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Deciphering the Inter Allelic Interactions for Yield Components and Urdbean Leaf Crinkle Disease Resistance in Black Gram [*Vigna mungo* (L.) Hepper] using Generation Mean Analysis

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ABSTRACT

Background: Urdbean leaf crinkle disease (ULCD) caused by urdbean leaf crinkle virus (ULCV) is one of the destructive viral diseases for black gram cultivation. Development of resistant cultivars along with higher yield is the most efficient and cheapest way to alleviate the prevalence of ULCD. But for which understanding of inheritance of complex quantitative traits along with ULCD resistance is essential. Proper understanding of genetic architecture of complex traits can be obtained by using six-parameter model of generation mean analysis.

Methods: Four diverse parents (VBN 8, DKU 87, LBG 623 and LBG 787) together with their six F_1s (obtained during *rabi*, 2021-22), six BC_1s, six BC_2s and six F_2s (obtained during *summer*, 2022) were evaluated for yield components in *kharif*, 2022 and *rabi*, 2022-23 and for ULCD during *rabi,* 2022-23 and *late rabi*, 2022-23 at Agricultural College Farm, Bapatla, Andhra Pradesh for estimation of components of gene effects controlling various traits.

Result: Additive-dominant model is inadequate for nine traits out of ten studied quantitative traits including ULCD except test weight. Dominant × Dominant [*l*] type of epistatic interaction, is predominant among the operating non-allelic interactions. Duplicate epistatic interaction in the inheritance is evident at least in few crosses for eight traits (Days to maturity, plant height, branches per plant, clusters per plant, pods per plant, pod length, seeds per pod and grain yield per plant).

Key words: Duplicate epistasis, Generation mean analysis, Non-allelic interactions, ULCD.

INTRODUCTION

Black gram [*Vigna mungo* (L.) Hepper] is a prominent annual legume crop with short duration. Among the pulses, black gram is one of the significant crop in India (Singh *et al*., 2022). This crop can be grown under different agro-climatic conditions and adapts well to drier regions of the tropics. It is the fourth most important pulse crop with 13% of area and 10% pulse production in India (Shashidhar *et al*., 2020). Among various biotic factors, the black gram crop is more susceptible to urdbean leaf crinkle virus (ULCV) which causes leaf crinkle disease and is a predominant disease which devastates the cultivation of blackgram. This disease has become one of the major production constraints in blackgram especially during *rabi* and *summer* under uplands and rice fallow situations. The causal agent is reported to be transmitted by whitefly, aphid, seed, sap (Palanivelu *et al*., 2021) and grafting (Kolte and Nene, 1972). Among the insect vectors, the virus was effectively transmitted by aphid, *Aphis craccivora* in a non-persistent manner and whitefly, *Bemisia tabaci*. The per cent transmission by aphids (83.3%) was higher compared to whiteflies (66.6%) (Sravika *et al*., 2018). Yield losses due to Urdbean Leaf Crinkle Disease (ULCD) ranges from 62-100% depending on the genotype, location, infection time and cropping season. Hence, for developing improved genotypes along with ULCD resistance, information on inheritance of yield components and resistance to ULCD need to be generated.

In any crop improvement programme, information on kind of gene action for various quantitative traits (QTs) helps in formulation of effective breeding strategies. Among various biometrical techniques which provides the estimates of gene action, Generation Mean Analysis proposed by Hayman and Mather (1955) and Mather (1949), is a useful technique in estimating the gene effects for quantitative traits. It provides unbiased estimates of additive [*d*] and dominant [*h*] genetic components and also has greatest merit in providing the information regarding

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epistatic or non-allelic or inter-allelic gene affects. Hence in present study, six parameter model of generation mean analysis was employed to estimate gene effects for ten yield related traits and resistance to ULCD.

MATERIALS AND METHODS

Experimental material

Four diverse black gram genotypes *viz*., VBN 8 (Resistant to ULCD), DKU 87 (Highly resistant to ULCD), LBG 623 (Highly susceptible to ULCD) and LBG 787 (Highly susceptible to ULCD) are selected (Barathi *et al*., 2023) and all possible single crosses without reciprocals were carried out during *rabi,* 2021-22 to obtain six F_1s [n(n-1)/2]. The six F_1s of the six crosses were back crossed to their respective parents and obtained six BC_1s (F_1 back crossed with first/female parent) and six BC_2s (F_1 backcrossed with second/male parent) during s*ummer*, 2022. Further, the six F_1s were selfed in the same season to obtain two sets of six F_2s. A total of 150 seed per each F_1 and 120 seed per each back cross were obtained to perform generation mean analysis. The analysis was carried out for each of the six crosses separately and the results were presented.

