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Research Article

Scrutiny of gene action underlying yield contributing traits and earliness in blackgram (*Vigna mungo* (L.) Hepper)

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Abstract

Understanding the genetic architecture of complex traits is the major thrust in plant breeding programs. Hence, the present investigation was carried out at a dry land farm of S.V. Agricultural College, Tirupati during *rabi*, 2020 to elucidate the gene action governing seed yield, yield related traits and earliness in blackgram. The experimental material consisted of six generations *viz.*, P₁, P₂, F₁, F₂, B₁ and B₂ of five blackgram crosses *viz.*, LBG-752 x TBG-104, LBG-752 x PU-31, LBG-752 x TU-40, TU-40 x TBG-104 and IPU-2-43 x TBG-104. The scaling tests suggested that the simple additive–dominance model is inadequate in elucidating gene action in all the crosses for all the traits. Generation mean analysis based on six parameter model made evident that gene interactions varied cross-wise as well as character-wise. A complementary type of epistasis was observed for majority of the yield attributing traits, while days to 50 % flowering and days to maturity had duplicate epistasis in majority of the cross combinations. High yielding and short duration blackgram varieties could be developed by exploiting both additive and non-additive gene effects in the present set of breeding material through inter-mating of desirable transgressive segregants in the early generations followed by simple pedigree selection.

Keywords: Blackgram, generation mean analysis, seed yield, earliness

INTRODUCTION

Blackgram is one of the widely grown grain legumes in India as a mixed crop, mulch crop, catch crop and inter crop highlighting the success of this crop as the best fit into multiple and intercropping systems which form the basis of a sustainable farming system. The nutritional profile of this crop underscores its potentiality to address the future food and nutritional challenges of the ever-growing population. Being a leguminous crop, blackgram potentially fixes nitrogen to an extent of 80% through biological nitrogen fixation which in turn enhances the yield of subsequent crops. Despite having all these

advantages, there is no impressive increase in the yield levels of blackgram over the past few years. The major factor back-stacking the yield enhancement of black gram is non-availability of stable high yielding varieties. In the present scenario of global climate change, matching crop maturity duration to prevailing conditions is a key strategy to avoid yield losses. Earliness not only makes the varieties fit well in different cropping windows, but also helps to escape various biotic and abiotic stresses. The selection of relevant breeding methods for the improvement of polygenic traits like yield largely depends

on the nature of gene action. For a polygenic trait like yield, a coherent understanding of the way how the genes act and interact will decide which breeding system can optimize gene action more effectively. In natural plant populations, epistatic variance is of the lowest magnitude. Over sighting or ignoring the effects of epistasis by the breeder may result in biased estimates of additive and dominance components of genetic variation that eventually would lead to faulty breeding procedures. Therefore, true knowledge on the gene actions underlying target traits is inevitable in deciding the appropriate breeding system. Generation mean analysis (Hayman, 1958) provides information about the components of genetic variation and the predominant type of gene action involved in the inheritance of traits. Available literature indicated that a few attempts were made on exploring the existence of non-allelic gene interactions in the expression of yield, yield components and earliness in blackgram. Therefore, the present work was undertaken to obtain more information on this line.

MATERIALS AND METHODS

Six generations (P_1 , P_2 , F_1 , F_2 , B_1 and B_2) of five crosses viz., LBG-752 x TBG-104, LBG-752 x PU-31, LBG-752 x TU-40, TU-40 x TBG-104 and IPU-2-43 x TBG-104 were sown in compact family block design with three replications during *rabi*, 2020 at the dry land farm of S.V. Agricultural College, Tirupati, ANGRAU. In each cross, the parents, F_1 , B_1 and B_2 generations were raised in two rows of three meter length and F_2 s were maintained in four rows following a spacing of 30 cm between the rows and 10 cm within a row. Common crop management practices like weeding, irrigation and plant protection measures were followed to maintain good crop growth. The recommended dose of chemical fertilizers (20 kg N, 40 kg P_2O_5 ha⁻¹) in the form of urea and single super phosphate were applied. Data was recorded on randomly selected ten plants in parents, F_1 s and 40 random plants in B_1 and B_2 , 80 random plants in F_2 in each entry in each replication for 12 traits.

The mean data on 12 traits obtained from six generations (P_1 , P_2 , F_1 , F_2 , B_1 and B_2) of the five crosses were subjected to generation mean analysis using six parameter model (Hayman, 1958). Before fitting models for estimating gene actions, scaling tests were performed (Mather, 1949). Data analysis was carried out using TNAU STAT (Manivannan, 2014).

