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Genetic architecture for yield and its components in greengram (*Vigna radiata* (L.) Wilczek.)

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Abstract
The genetic architecture of seed yield and related traits was investigated through generation mean analysis for four crosses in six generations in greengram. Involvement of both additive and non-additive gene actions with preponderance of non-additive gene actions for seed yield, its major yield components suggested that breeding can profitably be utilized for improving seed yield in greengram by exploiting dominance / non-additive gene action. However, to exploit both additive and non-additive types of gene actions observed for seed yield, its components, cyclic method of breeding involving conventional breeding approaches for selection of superior recombinants and their inter se crossing can alternatively be utilized for the development of high yielding inbred in greengram.

Keywords: Greengram, genetic architecture, gene action, generation mean

Introduction
Yield is the ultimate product of action and interaction of number of yield components, which are governed by a large number of genes having small effects and are greatly influenced by environment. Effect of small individual gene cannot be selected, collective effect of the genes can be estimated for any of the attributes. The estimation of gene effects involved in the inheritance of yield contributing or quantitative characters are helpful in planning breeding programs. Though gene effects for seed yield and other traits have been estimated in greengram, information on epistatic gene effects is negligible. To exploit the existing genetic variability in greengram 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 program. In the present studies, the detection of epistasis, and estimates of additive and dominance components of variation for yield components in four sets of greengram crosses were carried out by using generation mean analysis

Materials and Methods
The material comprised of four hybrids viz., MGG 347 x KM 11 564 (Cross-I), WGG 42 x RM 12-13 (Cross-II), LGG 543 x KM 11- 564 (Cross-III) and MGG-347 x RM 12-13 (Cross-IV) involving five diverse parents. The entire experimental material comprised of parents (P_1 and P_2), F_1, F_2, B_1 (F_1 x P_1) and B_2 (F_1 x P_2) generations of all four crosses, which was conducted in randomized block design with three replications in College Farm, College of Agriculture, Rajendranagar, Hyderabad during Kharif season, 2016. The row-length was always four meters but the number of rows varied as follows: three rows, for the non-segregating P_1, P_2 and F_1; 40 rows for the F_2; and 20 rows for the BC_1 and BC_2 generations. Since, the non-segregating generations represent the homogeneous population while the segregating generations represent the heterogeneous population the sample size (i.e., number of plants analyzed) varied as follows: 40 plants for the P_1, P_2 and F_1 generations, 300 plants for the F_2 generations and 100 plants in the BC_1 and BC_2 generations. The recommended agronomic practices were followed to raise healthy crop. The traits assessed were days to 50% flowering, days to maturity, number of primary branches, plant height (cm), number of clusters/plant, number of pods/plant, pod length (cm), number of seeds/pod, weight of 100 seed weight (g), seed yield/plant (g) protein content (%) and harvest index (%). From each replication data were recorded for twelve quantitative characters.

The data were subjected to different biometrical techniques namely scaling test and generation mean analysis by Hayman's six parameter model (Haymen, 19580 [4]. Three parameters viz., m, d and h defining the additive-dominance model was estimated using weighted least square (Mather and Jinks, 19820 [8]. This model provides χ 2 test for the goodness of fit of the model (Kearsey and Pooni, 19960 [7]. From these estimated parameters, the expected generation means were calculated as follows:

$P_1 = m - d$, $P_2 = m + [d]$, $F_1 = m + [h]$, $F_2 = m + (1/2)\ h$,

$B_1 = m - (1/2)\ d + (1/2)h$, $B_2 = m + (1/2)d + (1/2)h$

All the yield and yield contributing traits were analyzed statistically and tested for significance. The significance of the joint scaling test was determined by the using $\chi 2$ test and compared observed and expected't' values at 5 and 1% level of significance. In instances where the A, B, C and D values and $\chi 2$ test significantly deviated from zero in the joint scaling test of simple additive-dominance model, digenic interaction was assumed. Statistical analysis for scaling test, joint scaling test and $\chi 2$ test were carried out by using advanced biometrical Indostat statistical package, Hyderabad, India.