Experimental layout and screening for ULCD

The present experiment was executed at Agricultural College Farm, Bapatla, Andhra Pradesh, India which is located at 15.54°N latitude, 80.47°E longitude and 5.49 m altitude. Two separate generation mean analysis experiments were taken up to find out the gene actions pertaining to yield components and ULCD. First experiment of generation mean analysis for yield components was conducted to assess the gene effects for yield components during two seasons *viz*., *kharif*, 2022 and *rabi*, 2022-23. For which with all the six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the six crosses were sown in a randomized complete block design with two replications. The populations *viz*., P_1, P_2, F_1s, BC_1 and BC_2 were grown in two rows and F_2s of eight rows with four meter row length by adapting a spacing of 30×10 cm. The data on the ten traits *viz*., days to 50% flowering, days to maturity, plant height, branches per plant, clusters per plant, pods per plant, pod length, seeds per pod, test weight and grain yield per plant were collected on ten randomly chosen plants per replication in P_1, P_2 and F_1s. Data was collected on 20 plants per generation per replication in BC_1 and BC_2. Similarly, data on 100 plants per each F_2 generation per replication were also recorded.

The second experiment of generation mean analysis was conducted for ULCD resistance during two seasons *viz*., *rabi*, 2022-23 and late *rabi*, 2022-23 separately. Different *in vitro* screening methods like leaf disc method and pollen bio assay (Babu and Ravikumar, 2010) were available for screening against different biotic stresses. However, screening under natural disease conditions with a susceptible check is the best method. The second experiment was conducted in similar fashion as that of first experiment under natural conditions using a susceptible check without spraying insecticides during the entire cropping period in order to maintain the natural whitefly, aphids and beetle populations in the field. For every two rows of each entry susceptible check (LBG 623) was sown. Scoring was done by modifying the scale of Bashir *et al*. (2005). Disease was scored on individual plant basis only and not as per cent plants infected. In homogeneous populations *i.e*., P_1, P_2 and F_1 the plant which is showing maximum infection was considered for scoring of the respective population. However, in heterogenous populations (BC_1, BC_2 and F_2) disease on individual plants was scored. Susceptible check had a disease score of '5' (on a 1-5 scale) by the 45th day *i.e*., the day on which scoring was done on all the entries.

Statistical analysis

The data collected on the ten yield components and ULCD scores over two seasons were subjected to pooled ANOVA after validating the homogeneity of error variance through the Bartlett test (Gomez and Gomez, 1984) and subjected to generation mean analysis as per Singh and Choudhary (2010). Adequacy of additive-dominance model was tested using the four scaling tests (A, B, C and D) as suggested by Mather (1949). Joint Scaling test (Cavalli, 1952) was also employed and Additive-Dominance model was considered inadequate only when any one of the scaling test among the four scaling tests appeared to deviate significantly from zero and calculated chi-square value is significantly more than the table value. Once the inadequacy of additive-dominance model was observed, the six genetic parameters *viz*., mean [*m*], additive effect [*d*], dominant effect [*h*], Additive × Additive [*i*] effect, Additive × Dominant [*j*] and Dominant × Dominant [*l*] effects were estimated using six-parameter model of generation mean analysis (Hayman, 1958). To test the significance of both scaling tests and the genetic parameters, student t-test was used. While, chi-square test (Cavalli, 1952) was used to test the significance of Cavalli's joint scaling test.

RESULTS AND DISCUSSION

The generation mean analysis helps to understand the role of epistatic interactions in the expression of yield and its component characters, which is not possible with line × tester analysis or diallel analysis alone. Mean performance of six generations of six crosses for ULCD disease scores and yield components were indicated in the supplementary material.