RESULTS AND DISCUSSION

The mean performance of six generations of five crosses for 12 traits along with standard errors and the estimates of individual scaling tests (A, B, C and D) are presented in **Table 1**. The results pertaining to gene effects and gene action involved in the inheritance of traits are presented in **Tables 2 and 3**, respectively. There were significant differences across the generations for all the traits in all five crosses. The results of the scaling tests revealed the

significance of one or more scaling tests in all the five crosses that in turn confirms the presence of epistatic gene effects (**Table 1**). Hence, six parameter model was selected to test the presence of non-allelic interactions. The partitioning of generation means and estimation of genetic components revealed highly positive and significant mean [m] values for all the crosses.

For days to 50% flowering, positive estimates of dominance gene effects indicated that genes for late flowering dominated over genes for early flowering. The positive sign of [I] in all the crosses except LBG-752 x TU-40 suggested that selection could be practised in early segregating generations. In all the crosses except LBG-752 x PU-31 duplicate epistasis was observed for days to 50% flowering was observed. Except, IPU-2-43 x TBG-104 all the crosses expressed a duplicate type of gene action for days to maturity. Non-significant [d] effects for seed yield per plant indicated that this trait is under the control of a complex gene pathway involving several minor genes with small effects and different expressions. Seed yield per plant in all the crosses was predominantly governed by dominance and dominance x dominance interactions. The pedigree method of breeding followed by a simple selection in later segregating generations will be a meaningful breeding strategy for isolating high yielding segregants. The plausible reason behind the expression of heterosis in the crosses with complementary type of genic interaction is that [h] and [I] gene effects reinforce the effect of dominance, while the duplicate type of interaction opposes the effect of the dominance component (Bindra *et al.*, 2017).

The results of dominance [h] and dominance x dominance [I] type interactions revealed that the duplicate type of epistasis is primarily involved in controlling plant height in all the crosses except, TU-40 x TBG-104. For the number of primary branches per plant, opposite signs of [h] and [I] revealed that duplicate type of gene action in the crosses LBG-752 x TU-40 and TU-40 x TBG-104, while complementary gene action was noticed in the crosses LBG-752 x TBG-104, LBG-752 x PU-31 and IPU-2-43 x TBG-104. The number of clusters per plant recorded non-significant additive [d] gene effects in all the crosses indicating that additive gene effects do not play a major role in governing this trait. Positively significant estimates of dominance gene effects in all the crosses revealed that genes for high cluster number dominated over genes for less cluster number. Complementary epistasis was noticed for the number of clusters per plant in all the crosses except, IPU-2-43 x TBG-104 that discerned duplicate types of gene action. Duplicate type of gene action was observed for the number of pods per cluster in the crosses viz., LBG-752 x TU-40, TU-40 x TBG-104 and IPU-2-43 x TBG-104, whereas LBG-752 x TBG-104 and LBG-752 x PU-31 revealed a complementary type of non allelic interaction.

Table 1. Estimates of scaling tests for 12 characters in five crosses of blackgram