Results and Discussion

The analysis of variance for the four crosses for twelve characters is presented in Table 1. The analysis of variance revealed the significant differences among the generations for eleven characters out of twelve characters studied in all the four crosses except for pod length in MGG 347 × KM 11 - 564; protein content in WGG 42 × RM 12-13; days to maturity in LGG 543 × KM 11-564; number primary branches per plant in MGG 347 × RM 12-13. Whenever the differences between generation means were found to be non-significant, further analysis was avoided and if generation means were found significant, the data were subjected to generation mean analysis to know the gene action controlling the traits.

Significant scaling test for different traits was observed in almost all crosses indicating the presence of digenic or higher order interactions. The scaling tests were applied to the data to detect the presence or absence of non-allelic interactions. The estimates of genetic parameters m, [d] and [h] were obtained for all the 12 traits in four crosses. The results of the scaling tests in four hybrids showed significant values of A, B, C and D scales for all the traits under study. Majority of the hybrids coupled with traits showed deviation from zero indicated that simple additive-dominance model was inadequate. The joint scaling test were analyzed and found that mean, additive [d] and dominance [h] gene effects coupled with $\chi 2$ test was highly significant for all the traits, and values deviated from zero. For traits like pod length in cross 1 (MGG 347 x KM 11- 564), protein content in cross 2 (WGG 42 x RM 12-13), days to maturity in cross 3 (LGG 543 x KM 11-564) and number of primary branches per plant in cross 4 (MGG 347 x RM 12- 13) additive-dominance model were adequate, so data for these traits was not subjected to further analysis.

(i) Cross 1(MGG 347 x KM 11-564) In this cross, dominance (h) and dominance × dominance (l) gene effects displayed opposite signs for the traits, namely, days to 50% flowering, days to maturity, plant height, number of clusters per plant, 100-seed weight and protein content indicating duplicate epistasis. The values of dominance (h) and dominance × dominance (l) interaction were in the same direction for traits like pods per plant, pod length, seed yield per plant and harvest index and the interaction followed the complementary mode of nonallelic gene interaction. 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. In the present investigation, genotypes MGG 347 and KM 11-564 could be identified as the best parents since their respective crosses showed complementary gene action for number of pods per plant, seed yield per plant and harvest index. These findings are in accordance with the results published by Ajay *et al*. 2012 [1]. The classification of gene interaction depends on the magnitude and sign of the estimates of dominance (h) and dominance × dominance (l) effects, when there are many pairs of interacting genes. The sign associated with the estimates of additive effects (d) and dominance effects (h) indicates the parent who concentrates the highest number of genes or positive alleles for increasing the traits. Therefore, the significant but positive d for harvest index indicates that additive effect of the gene is predominant and selection for this trait can be done by simple selection. The significant negative value of d for traits number of clusters per plant, number of seeds per pod, 100 seed weight indicated that the inheritance of these traits is not controlled by additive gene action. Similarly, the significant and positive value of h for plant height and 100-seed weight showed that the dominant effect of gene is predominant. Presence of h indicates that selection should be delayed until heterozygosity is reduced in population. The earlier findings reported that traits with high magnitude of dominance than additive can be improved through conventional breeding approach such as pedigree or bulk or single seed descent method if selection is delayed until later generation when the dominance effect would have diminished (Parihar *et al*. 2016 and Punia *et al*. 20110 [10, 13]. On the contrary, the significant but negative values of h, i, j and l for some traits showed that negative alleles were also dispersed in the parents involved in the cross. Negative sign of h in cross for any trait indicates that dominance effects were contributed by the parents having alleles responsible for low value for the traits, for example, in plant heights of MGG 347 and KM 11-564 in respective crosses. Thus, selection for these traits should also be delayed to later generation when desirable segregants become available. The significant but similar sign of d and h for primary branches indicated predominant role of additive and dominant effects for the inheritance of these traits. The type of epistatic interaction additive × additive (i) was significant for plant height. Additive × dominance type of epistasis (j) was nonsignificant with negative sign for most of the traits in this cross, which indicate that this type of epistasis is not contributing in inheritance of any trait in the crosses. The d effect for seed yield per plant, pods per plant and protein content was nonsignificant indicating involvement of several genes with small effects (Ajay *et al*. 20120 [1].

