Harer and Deshmukh (1991), Sharma and Phul (1994), Khattab (1998) and Maloo and Nair (2005). The additive and dominance gene effects were positively significant for cross Kalitur × MACS-450. The predominance of additive gene action for this character was reported by Malik and Singh (1987), Mehetre *et al.* (1998) and Agrawal *et al.* (1999).

Duplicate epistasis was observed for the cross Kalitur × DS-9712. Importance of duplicate epistasis in control of this character was reported by Rahangdale and Raut (2002) and Datt *et al.* (2011). Complementary epistasis was observed for cross Kalitur × MACS-450 which suggests that improvement in the character can be done by selection in F_3 generation onwards such that the desired recombinants become available in the population.

The significant values of additive and the non-allelic gene interactions *i.e.* additive x additive (i), additive x dominance (j) and dominance x dominance (l) for number of pods per plant in cross II showed less complexity in the inheritance of the trait. These results are in agreement with earlier reports of Mehetre *et al.* (1998) and Agrawal *et al.* (1999).

Number of clusters per plant: Additive gene effects were observed in all the three crosses for no. of clusters per plant. The perusal of data indicated significant non additive (dominance and epistasis) gene actions with duplicate epistasis in the inheritance of this trait in the crosses II and III, which revealed that number of clusters per plant was predominantly under non-additive genetic control. Both additive and dominance gene effects were significant in crosses II and III.

Number of pods per cluster: Significant additive and non-additive (dominance and epistasis) gene actions with duplicate epistasis was observed for the inheritance of the trait, number of pods per clusters in the cross II (Kalitur × DS-9712) which revealed that selection through biparental mating is suggested for duplicate epistasis. The dominance effect suggested that selection of high yielding genotype would be proposed till latter generation when the dominant effect would have diminished.

Number of seeds per pod: This trait showed the both additive and dominance effect in two crosses expression for this character. In addition to additive and dominance effect additive x additive and dominance x dominance in both the cross I (Monetta × MACS-450) and additive x additive, additive x dominance in cross III (Kalitur × MACS-450) and dominance x dominance non allelic interaction significantly involved in cross II (Kalitur × DS-9712). The relative magnitude of dominance component *i.e.* non-additive gene action was greater than respective additive component, in general, suggesting its important role in the expression of this character.

100 Seed weight (g): Additive gene effect was observed for the 100 seed weight trait in cross Monetta × MACS 450. Among non-allelic interaction all three additive x additive (i), additive x dominance (j) and dominance x dominance (l) effects were significant for the cross Monetta × MACS 450. Additive x additive non-allelic gene interaction was observed in cross I and III for inheritance of this character. Similar results were also reported by Sharma and Phul (1994) and Maloo and Nair (2005).
Duplicate epistasis was observed for the cross Monetta × MACS 450. Biparental mating is suggested for duplicate epistasis.

Seed yield per plant (g): Predominance of additive gene effect was observed for the trait in crosses Kalitur × DS-9712 and Kalitur × MACS-450. Importance of additive gene action for inheritance of this trait was reported by Srinivas and Sutakom (1986), Ganesamurthy and Seshadri *et al.* (2002) and Maloo and Nair (2005).

The effect of dominance gene in cross II (Kalitur × DS-9712) and cross III (Kalitur × MACS-450) suggested that selection of high yielding genotypes would be postponed till later generations when the dominance effect would have reduced. Estimates of additive effects is small due to a high degree of dispersion of increasing alleles between parents and the dominance effect is large due to its bi-directional nature. The presence of duplicate epistasis in all three crosses for the trait can hinder progress and make it difficult to fix genotypes at a high level of manifestation.

The selection in early generations would not be effective for want of fixable components of

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variation. Such gene effects can however, be exploited by intermating the selected segregants and delaying the selections to the advanced generations. Duplicate epistasis involving in the inheritance of this trait was reported by Rahangdale and Raut (2002), Datt *et al.* (2011) and Bhor *et al.* (2014). The involvement of non-additive gene action in control of this trait was reported by Sharma and Phul *et al.* (1994) and Khattab (1998). Significant additive x additive gene effects for controlling this trait was observed for all the three crosses. The importance of both additive and non-additive gene effects were equally important as reported by Harer and Deshmukh (1991).

It can be concluded that dominance gene action was observed for the inheritance of yield contributing characters like number of pods per plant and 100 seed weight, thus suggesting that conventional selection procedure may not be rewarding for improvement of these characters. Thus, it appears that selections should be postponed to 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 accumulation of favourable alleles for improvement of these traits.

Both additive and non-additive gene effects were involved in the expression of cross I for maturity, plant height (cm), no. of seeds/pod, 100 seed weight (g) whereas, cross II and III for number of clusters per plant and all three crosses for yield per plant (g) duplicate epistasis, suggesting the reciprocal recurrent selection or bi-parental mating design to improve these characters. Complementary epistasis was observed for cross Kalitur × DS-9712 for plant height (cm) and cross Kalitur × MACS-450 for number of pods per plant suggesting selection can be practiced from F_3 generation onwards for the improvement of these characters.