Character	Scale	LBG-752 x TBG-104	LBG-752 x PU-31	LBG-752 x TU-40	TU-40 x TBG-104	IPU-2-43 x TBG-104
Days to 50% flowering	A	1.90 ** ± 0.44	-1.65** ± 0.58	-3.09 ** ± 0.50	2.08 ** ± 0.45	1.77 ** ± 0.46
	B	-0.13 ± 0.56	-1.20* ± 0.56	-0.47 ± 0.50	1.88 ** ± 0.54	1.45** ± 0.46
	C	-3.40 ** ± 0.73	-4.70 ** ± 0.89	-3.40** ± 0.90	-0.67 ± 0.67	-1.83** ± 0.67
	D	-2.58 ** ± 0.35	-0.93** ± 0.36	0.08 ± 0.30	-2.32 ** ± 0.33	-2.53** ± 0.31
Days to maturity	A	3.50 ** ± 0.64	1.03 ± 0.54	0.45 ± 0.52	3.42 ** ± 0.45	2.43** ± 0.57
	B	3.45 ** ± 0.53	3.57 ** ± 0.55	5.05 ** ± 0.48	2.65 ** ± 0.58	1.40* ± 0.56
	C	-1.25 ± 0.69	-1.92 ± 1.03	2.53 ** ± 0.92	2.95 ** ± 0.69	7.17** ± 0.84
	D	-4.10 ** ± 0.43	-3.26 ** ± 0.48	-1.48 ** ± 0.35	-1.56 ** ± 0.39	1.67** ± 0.45
Plant height	A	6.37** ± 1.51	6.28** ± 1.04	-0.72 ± 1.18	-4.64 ** ± 1.69	6.07 ** ± 1.23
	B	5.33** ± 1.54	7.12** ± 1.22	2.08 ± 1.21	-4.31 ** ± 1.15	0.53 ± 0.97
	C	13.27** ± 2.53	15.01** ± 1.77	10.32** ± 1.79	-4.43 ± 2.27	-7.88 ** ± 1.64
	D	0.78 ± 1.14	0.81 ± 0.95	4.48 ** ± 0.99	2.26 ** ± 0.96	-7.24 ** ± 0.89
Number of primary branches per plant	A	-1.78 ** ± 0.22	-0.53* ± 0.21	-1.87 ** ± 0.20	-1.13 ** ± 0.17	-1.97 ** ± 0.20
	B	-1.57** ± 0.21	-0.45 ± 0.21	-2.00 ** ± 0.20	-1.17 ** ± 0.19	-2.50 ** ± 0.17
	C	-3.10** ± 0.34	-1.53** ± 0.33	-1.97 ** ± 0.35	-1.45 ** ± 0.31	-4.38 ** ± 0.34
	D	0.13 ± 0.14	-0.28 ± 0.14	0.95 ** ± 0.13	0.43 ** ± 0.14	0.04 ± 0.15
Number of clusters per plant	A	-9.85 ** ± 1.21	-2.67 ** ± 0.77	-5.56 ** ± 0.70	-3.83** ± 0.79	0.15 ± 0.69
	B	-10.77** ± 1.10	-3.27 ** ± 0.73	-4.00 ** ± 0.63	-4.90** ± 0.87	-1.43 ± 0.66
	C	-18.92** ± 2.08	-5.90 ** ± 0.89	-10.02 ** ± 1.06	-11.03** ± 1.40	-6.07** ± 0.98
	D	0.85** ± 0.55	0.02 ± 0.52	-0.23 ± 0.33	-1.15* ± 0.55	-2.39 ** ± 0.53
Number of pods per cluster	A	-0.67** ± 0.18	-0.35 ± 0.20	-0.90 ** ± 0.18	-0.47* ± 0.22	-1.57 ** ± 0.17
	B	-0.97** ± 0.16	-0.57** ± 0.17	-1.23 ** ± 0.18	-0.93** ± 0.20	-1.45 ** ± 0.15
	C	-2.30** ± 0.29	-0.68* ± 0.29	-0.92 ** ± 0.29	-0.87** ± 0.31	-2.42 ** ± 0.28