Scaling tests and Cavalli's Joint scaling test

The overall results of generation mean analysis revealed that additive-dominant model is adequate only for a single trait *i.e*. test weight (Fig 1). All the other nine traits *viz.,* days to 50% flowering, plant height, branches per plant, clusters per plant, days to maturity, pods per plant, pod length, seeds

per pod, grain yield per plant and reaction to ULCV had significance for one or more scaling tests *viz*., A, B, C and D and also had significant chi-square values of joint scaling tests. This clearly indicated the inadequacy of additive-dominant model in explaining the inheritance of these traits emphasizing the complex nature of inheritance, indicating simple selection procedures may not be sufficient to improve the above yield and its contributing traits. Hence, the estimates of inter-allelic or non-allelic gene effects ([*i*], [*j*] and [*l*]) were obtained using six parameter model of generation mean analysis. Ayesha and Babu (2023) also reported adequacy for additive-dominant model for test weight and inadequacy for various yield traits.

Estimates of inter-allelic interactions Urdbean Leaf Crinkle Virus (ULCV) resistance

From Table 1, it was evident that the estimates of dominant × dominant [*l*] kind of gene effects are significant and higher in magnitude than that of both additive [*d*] and additive × additive [*i*] estimates in four crosses *viz*., VBN 8 × LBG 623, VBN 8 × LBG 787, DKU 87 × LBG 623 and DKU 87 × LBG 787 indicating the predominance of dominant × dominant [*l*] type of inter-allelic interactions in the inheritance of this character in these crosses. Though, additive and additive × additive gene effects are significant in three crosses (VBN 8 × LBG 623, VBN 8 × LBG 787 and DKU 87 × LBG 787) along with additive × dominant effects