(ii) Cross 2 (WGG 42 x RM 12-13) In this cross dominance (h) and dominance × dominance (l) gene effects displayed opposite signs for all the traits except number of clusters per plant and number of pods per plant witnessed duplicate epistasis. The opposite signs of h and l counterbalance each other, thus leading to reduced heterosis (Suresh *et al*. 2010 and Ajay *et al*. 20120 [14, 1]. The positive sign of additive effects (d) for all the traits except 100-seed weight indicates that the additive effect of gene is predominant for all traits, and 100-seed weight exhibited negative value of d suggest that these traits are not controlled by additive gene action. In this case as magnitude of d was less, we could move for heterosis breeding. The estimates of h, i and l were found

significant with negative signs suggesting that selection for the traits, namely, plant height, pods per plant and seed per pod should be delayed to later generation, so that negative alleles are removed. Hence, improvement of these traits could be achieved through recurrent selection procedure. The significant but similar signs of d and h for primary branches indicated predominant role of additive and dominant effects for the inheritance of this trait. Both additive and nonadditive gene effects were also reported in earlier studies. Nonsignificant d effects for harvest index and 100-seed weight indicates that these traits are under the control of several genes (Ajay *et al*. 2012 and Eswaran *et al*. 20180 [1, 3].

(iii) Cross 3 (LGG 543 x KM 11-564) Opposite sign for dominance (h) and dominance × dominance (l) type of interaction was recorded for all the traits except number of clusters per plant, harvest index and seed yield per plant. It indicates that all the traits depicted duplicate type of epistasis and number of clusters per plant, harvest index and seed yield per plant displayed complementary type of epistatic effect. The complementary type suggested the possibility of considerable amount of heterosis for these three traits in this particular cross (Punia *et al*. 20110 [13]. Duplicate type of nonallelic gene interaction for most of studied traits with few exceptions further confirms the prevalence of dominance effects (Chandra mohan *et al*. 2016) [6]. Presence of duplicate epistasis indicates that variability in segregating generations may be reduced which hinder the selection process, hence it is difficult to utilize them in breeding programme (Vadivel *et al*. 20190 [15]. The positive sign of additive effect (d) for number of clusters per plant, harvest index and seed yield per plant indicated that these traits are governed by additive effect of genes. Significant but negative value of d for most of the traits indicted that the inheritance of these traits in this particular cross combination is not controlled by additive genes. The significant but similar sign of d and h for primary branches and seed yield per plant indicated predominant role of additive and dominant effect for the inheritance of these traits. In this cross protein content and 100-seed weight lacked significant d effects indicated that these traits are under the control of complex gene pathway in this cross involving several minor genes with small effect and different expressions (Payasi *et al*. 2010 and Pathak *et al*. 20140 [12, 11]. The estimates of h and l were found significant with positive sign for some traits indicated predominant role of dominant component in the inheritance of these traits. Significant but positive sign of i (additive × additive) for any of the traits portrayed that the inheritance of these traits in a particular cross is controlled by additive gene action. Overall additive gene effects were exhibited by three characters out of twelve characters studied, however, the relative magnitude of these effects to the mean effects (m) suggests that they are of minor importance in the explanation of traits variation. The positive sign of additive effects (d) for seed yield per plant indicated predominant role of additive gene action for the inheritance of this trait. Hence this cross is desirable for future breeding programmes.