	D	-0.33** ± 0.11	0.12 ± 0.12	0.61 ** ± 0.11	0.27* ± 0.13	0.30 ± 0.12
Number of pods per plant	A	-27.85 ** ± 4.32	-8.90** ± 1.90	-18.18** ± 2.55	-4.63* ± 1.98	-13.48 ** ± 2.43
	B	-35.70 ** ± 4.18	-7.32** ± 1.56	-14.40 ** ± 2.51	-19.80** ± 2.12	-14.27 ** ± 2.09
	C	-67.28 ** ± 8.20	-14.68** ± 2.79	-40.33 ** ± 3.88	-24.02 ** ± 3.40	-35.32** ± 4.02
	D	-1.87 ± 1.74	0.77 ± 1.57	-3.88 ± 1.61	0.21 ± 1.63	-3.78 ± 1.53
Pod length	A	-0.93 ** ± 0.10	-1.12** ± 0.10	-0.63 ** ± 0.15	-0.32 ** ± 0.08	-0.38 ** ± 0.07
	B	-0.58 ** ± 0.07	-0.38** ± 0.07	-0.79 ** ± 0.13	-0.39 ** ± 0.09	-0.20 ± 0.09
	C	-1.97 ** ± 0.15	-0.64 ** ± 0.15	-0.87 ** ± 0.25	-0.50 ** ± 0.12	-0.31 ± 0.15
	D	-0.23 ** ± 0.05	0.43 ** ± 0.05	0.28 ** ± 0.06	0.10 ± 0.06	0.13 ± 0.07
Number of seeds per pod	A	-2.33 ** ± 0.27	-0.63* ± 0.27	-1.08** ± 0.27	-1.07 ** ± 0.27	-1.32 ** ± 0.26
	B	-1.45 ** ± 0.27	-1.60** ± 0.28	-1.40 ** ± 0.27	-0.88 ** ± 0.24	-1.33 ** ± 0.26
	C	-3.83 ** ± 0.45	-1.25* ± 0.44	-2.77 ** ± 0.46	-2.32 ** ± 0.40	-1.65 ** ± 0.44
	D	-0.03 ± 0.21	0.49** ± 0.21	-0.14 ± 0.22	-0.18 ± 0.20	0.50 ± 0.19
Seed yield per plant	A	-6.82** ± 1.29	-3.76** ± 0.60	-5.31 ** ± 0.53	-2.30** ± 0.56	-3.75** ± 0.57
	B	-9.37 ** ± 1.28	-3.61 ** ± 0.55	-4.60 ** ± 0.62	-4.00** ± 0.64	-3.69 ** ± 0.58
	C	-16.50 ** ± 2.50	-6.91 ** ± 0.92	-9.64 ** ± 0.79	-7.70 ** ± 1.03	-9.28 ** ± 0.98
	D	-0.15 ± 0.51	0.23 ± 0.49	0.14 ± 0.45	-0.69* ± 0.49	-0.92 ± 0.45
100 seed weight	A	-1.02** ± 0.14	-0.67** ± 0.12	-0.97** ± 0.15	-0.36* ± 0.15	-1.27 ** ± 0.19
	B	-0.81** ± 0.11	-1.00** ± 0.15	-1.63 ** ± 0.19	-0.73** ± 0.16	-1.92 ** ± 0.22
	C	-1.87** ± 0.19	-0.53** ± 0.19	-1.88 ** ± 0.29	-0.40 ± 0.26	-4.02 ** ± 0.31
	D	-0.02 ± 0.11	0.57** ± 0.09	0.36 ** ± 0.11	0.34** ± 0.11	-0.42 ± 0.19
Harvest index	A	-18.98 ** ± 2.02	-7.84 ** ± 1.42	-10.45** ± 1.67	-15.52** ± 1.28	-9.09 ** ± 1.90
	B	-20.98 ** ± 2.14	-8.29** ± 1.99	-11.47 ** ± 1.88	-16.32** ± 1.37	-9.32** ± 2.25
	C	-38.70 ** ± 3.82	-18.34** ± 2.62	-30.27 ** ± 3.23	-34.69** ± 2.94	-19.27** ± 3.56
	D	0.63 ± 1.21	-1.11 ± 1.44	-4.18 ** ± 0.96	-1.43 ± 1.02	-0.43 ± 1.10