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Table 1. Estimates of individual and joint scaling test (x^2) for detecting non-allelic interaction for yield and yield contributing characters in soybean

Characters	Crosses	Scaling tests				x^2
		A	B	C	D	
Days to 50% flowering	MONETTA x MACS-450	-1.40**	4.20**	-0.07	-1.43**	112.78**
	KALITUR x DS-9712	1.27**	-1.73**	-2.02*	-0.78	28.23**
	KALITUR x MACS-450	-2.80**	1.13*	-3.07**	-0.70	61.42**
Days to maturity	MONETTA x MACS-450	-6.07	8.33**	24.91**	8.32**	763.89**
	KALITUR x DS-9712	3.60**	-1.80**	0.42	-0.69	113.14**
	KALITUR x MACS-450	8.07**	-1.53**	3.78**	-1.38	176.17**
Plant height (cm)	MONETTA x MACS-450	-15.02**	3.07*	8.81**	10.38**	265.31**
	KALITUR x DS-9712	9.03**	-40.66**	-20.14**	5.75**	1408.84**
	KALITUR x MACS-450	8.27**	-15.13**	-20.76**	-6.95**	142.40**
No. of primary branches/plant	MONETTA x MACS-450	-0.80*	-0.73*	-2.62**	-0.54	22.50**
	KALITUR x DS-9712	-1.67**	-1.47**	-2.20**	0.47	21.59**
	KALITUR x MACS-450	-1.00*	-1.47**	-1.49*	0.49	16.16**
No. of pod per plant	MONETTA x MACS-450	-7.47**	-8.80**	5.62*	10.94**	64.56**
	KALITUR x DS-9712	-16.20**	-46.13**	55.36**	58.84**	2297.50**
	KALITUR x MACS-450	-9.80**	-24.73**	-36.56**	-1.01	142.28**
No. of clusters per plant	MONETTA x MACS-450	3.47*	-3.07**	5.80*	2.70	16.90**
	KALITUR x DS-9712	3.47*	-14.33**	17.04**	13.96**	150.67**
	KALITUR x MACS-450	-3.60**	-12.26**	11.38**	13.62**	96.49**
No. of pods per cluster	MONETTA x MACS-450	-0.21	-0.26*	-1.67**	-0.60**	23.93**
	KALITUR x DS-9712	-0.20*	-0.19*	0.47*	0.43**	18.42**
	KALITUR x MACS-450	-0.46*	-0.45*	-0.84*	0.03	13.03**
No. of seeds per pod	MONETTA x MACS-450	-0.25**	-0.15	0.28	0.34**	24.07**
	KALITUR x DS-9712	-0.23*	-0.36**	-0.42*	0.08	10.27*
	KALITUR x MACS-450	-0.24*	0.03	-0.53**	-0.16	10.88**
100 seed weight (g)	MONETTA x MACS-450	-1.03**	-3.86**	-1.49*	1.70**	94.46**
	KALITUR x DS-9712	-1.49**	-0.77	-1.81*	0.23	12.99**
	KALITUR x MACS-450	-4.08**	-2.68**	-11.50**	-2.37**	174.36**
Yield per plant (g)	MONETTA x MACS-450	-3.08*	-1.78	6.48**	5.67**	20.91**
	KALITUR x DS-9712	-2.20	-8.94**	3.63	7.39**	60.96**
	KALITUR x MACS-450	6.25**	-8.25**	9.12**	-3.56**	78.22**

*, ** significant at 5 and 1 per cent level respectively

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Table 2. Estimates of gene effects in three crosses for the quantitative traits in soybean