(iv) Cross4 (MGG 347 x RM 12-13) This cross showed opposite sign for dominance (h) and dominance × dominance (l) type of interaction for all the traits except number of pods per plant and pod length. It indicates that all the traits depicted duplicate type of epistasis and number of pods per plant and pod length displayed complementary type of epistatic effect. The complementary type suggested the possibility of considerable amount of heterosis for these three traits in this particular cross (Punia *et al*. 20110 [13]. Duplicate type of nonallelic gene interaction for most of studied traits with few exceptions further confirms the prevalence of dominance effects (Chandra mohan *et al*. 20160 [6]. Presence of duplicate epistasis indicates that variability in segregating generations may be reduced which hinder the selection process, hence it is difficult to utilize them in breeding programme (Mir Ghulam *et al*. 2015 and Jog *et al*. 20160 [9, 6]. For seed yield per plant, number of seeds per pod both additive (d) and dominant (h) gene action are playing a role in the inheritance of this trait, but predominantly dominant gene action is contributing higher in magnitude than additive effects. Dominant gene action is more important than additive in case of number of clusters per plant, number of pods per plant and harvest index indicating non additive gene effects. Among the interactions additive x additive (i) and dominant x dominant (l) were generally higher in magnitude and exceeds the additive x dominant (j) effect for all the traits under study. Negative sign of dominant effect (h) for days to flowering and days to maturity shows reducing alleles involving dominant phenotype (Parihar *et al*. 2016 and Hemanth *et al*. 2014) [10, 5].

The mean comparison of six generations indicated that, the F_1 means were higher than mid-parental values and/or comparable to better parent mean values in respect of all the traits except days to 50 per cent flowering indicated presence of both partial and over dominance. The F_2 means were lesser than the F_1 mean values in all the crosses for most of the traits. The means of backcross populations tended towards their respective parents. These results indicate predominant role of non-additive gene action which includes both dominance as well as epistatic interactions. Results of A, B, C and D scaling tests revealed that simple additive - dominance model is inadequate for all the crosses and almost all the traits studied except for pod length (cm) in MGG 347 × KM 11-564; protein content (%) in WGG 42 × RM 12-13,days to maturity in LGG-543 × KM 11-564; and number of primary branches per plant in MGG 347 × RM 12-13, where in all the four scales were found to be non significant. It suggests the importance of epistatic effects besides the major components viz., (d) and (h) for important yield and yield attributes of the material studied in the investigation.

Estimates of gene effects through joint scaling test of three and six parameter and sequential fit model in four crosses for different characters were investigated. It was noticed that simple additive dominance model exhibited lack of good fit for eleven traits out of twelve traits studied indicating the role of non-allelic interactions. So, sequential fit model was searched after eliminating the non-significant parameters of six parameter model. Additive × additive (i) type of epistasis was significantly predominant in all the four crosses for plant height; three crosses for days to flowering and number of primary branches per plant. For days to maturity and number of pods per plant additive × additive (i) component was significant in two crosses and in one cross for pod length. But these are mostly with negative sign implied that sum of the contributions made to this type of interaction by dispersed pairs of genes was more than by associated pairs. Additive × dominance (j) gene effects are mostly important for pod length in four crosses; for days to 50 per cent flowering in three crosses and for days to maturity and number of seeds per pod in two crosses; plant height, number of clusters per plant and protein content in single crosses. Dominance × dominance (l) gene effects were significant in all the four crosses for plant height and number of pods per plant; three crosses 100 seed weight and harvest index; in two crosses for days to 50 per cent flowering, number of clusters per plant