*Significant at 5% level; ** Significant at 1 % level

Table 2. Estimates of gene effects for 12 characters in five crosses of blackgram

Character	Scale	LBG-752 x TBG-104	LBG-752 x PU-31	LBG-752 x TU-40	TU-40 x TBG-104	IPU-2-43 x TBG-104
Days to 50% flowering	<i>m</i>	35.66 ± 0.11	36.43 ± 0.11	34.62 ± 0.11	33.25 ± 0.09	34.97 ± 0.09
	<i>d</i>	2.30 ± 0.27	0.34 ± 0.27	1.02 ± 0.20	-1.40 ± 0.26	0.58 ± 0.23
	<i>h</i>	4.48 ± 0.77	1.65 ± 0.81	-1.49 ± 0.72	0.60 ± 0.71	2.27 ± 0.67
	<i>i</i>	5.17 ± 0.71	1.85 ± 0.72	-0.16 ± 0.60	4.63 ± 0.66	5.05 ± 0.62
	<i>j</i>	1.02 ± 0.31	-0.23 ± 0.32	-1.31 ± 0.23	0.10 ± 0.32	0.16 ± 0.28
	<i>l</i>	-6.93 ± 1.32	1.00 ± 1.43	3.71 ± 1.21	-8.60 ± 1.25	-8.27 ± 1.17
Days to maturity	<i>m</i>	73.25 ± 0.11	75.40 ± 0.19	73.98 ± 0.14	72.99 ± 0.12	76.59 ± 0.15
	<i>d</i>	1.27 ± 0.36	1.10 ± 0.27	1.63 ± 0.22	-2.75 ± 0.30	-1.82 ± 0.33
	<i>h</i>	2.42 ± 0.90	9.15 ± 1.02	4.47 ± 0.80	2.28 ± 0.82	-0.67 ± 0.94
	<i>i</i>	8.20 ± 0.86	6.52 ± 0.96	2.97 ± 0.72	3.12 ± 0.78	-3.33 ± 0.90
	<i>j</i>	0.03 ± 0.39	-1.27 ± 0.34	-2.30 ± 0.27	0.38 ± 0.35	0.52 ± 0.36
	<i>l</i>	-15.15 ± 1.60	-11.12 ± 1.51	-8.47 ± 1.26	-9.18 ± 1.40	-0.50 ± 1.56
Plant height (cm)	<i>m</i>	33.23 ± 0.42	30.28 ± 0.33	28.75 ± 0.34	27.39 ± 0.40	23.57 ± 0.31
	<i>d</i>	-0.20 ± 0.78	1.93 ± 0.67	1.46 ± 0.71	-3.60 ± 0.53	-0.02 ± 0.62
	<i>h</i>	4.68 ± 2.48	4.53 ± 1.99	-4.49 ± 2.07	5.07 ± 2.08	17.95 ± 1.56
	<i>i</i>	-1.57 ± 2.29	-1.62 ± 1.90	-8.95 ± 1.99	-4.53 ± 1.92	14.48 ± 1.78
	<i>j</i>	0.52 ± 0.89	-0.42 ± 0.71	-1.40 ± 0.78	-0.17 ± 0.63	2.77 ± 0.76
	<i>l</i>	-10.13 ± 4.04	-11.78 ± 3.23	7.59 ± 3.36	13.48 ± 3.12	-21.08 ± 3.00
Number of primary branches per plant	<i>m</i>	3.09 ± 0.04	2.83 ± 0.05	3.03 ± 0.04	3.18 ± 0.05	2.87 ± 0.06
	<i>d</i>	-0.34 ± 0.10	0.36 ± 0.09	-0.04 ± 0.08	-0.10 ± 0.08	0.34 ± 0.09
	<i>h</i>	0.08 ± 0.31	0.85 ± 0.31	-2.00 ± 0.30	-1.27 ± 0.30	0.12 ± 0.32
	<i>i</i>	-0.25 ± 0.28	0.55 ± 0.28	-1.90 ± 0.26	-0.85 ± 0.28	-0.08 ± 0.30