Characters	Crosses	Genetic parameters						Type of epistasis
		M	d	h	*i*	*j*	*l*	
Days to 50% flowering	MONETTA x MACS-450	36.73**±0.23	-5.97**±0.24	0.70 ±1.06	2.87**±1.03	-2.80**±0.29	-5.67**±1.43	-
	KALITUR x DS-9712	37.84**±0.21	1.87**±0.27	-1.14 ±1.01	1.56 ±0.99	1.50**±0.31	-1.09 ±1.44	-
	KALITUR x MACS-450	39.40**±0.19	-2.83**±0.26	0.80 ±0.96	1.40 ±0.94	-1.97**±0.29	0.27 ±1.38	-
Days to maturity	MONETTA x MACS-450	91.58**±0.20	-8.90**±0.26	-19.08**±1.01	-16.64**±0.94	-4.20**±0.30	8.38**±1.51	Duplicate
	KALITUR x DS-9712	97.96**±0.20	6.47**±0.23	0.34 ±0.94	1.38 ±0.92	2.70**±0.26	-3.18*±1.28	-
	KALITUR x MACS-450	96.78**±0.31	10.13**±0.37	-0.38 ±1.46	2.76 ±1.44	4.80**±0.39	-9.30**±1.98	-
Plant height (cm)	MONETTA x MACS-450	54.95**±0.59	-23.08**±0.71	-11.72**±2.84	-20.77**±2.75	-9.04**±0.82	32.72**±3.98	Duplicate
	KALITUR x DS-9712	64.65**±0.62	49.83**±0.71	6.25*±2.96	-11.49**±2.85	24.85**±0.84	43.19**±4.09	Complementary
	KALITUR x MACS-450	70.26**±0.69	22.67**±0.99	17.28**±3.52	13.90**±3.38	11.70**±1.16	-7.05 ±5.20	-
No. of primary branches per plant	MONETTA x MACS-450	5.38**±0.11	-0.43*±0.19	1.82**±0.61	1.09 ±0.58	-0.03 ±0.23	0.44 ±0.96	-
	KALITUR x DS-9712	6.33**±0.16	0.13 ±0.24	-0.57 ±0.83	-0.93 ±0.79	-0.10 ±0.30	4.07**±1.27	-
	KALITUR x MACS-450	6.24**±0.14	0.53*±0.24	-0.74 ±0.79	-0.98 ±0.75	0.23 ±0.29	3.44**±1.22	-
No. of pod per plant	MONETTA x MACS-450	95.49**±0.54	-4.30**±1.02	-3.12 ±3.11	-21.89**±2.97	0.67 ±1.11	38.16**±4.98	-
	KALITUR x DS-9712	117.42**±0.55	37.20**±1.12	-75.26**±2.87	-117.69**±3.15	14.98**±1.19	180.02**±5.21	Duplicate
	KALITUR x MACS-450	103.24**±1.54	15.17**±1.27	17.92**±6.67	2.02 ±6.68	7.47**±1.41	32.51**±8.32	Complementary
No. of clusters per plant	MONETTA x MACS-450	39.07**±0.56	4.10**±0.87	-3.70 ±2.99	-5.40 ±2.84	3.27**±0.97	5.00 ±4.54	-
	KALITUR x DS-9712	43.64**±0.99	19.93**±0.98	-17.61**±4.49	-27.91**±4.45	8.90**±1.07	38.78**±5.73	Duplicate
	KALITUR x MACS-450	47.38**±0.65	7.63**±0.98	-19.51**±3.37	-31.71**±3.27	2.10 ±1.09	57.24**±4.99	Duplicate
No. of pods per cluster	MONETTA x MACS-450	2.19**±0.08	-0.03 ±0.04	1.22**±0.32	1.21**±0.31	0.03 ±0.07	-0.74 ±0.38	-
	KALITUR x DS-9712	2.68**±0.05	-0.16**±0.04	-0.58*±0.23	-0.86**±0.22	-0.00 ±0.06	1.25**±0.30	Duplicate
	KALITUR x MACS-450	2.43**±0.06	-0.12 ±0.09	0.15 ±0.36	-0.07 ±0.32	-0.00 ±0.12	0.97 ±0.56	-
No. of seeds per pod	MONETTA x MACS-450	2.35**±0.03	-0.21**±0.04	-0.43*±0.15	-0.68**±0.15	-0.05 ±0.05	1.08**±0.23	Duplicate
	KALITUR x DS-9712	2.22**±0.04	-0.04 ±0.05	0.06 ±0.20	-0.17 ±0.18	0.07 ±0.07	0.76*±0.30	-
	KALITUR x MACS-450	2.16**±0.03	0.17**±0.07	0.56**±0.21	0.43*±0.19	0.27**±0.08	-0.43 ±0.35	-
100 seed weight (g)	MONETTA x MACS-450	14.15**±0.14	0.43*±0.20	-2.09**±0.74	-3.40**±0.69	1.41**±0.24	8.28**±1.11	Duplicate
	KALITUR x DS-9712	11.80**±0.18	-0.77**±0.24	0.74 ±0.89	-0.45 ±0.87	-0.36 ±0.28	2.71*±1.29	-
	KALITUR x MACS-450	11.76**±0.20	-1.69**±0.28	6.86**±1.00	4.74**±0.96	-0.70*±0.32	2.02 ±1.46	-
Yield per plant (g)	MONETTA x MACS-450	24.33**±0.49	-3.85**±0.80	-1.83 ±2.62	-11.34**±2.54	-0.65 ±0.92	16.19**±3.98	Duplicate
	KALITUR x DS-9712	26.25**±0.47	7.18**±0.79	-6.14*±2.50	-14.78**±2.45	3.37**±0.88	25.92**±3.78	Duplicate
	KALITUR x MACS-450	34.08**±0.41	5.86**±0.75	-19.94**±2.39	-38.14**±2.21	4.08**±0.89	68.46**±3.86	Duplicate

*, ** significant at 5 and 1 per cent level respectively