and seed yield per plant, whereas for days to maturity and number of primary branches per plant significant in one cross. These findings indicate that additive, dominance and epistatic interaction effects are contributing significantly in the inheritance of the traits in greengram. Results of dominance (h) and dominance × dominance (l) type interactions revealed the operation of duplicate type of epistasis in MGG 347 × KM 11-564 for days to maturity, number of primary branches per plant, plant height, number of clusters per plant, number of pods per plant, pod length, number of seeds per pod, 100 seed weight, seed yield per plant, protein content and harvest index, and in WGG 42 × RM 12-13 for days to 50% flowering, days to maturity, number of primary branches per plant, plant height, number of pods per plant, pod length, 100 seed weight, seed yield per plant, protein content and harvest index; in LGG 543 × KM 11-564 for days to 50% flowering, days to maturity, number of primary branches per plant, plant height, number of clusters per plant, number of pods per plant, pod length, number of seeds per pod, seed yield per plant, protein content and harvest index; in MGG 347 × RM 12-13 for days to 50 per cent flowering, days to maturity, number of primary branches per plant, plant height, number of pods per plant, pod length, number of seeds per pod, 100 seed weight, seed yield per plant, protein content and harvest index.

Table 1: Analysis of variance (mean squares) between crosses and between generations within cross of six generations for different characters in greengram

Source of varaiation	df	Days to flowering	Days to maturity	Primary branches	Plant height	No. of clusters/ plant	No. of pods/ plant	Pod length	No. of seeds/ pod	100 seed wt	Seed yield /plant (g)	Protein content (%)	Harvest index (%)
Analysis of variation between crosses													
Replications	2	0.27	0.02	0.02	0.09	0.01	1.52	0.01	0.00	0.00	1.73	0.07	3.61
genotypes	5	3.78**	5.14**	0.15**	21.06**	1.22**	76.69**	0.85**	2.67**	1.38**	12.91**	1.98**	14.05**
Error	10	0.47	1.14	0.07	1.48	0.03	0.10	0.12	0.09	0.01	1.13	0.01	3.86
Analysis of variation between generations within cross													
				Cross 1	**MGG 347 x KM 11-564**								
Replications	2	0.88	0.18	0.20	5.63	0.65	9.96	0.07	0.23	0.01	8.48	0.50	6.14
genotypes	5	1.73**	8.28**	0.015**	12.86**	1.83**	54.41**	0.16	1.92**	0.13**	18.52**	1.05**	16.40**
Error	10	0.86	1.52	0.08	3.68	0.41	12.36	0.13	0.29	0.02	0.87	0.66	3.20
				Cross 2	**WGG-42 x RM 12-13**								
Replications	2	0.55	2.49	0.09	7.42	0.01	1.24	0.33	0.11	0.03	2.11	0.21	4.87
genotypes	5	5.78**	4.30**	0.11**	15.23**	0.69*	102.10**	1.13**	1.39*	0.16**	7.67**	0.09	22.54**
Error	10	0.91	0.99	0.05	2.86	0.49	7.87	0.09	0.50	0.02	2.98	0.53	2.99
				Cross 3	**LGG-540 x KM 11-564**								
Replications	2	0.76	0.70	0.02	7.51	1.35	17.28	0.23	0.34	0.03	0.92	1.19	3.63
genotypes	5	1.98**	4.45**	0.09**	33.61**	0.71*	81.34**	0.95**	1.03	0.13**	8.12**	1.55**	7.11
Error	10	1.38	1.15	0.10	2.20	0.40	10.31	0.08	0.44	0.06	1.77	0.43	2.65
				Cross 4	**MGG347 x RM 12-13**								
Replications	2	0.95	0.05	0.10	0.53	0.24	2.96	0.13	3.04	0.18	0.46	0.41	0.19
genotypes	5	5.62**	3.54**	0.05	26.44**	1.44**	68.94**	0.66**	4.15**	0.13**	5.65**	1.23**	14.28**
Error	10	2.76	0.93	0.03	9.17	0.94	9.57	0.13	0.39	0.04	1.77	0.70	6.57

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

Table 2: Summary of estimates of gene effects based on joint scaling test of three and sequential best fit model for four crosses in greengram