	<i>j</i>	-0.11 ± 0.13	-0.04 ± 0.13	0.07 ± 0.10	0.02 ± 0.11	0.27 ± 0.11
	<i>l</i>	3.60 ± 0.53	0.43 ± 0.52	5.77 ± 0.50	3.15 ± 0.47	4.55 ± 0.49
Number of clusters per plant	<i>m</i>	9.10 ± 0.21	9.93 ± 0.15	9.18 ± 0.12	8.55 ± 0.20	8.50 ± 0.18
	<i>d</i>	-0.14 ± 0.35	0.63 ± 0.43	0.25 ± 0.23	-0.25 ± 0.38	0.43 ± 0.38
	<i>h</i>	5.70 ± 1.46	4.77 ± 1.10	3.62 ± 0.82	5.28 ± 1.25	4.88 ± 1.11
	<i>i</i>	-1.70 ± 1.11	-0.03 ± 1.05	0.45 ± 0.67	2.30 ± 1.11	4.78 ± 1.06
	<i>j</i>	0.46 ± 0.44	0.30 ± 0.51	-0.78 ± 0.40	0.53 ± 0.46	0.79 ± 0.45
	<i>l</i>	22.32 ± 2.53	5.97 ± 1.95	9.11 ± 1.41	6.43 ± 2.09	-3.50 ± 1.83
Number of pods per cluster	<i>m</i>	2.76 ± 0.04	3.04 ± 0.04	3.10 ± 0.03	2.97 ± 0.04	2.95 ± 0.04
	<i>d</i>	0.09 ± 0.07	0.06 ± 0.08	0.20 ± 0.08	0.20 ± 0.10	-0.25 ± 0.08
	<i>h</i>	0.80 ± 0.25	0.02 ± 0.28	-1.15 ± 0.26	-0.57 ± 0.30	-0.05 ± 0.27
	<i>i</i>	0.67 ± 0.22	-0.23 ± 0.25	-1.22 ± 0.23	-0.53 ± 0.27	-0.60 ± 0.25
	<i>j</i>	0.15 ± 0.10	0.11 ± 0.12	0.17 ± 0.11	0.23 ± 0.13	-0.06 ± 0.10
	<i>l</i>	0.97 ± 0.42	1.15 ± 0.46	3.35 ± 0.45	1.93 ± 0.52	3.62 ± 0.43
Number of pods per plant	<i>m</i>	24.90 ± 0.66	28.27 ± 0.59	22.07 ± 0.50	26.37 ± 0.60	24.71 ± 0.59
	<i>d</i>	1.16 ± 1.13	1.76 ± 1.02	1.75 ± 1.26	1.23 ± 1.11	-1.43 ± 0.97
	<i>h</i>	30.83 ± 5.22	15.12 ± 3.22	28.38 ± 3.62	15.10 ± 3.49	16.42 ± 3.47
	<i>i</i>	3.73 ± 3.49	-1.53 ± 3.14	7.75 ± 3.22	-0.42 ± 3.27	7.57 ± 3.07
	<i>j</i>	3.93 ± 1.32	-0.79 ± 1.20	-1.89 ± 1.44	7.58 ± 1.24	0.39 ± 1.26
	<i>l</i>	59.82 ± 9.38	17.75 ± 4.95	24.83 ± 6.36	24.85 ± 5.60	20.18 ± 5.59
Pod length (cm)	<i>m</i>	4.58 ± 0.01	4.97 ± 0.01	4.68 ± 0.02	4.64 ± 0.01	4.61 ± 0.02
	<i>d</i>	0.06 ± 0.03	-0.07 ± 0.03	0.17 ± 0.04	0.18 ± 0.05	-0.17 ± 0.04
	<i>h</i>	0.59 ± 0.11	-0.59 ± 0.12	-0.70 ± 0.17	-0.57 ± 0.13	-0.22 ± 0.15
	<i>i</i>	0.45 ± 0.10	-0.86 ± 0.10	-0.55 ± 0.12	-0.21 ± 0.12	-0.26 ± 0.14
	<i>j</i>	-0.18 ± 0.05	-0.37 ± 0.05	0.08 ± 0.07	0.03 ± 0.05	-0.09 ± 0.04
	<i>l</i>	1.06 ± 0.19	2.37 ± 0.19	1.98 ± 0.31	0.92 ± 0.23	0.84 ± 0.23