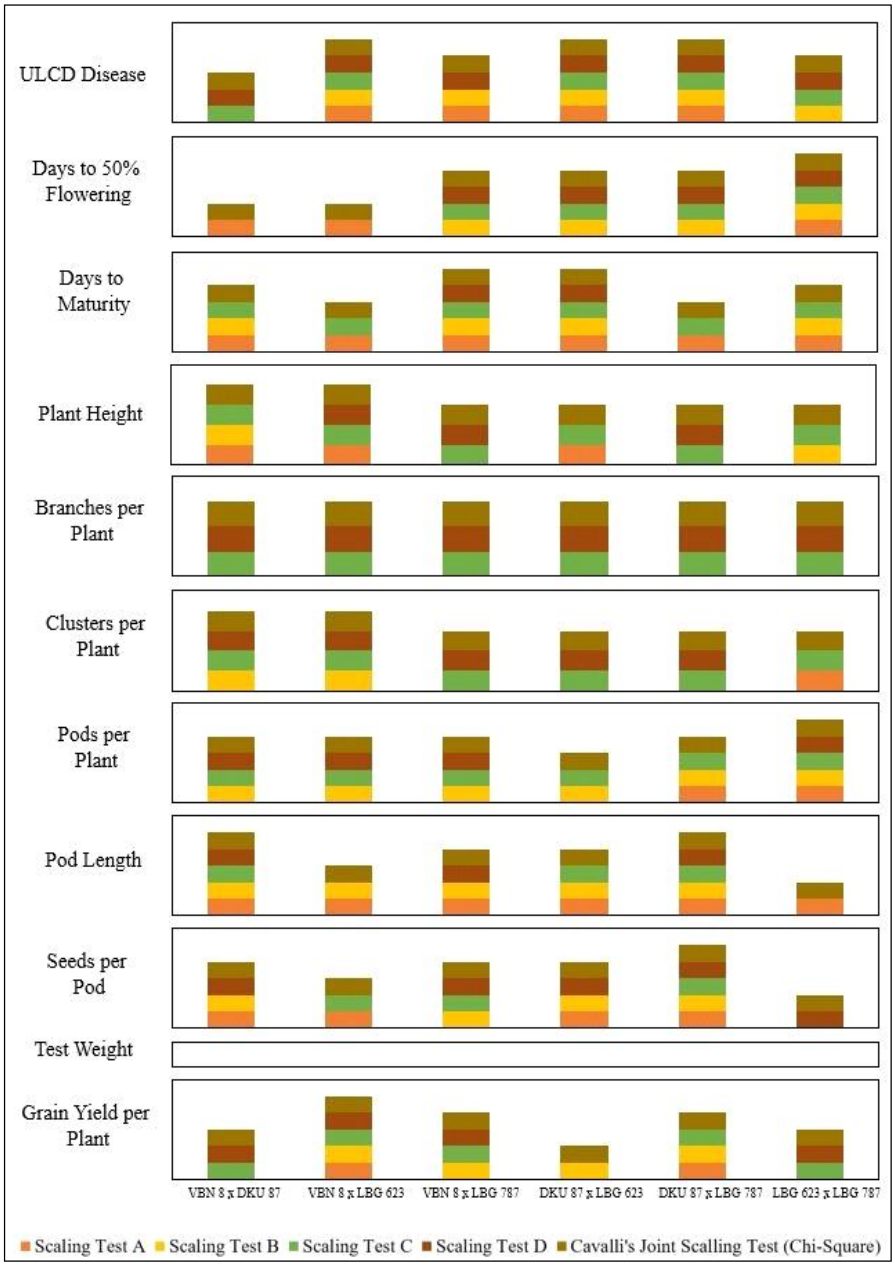

Fig 1: Significant estimates of Scaling tests and Joint scaling test of six crosses for ULCD and yield components.

Table 1: Estimates of components of gene effects and type of epistasis for ULCD and yield components.

Cross	m	d	h	i	j	l	Epistasis
Urdbean leaf crinkle disease (ULCD)							
VBN 8 × DKU 87	0.85±0.04**	0.33±0.13*	-1.68±0.32**	-1.25±0.30**	-0.15±0.14	0.75±0.58	-
VBN 8 × LBG 623	2.30±0.14**	-2.13±0.17**	0.67±0.64	2.67±0.63**	-0.23±0.17	-6.52±0.87**	-
VBN 8 × LBG 787	2.32±0.13**	-2.28±0.23**	0.94±0.69	2.79±0.68**	-0.38±0.23	-6.54±1.06**	-
DKU 87 × LBG 623	2.17±0.15**	-2.80±0.19**	0.74±0.71	2.94±0.70**	-0.50±0.20*	-9.14±0.98**	-
DKU 87 × LBG 787	2.19±0.14**	-2.68±0.28**	0.62±0.80	2.79±0.79**	-0.45±0.29	-8.79±1.27**	-
LBG 623 × LBG 787	4.97±0.02**	-0.38±0.09**	-1.18±0.25**	-1.13±0.20**	-0.43±0.12**	0.88±0.48	-
Days to 50% flowering							
VBN 8 × DKU 87	40.13±0.21**	1.73±0.37**	-1.25±1.13	-0.07±1.12	1.65±0.38**	-1.63±1.75	-
VBN 8 × LBG 623	40.69±0.22**	0.80±0.56	2.81±1.46	2.66±1.44	1.05±0.58	-6.36±2.47*	-
VBN 8 × LBG 787	41.41±0.14**	-0.40±0.20*	-3.72±0.79**	-3.04±0.68**	-0.47±0.29	0.19±1.24	-
DKU 87 × LBG 623	41.13±0.12**	-1.30±0.27**	-2.57±0.80**	-2.72±0.72**	-1.35±0.34**	1.62±1.36	-
DKU 87 × LBG 787	38.42±0.15**	1.08±0.52*	4.39±1.28**	4.89±1.20**	1.23±0.58*	-3.64±2.35	-
LBG 623 × LBG 787	41.13±0.09**	0.83±0.17**	0.28±0.64	1.03±0.49*	1.08±0.30**	-6.88±1.11**	-
Days to maturity							
VBN 8 × DKU 87	80.30±0.13**	1.30±0.36**	3.17±0.92**	-1.38±0.90	0.25±0.37	-8.92±1.59**	D
VBN 8 × LBG 623	81.78±0.32**	0.58±0.70	1.08±1.93	-1.07±1.90	3.23±0.72**	-5.68±3.14	-