Model	Days to 50% flowering	Days to maturity	No. of primary branches	Plant height (cm)	No.of clusters/ plant	No. of pods/ plant	Pod length (cm)	No. of seeds/ pod	100 seed wt. (g)	Protein content (%)	Harvest index (%)	Seed yield /plant (g)
Adequate $\chi^2_{(3)}$ for 3 parameter model												
5 -parameter model	3 (mdhjl) 4 (mdhil)	-	2 (mdhil) 3 (mdhil)	1 (mdhil) 4 (mdhil)	1 (mdhil)	1 (mhijl) 4 (mdhil)	2 (mdhjl)	4 (mdhil)	2 (mdhil) 3 (mdhjl) 4 (mdhil)	3 (mdhil)	1 (mdhjl) 4 (mdhil)	1 (mdhil) 2(mdhil) 3(mdhil) 4(mdhil)
Sequential fit after elimination of non significant parameters from 6 parameter model, $\chi^2_{(6-p)}$ being non-significant and tested parameters being Model significant												
4- parameter	1 (mhjl)	4 (mdhl)	4 (mdhl)	-	-	2(mhil)	-	-	-	-	-	-
3- parameter	2 (mdi)	3 (mhl)	-		3(mhl) 4(mhl)	-	1 (mhl) 4 (mdhl)	2 (mhl)	-	-	-	-
2 -parameter	-	-	-	-	-		3 (mh)	-	-	-	-	-
Digenic interaction model with $\chi^2_{(6-p)}$ non significance indicates all the three parameters tested were significant												
	-	1,2	1	2,3	2	3	-	1,3	1	1,2,4	2,3	-

1: Cross 1 (MGG 347 x KM 11-564) 2: Cross 2 (WGG 42 x RM 12-13)
3: Cross 3 (LGG 543 x KM 11-564) 4: Cross 4(MGG 347 x RM 12-13)

Table 3: Direction of dominance gene [h] and dominance x dominance [l] for various characters in 4 crosses of Greengram

Character	Gene action	Cross 1 to 4			
		1	2	3	4
Days to 50% flowering	[h]	+	-	-	-
	[l]	-	-	+	+
Days to maturity	[h]	-	-	-	-
	[l]	+	-	+	+
Number of primary branches	[h]	0	-	-	+
	[l]	0	+	+	+
Plant height (cm)	[h]	-	0	+	-
	[l]	+	0	+	+
Number of clusters/ plant	[h]	-	0	+	+
	[l]	+	0	+	+
Number of pods/ plant	[h]	+	-	-	-
	[l]	+	+	+	+
Pod length (cm)	[h]	+	+	+	+
	[l]	+	+	+	-
Number of seeds/pod	[h]	0	+	0	+
	[l]	0	-	0	+
100 Seed weight (g)	[h]	+	0	+	-
	[l]	-	0	+	+
Protein content (%)	[h]	-	0	+	0
	[l]	+	0	-	0
Harvest index (%)	[h]	+	0	0	+
	[l]	+	0	0	+
Seed yield/plant (g)	[h]	+	-	+	-
	[l]	+	+	+	-

1: Cross 1 (MGG 347 x KM 11-564)
2: Cross 2 (WGG 42 x RM 12-13)
3: Cross 3 (LGG 543 x KM 11-564)
4: Cross 4(MGG 347 x RM 12-13)

Conclusion

All the traits examined in the present study have shown complex genetic behaviour. The simple selection procedure in the early segregating generation may not contribute significantly for the improvement of these traits. The complex genetic behavior particularly additive and dominance components could be successfully exploited in later generation. It was evident from the results that the components of seed yield could be improved by exploiting both additive and non-additive types of gene effects in the present set of biological material through inter-mating of superior segregants at early generations followed by biparental mating and recurrent selection especially reciprocal recurrent selection. The transgressive segregants produced as a result of this will lead to the development of desirable high yielding genotypes of greengram.

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