Table 2. Continued..

Character	Scale	LBG-752 x TBG-104	LBG-752 x PU-31	LBG-752 x TU-40	TU-40 x TBG-104	IPU-2-43 x TBG-104
Number of seeds per pod	<i>m</i>	6.12 ^{**} ± 0.07	6.39 ^{**} ± 0.07	6.13 ^{**} ± 0.08	6.32 ^{**} ± 0.70	6.06 ^{**} ± 0.07
	<i>d</i>	-0.50 ^{**} ± 0.14	0.32 [*] ± 0.14	0.36 [*] ± 0.14	-0.33 [*] ± 0.14	0.14 ± 0.12
	<i>h</i>	0.83 ± 0.45	-0.85 ± 0.45	0.59 ± 0.47	1.03 [*] ± 0.42	-1.48 ^{**} ± 0.41
	<i>i</i>	0.05 ± 0.42	-0.98 [*] ± 0.42	0.29 ± 0.44	0.37 ± 0.40	-1.00 [*] ± 0.38
	<i>j</i>	-0.44 ^{**} ± 0.17	0.48 ^{**} ± 0.18	0.16 ± 0.17	-0.09 ± 0.16	0.01 ± 0.15
	<i>l</i>	3.73 ^{**} ± 0.73	3.22 ^{**} ± 0.72	2.20 ^{**} ± 0.73	1.58 [*] ± 0.69	3.65 ^{**} ± 0.66
Seed yield per plant (g)	<i>m</i>	6.02 ^{**} ± 0.19	6.51 ^{**} ± 0.17	5.87 ^{**} ± 0.14	5.80 ^{**} ± 0.18	5.61 ^{**} ± 0.17
	<i>d</i>	0.34 ± 0.33	0.68 ± 0.34	0.06 ± 0.35	-0.04 ± 0.32	-0.48 ± 0.30
	<i>h</i>	7.39 ± 1.57	3.94 ^{**} ± 1.03	4.72 ^{**} ± 0.95	4.42 ^{**} ± 1.05	2.97 ^{**} ± 0.98
	<i>i</i>	0.30 ± 1.03	-0.46 ± 0.98	-0.27 ± 0.92	1.39 ± 0.98	1.85 [*] ± 0.91
	<i>j</i>	1.27 ± 0.37	-0.07 ± 0.35	-0.36 ± 0.36	0.85 [*] ± 0.35	-0.03 ± 0.34
	<i>l</i>	15.89 ^{**} ± 2.84	7.83 ^{**} ± 1.66	10.19 ^{**} ± 1.63	4.92 ^{**} ± 1.67	5.59 ^{**} ± 1.56
100 seed weight (g)	<i>m</i>	4.78 ^{**} ± 0.04	4.84 ^{**} ± 0.03	4.96 ^{**} ± 0.04	4.63 ^{**} ± 0.04	3.84 ^{**} ± 0.06
	<i>d</i>	0.03 ± 0.07	0.27 ^{**} ± 0.07	0.39 ^{**} ± 0.07	0.12 ± 0.07	0.12 ± 0.13
	<i>h</i>	0.43 ^{**} ± 0.23	-1.48 ^{**} ± 0.20	-0.40 ± 0.25	-0.85 ^{**} ± 0.25	1.29 ^{**} ± 0.38
	<i>i</i>	0.04 ± 0.23	-1.14 ^{**} ± 0.19	-0.72 ^{**} ± 0.22	-0.69 ^{**} ± 0.22	0.84 [*] ± 0.38
	<i>j</i>	-0.10 ± 0.08	0.16 ± 0.08	0.33 ^{**} ± 0.10	0.19 [*] ± 0.09	0.32 [*] ± 0.13
	<i>l</i>	1.80 ^{**} ± 0.37	2.81 ^{**} ± 0.36	3.32 ^{**} ± 0.42	1.78 ^{**} ± 0.40	2.35 ^{**} ± 0.62
Harvest index (%)	<i>m</i>	32.53 ^{**} ± 0.45	33.26 ^{**} ± 0.52	32.14 ^{**} ± 0.34	32.40 ^{**} ± 0.34	32.10 ^{**} ± 0.38
	<i>d</i>	-0.51 ± 0.79	1.31 ± 0.97	-1.48 [*] ± 0.67	0.77 ± 0.76	1.49 ± 0.78
	<i>h</i>	10.12 ^{**} ± 2.95	9.82 ^{**} ± 2.98	13.64 ^{**} ± 2.42	8.42 ^{**} ± 2.16	-0.39 ± 2.72
	<i>i</i>	-1.26 ± 2.42	2.21 ± 2.88	8.36 ^{**} ± 1.93	2.85 ± 2.05	0.86 ± 2.20
	<i>j</i>	1.00 ± 0.93	0.22 ± 1.20	0.51 ± 0.77	0.40 ± 0.85	0.11 ± 1.06
	<i>l</i>	41.22 ^{**} ± 4.98	13.91 ^{**} ± 4.70	13.56 ^{**} ± 4.20	28.98 ^{**} ± 3.6	17.55 ^{**} ± 4.78

^{*}Significant at 5% level; ^{**} Significant at 1% level

Table 3. Gene action involved in the inheritance of 12 traits in five crosses of blackgram

Characters	LBG-752 x TBG-104	LBG-752 x PU-31	LBG-752 x TU-40	TU-40 x TBG-104	IPU-2-43 x TBG-104
Days to 50 % flowering	Duplicate	Complementary	Duplicate	Duplicate	Duplicate
Days to maturity	Duplicate	Duplicate	Duplicate	Duplicate	Complementary
Plant height	Duplicate	Duplicate	Duplicate	Complementary	Duplicate
Number of primary branches per plant	Complementary	Complementary	Duplicate	Duplicate	Complementary
Number of clusters per plant	Complementary	Complementary	Complementary	Complementary	Duplicate
Number of pods per cluster	Complementary	Complementary	Duplicate	Duplicate	Duplicate
Number of pods per plant	Complementary	Complementary	Complementary	Complementary	Complementary
Pod length	Complementary	Duplicate	Duplicate	Duplicate	Duplicate
Number of seeds per pod	Complementary	Duplicate	Complementary	Complementary	Duplicate
Seed yield per plant	Complementary	Complementary	Complementary	Complementary	Complementary
100- seed weight	Complementary	Duplicate	Duplicate	Duplicate	Complementary
Harvest index	Complementary	Complementary	Complementary	Complementary	Duplicate

For the number of pods per plant, none of the crosses exhibited significant additive [*d*] gene effects suggesting the meagre role of additive gene action. Positively

significant dominance [*h*] gene effects in all the crosses indicated that genes for more number of pods per plant were dominant over less number of pods per plant.