VBN 8 × LBG 787	81.35±0.30**	0.05±0.70	6.85±1.89**	4.60±1.86*	2.05±0.73**	-17.70±3.14**	D
DKU 87 × LBG 623	81.24±0.23**	-1.33±0.44**	-0.92±1.30	-2.89±1.28*	1.65±0.46**	-7.11±2.04**	-
DKU 87 × LBG 787	79.38±0.26**	-0.98±0.87	2.38±2.03	0.33±2.02	1.93±0.88*	-5.68±3.66	-
LBG 623 × LBG 787	82.03±0.28**	0.77±0.79	-1.97±1.95	-0.37±1.94	0.27±0.81	-8.58±3.40*	-
Plant height							
VBN 8 × DKU 87	42.80±0.38**	-3.91±0.71**	8.76±2.08**	-0.74±2.07	-9.43±0.71**	-12.40±3.25**	D
VBN 8 × LBG 623	47.06±0.40**	-3.60±1.71*	-11.3±23.77**	-14.29±3.76**	-0.13±1.71	21.21±7.02**	D
VBN 8 × LBG 787	48.02±0.27**	0.20±1.52	-30.02±3.23**	-31.24±3.22**	-0.87±1.52	29.18±6.18**	D
DKU 87 × LBG 623	44.78±0.43**	-1.94±1.19	9.55±2.95**	2.32±2.93	6.91±1.21**	-16.54±5.10**	D
DKU 87 × LBG 787	39.82±0.27**	-3.52±1.11**	-5.06±2.50*	-10.64±2.47**	1.43±1.13	9.34±4.63**	D
LBG 623 × LBG 787	48.11±0.39**	-0.61±0.99	10.71±2.55**	4.35±2.54	-4.91±1.02**	-15.59±4.31**	D
Branches per plant							
VBN 8 × DKU 87	3.06±0.09**	0.08±0.22	2.68±0.61**	2.13±0.59**	0.03±0.24	-1.18±1.03	-
VBN 8 × LBG 623	3.28±0.10**	-0.20±0.31	2.38±0.76**	2.08±0.73**	-0.15±0.34	-2.08±1.35	-
VBN 8 × LBG 787	3.02±0.10**	0.33±0.29	2.45±0.75**	2.17±0.69**	0.15±0.32	-2.17±1.35	-
DKU 87 × LBG 623	3.21±0.10**	-0.13±0.29	2.16±0.74**	2.01±0.69**	-0.03±0.33	-2.16±1.31	-
DKU 87 × LBG 787	3.14±0.09**	0.18±0.22	1.61±0.65*	1.31±0.56*	0.07±0.26	-0.96±1.14	-
LBG 623 × LBG 787	3.18±0.09**	0.13±0.22	2.93±0.63**	2.53±0.57**	-0.08±0.26	-2.98±1.11**	D
Clusters per plant							
VBN 8 × DKU 87	10.17±0.18**	1.55±0.58**	6.59±1.38**	5.04±1.37**	0.95±0.59	-3.24±2.47	-
VBN 8 × LBG 623	9.71±0.19**	0.90±0.57	7.86±1.39**	6.56±1.37**	-0.60±0.57	-8.56±2.43**	D