The presence of positive estimates of $[h]$ indicates that selection should be delayed until heterozygosity is reduced in the population. A higher magnitude of dominance effects than additive effects suggests that the number of pods per plant can be improved through a conventional breeding approach such as pedigree or bulk or single seed descent method. The predominance of complementary types of non allelic gene interaction was evident in all the crosses for the number of pods per plant. The pedigree method of breeding followed by a simple selection in later segregating generations will be a meaningful breeding strategy to be followed to obtain desirable segregants with more pod bearing ability.

The $[h]$ and $[l]$ components took opposite signs (Duplicate gene action) for pod length in all the crosses except, LBG-752 x TBG-104. For the number of seeds per pod, a complementary type of gene action played a predominant role in the crosses LBG-752 x TBG-104, LBG-752 x TU-40 and TU-40 x TBG-104, while duplicate gene action was noticed in the crosses LBG-752 x PU-31 and IPU-2-43 x TBG-104. For the trait 100 seed weight, the opposite signs of $[h]$ and $[l]$ for the crosses LBG-752 x PU-31, LBG-752 x TU-40 and TU-40 x TBG-104 revealed the existence of a duplicate type of gene action, whereas the crosses LBG-752 x TBG-104 and IPU-2-43 x TBG-104 exhibited the involvement of complementary type of gene action. All the crosses except IPU-2-43 x TBG-104 displayed the predominance of complementary type of gene action for harvest index.

The presence of both positive or negative signs of additive \times additive $[l]$ for most of the traits revealed association and dispersion of alleles in parents, respectively. The predominance of duplicate gene action for days to 50% flowering was reported by Rao *et al.* (1984), Lalitha (2003), Bindra *et al.* (2017), Prasad and Murugan (2021) and Vadodariya *et al.* (2020). The preponderance of complementary epistasis for days to 50% flowering was reported by Bindra *et al.* (2017) and Panigrahi *et al.* (2020). Rao *et al.* (1984), Chakraborty and Borua (1998), Lalitha (2003) and Vadodariya *et al.* (2020) registered duplicate gene action for days to maturity, while the preponderance of complementary epistasis for days to maturity was reported by Bindra *et al.* (2017) and Panigrahi *et al.* (2020). Ranwah and Sharma (2000), Kant and Srivatsava (2012) reported the presence of a duplicate type of gene action for clusters per plant, whereas Chakraborty and Borua (1998), Vadivel *et al.* (2019), Panigrahi *et al.* (2020) and Prasad and Murugan (2021) documented the existence of complementary epistasis. Dahiya and Waldia (1982) and Haque *et al.* (2013) recorded a predominance of duplicate epistasis for pods per plant, while complementary epistasis was reported by Kant and Srivatsava (2012). Vadivel *et al.* (2019) and Prasad and Murugan (2021) reported the existence of a complementary type of epistasis for seed yield. Lalitha (2003), Panigrahi *et al.* (2020) and Sinha *et al.* (2020) registered duplicate gene action for seed yield.

In the present study, the presence of a complementary type of epistasis was observed for majority of the yield attributing traits indicating that the parents selected in the present study are diverse. Days to 50 % flowering and maturity had duplicate epistasis in almost all the crosses. Duplicate epistasis hinders the improvement through selection as it decreases the variation in F_2 and subsequent generations. Hence, the selection should be postponed till a high level of gene fixation is attained.

The results showed that genic interactions varied cross-wise as well as trait-wise. Hence, a specific breeding strategy has to be implemented for each cross for effective improvement. All the traits examined in the present study have shown complex genetic behavior. The results of this study showed that as a consequence of the higher magnitude of gene interactions, the non-fixable gene effects were higher than the fixable indicating the major role of non-additive gene effects. By and large, based on generation mean studies, we can conclude that the simple selection in the early segregating generations may not significantly contribute towards the improvement of these crosses for our target traits. Therefore, the successful breeding strategy will be the one, which can pool up genes to form superior gene constellations interacting in a favorable manner. For effective selection, recurrent selection followed by a modified pedigree method as well as intermating of superior lines in segregating generations will be useful. The desirable segregants produced from these crosses may lead to the development of short duration and high yielding blackgram varieties that fit well into different ecological niches.

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