Table 1: Continue...

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VBN 8 × LBG 787	8.40±0.20**	0.78±0.64	13.30±1.54**	12.05±1.51**	0.38±0.66	-10.80±2.75**	D
DKU 87 × LBG 623	7.87±0.21**	1.05±0.59	6.54±1.46**	6.42±1.45**	0.18±0.60	-5.77±2.54*	D
DKU 87 × LBG 787	9.72±0.26**	-0.35±0.68	6.27±1.73**	4.64±1.72**	-0.28±0.69	-2.39±2.95	-
LBG 623 × LBG 787	9.15±0.23**	-2.25±0.46**	-0.23±1.31	-0.78±1.29	-1.25±0.48*	4.88±2.09*	-
Pods per plant							
VBN 8 × DKU 87	32.14±0.49**	8.28±1.24**	9.61±3.17**	7.91±3.16*	6.83±1.24**	2.84±5.34	-
VBN 8 × LBG 623	33.27±0.56**	-4.10±1.77*	11.99±4.19**	13.74±4.18**	-10.20±1.77**	-39.6±47.43**	D
VBN 8 × LBG 787	33.08±0.57**	2.53±1.33	18.78±3.53**	16.25±3.51**	3.90±1.35**	-3.25±5.85	-
DKU 87 × LBG 623	30.88±0.48**	7.33±0.90**	10.20±2.65**	4.75±2.62	2.48±0.93**	-3.10±4.15	-
DKU 87 × LBG 787	32.89±0.67**	4.03±1.19**	3.26±3.60	6.11±3.58	6.98±1.21**	-0.06±5.51	-
LBG 623 × LBG 787	30.32±0.69**	-0.48±1.24	19.77±3.74**	16.57±3.70**	7.23±1.27**	-17.02±5.78	D
Pod length							
VBN 8 × DKU 87	4.80±0.05**	0.35±0.07**	-0.30±0.25	-0.87±0.24**	-0.60±0.08**	0.51±0.38	-
VBN 8 × LBG 623	5.00±0.02**	-0.16±0.06*	0.36±0.17*	-0.04±0.16	-0.39±0.07**	0.38±0.29	-
VBN 8 × LBG 787	4.89±0.02**	-0.18±0.06**	-0.44±0.16**	-0.37±0.15*	-0.38±0.07**	0.70±0.28*	D
DKU 87 × LBG 623	4.83±0.03**	-0.18±0.06**	0.73±0.18**	-0.13±0.16	0.49±0.07**	-1.61±0.31**	D
DKU 87 × LBG 787	4.69±0.04**	-0.15±0.07*	1.57±0.23**	0.80±0.21**	0.58±0.08**	-2.90±0.36**	D
LBG 623 × LBG 787	4.94±0.06**	0.23±0.10*	0.08±0.33	-0.33±0.32	0.27±0.10**	0.31±0.49	-
Seeds per pod							
VBN 8 × DKU 87	6.73±0.10	-0.13±0.10	3.51±0.47**	2.53±0.47**	-1.05±0.12**	-5.53±0.61**	D
VBN 8 × LBG 623	7.08±0.08	-0.05±0.23	0.55±0.57	-0.40±0.57	-0.25±0.24	2.00±1.00*	-
VBN 8 × LBG 787	7.33±0.05	-0.30±0.13*	-0.90±0.32**	-1.12±0.32**	-0.57±0.18**	0.27±0.64	-
DKU 87 × LBG 623	6.69±0.11	-0.30±0.13*	2.37±0.49**	1.44±0.49**	0.18±0.17	-3.69±0.73**	D
DKU 87 × LBG 787	6.92±0.09	-0.27±0.15	1.92±0.46*	0.97±0.46*	0.33±0.23	-3.32±0.80**	D
LBG 623 × LBG 787	7.10±0.07	0.23±0.25	-1.01±0.57**	-1.63±0.57**	0.10±0.30	2.63±1.14*	-
Test weight							
VBN 8 × DKU 87	4.34±0.04**	0.42±0.23	-0.58±0.50	-0.56±0.49	0.26±0.24	1.50±0.95	-
VBN 8 × LBG 623	4.72±0.07**	-0.35±0.28	0.30±0.62	0.50±0.61	-0.24±0.28	-1.63±1.16	-
VBN 8 × LBG 787	4.43±0.03**	0.11±0.09	-0.48±0.25	-0.10±0.22	0.10±0.11	0.03±0.45	-
DKU 87 × LBG 623	4.36±0.04**	-0.23±0.12	0.40±0.30	0.45±0.28	-0.05±0.13	-0.57±0.54	-
DKU 87 × LBG 787	4.34±0.06**	-0.20±0.20	-0.04±0.47	0.28±0.45	0.01±0.20	-0.54±0.85	-
LBG 623 × LBG 787	4.73±0.03**	-0.05±0.10	-0.18±0.27	-0.28±0.24	-0.07±0.14	0.86±0.49	-
Grain yield per plant							
VBN 8 × DKU 87	7.01±0.21**	0.76±1.56**	7.44±1.56**	8.11±1.55**	0.03±0.66	-10.37±2.76**	D
VBN 8 × LBG 623	6.74±0.23**	-0.35±1.35**	4.63±1.35**	4.48±1.34**	-2.05±0.49**	-4.27±2.16*	D
VBN 8 × LBG 787	8.04±0.23**	0.21±1.33	2.42±1.33	2.68±1.32*	0.02±0.47	-0.81±2.13	-
DKU 87 × LBG 623	6.87±0.22**	1.08±1.32	-1.08±1.32	-1.41±1.32	0.11±0.50	4.50±2.17*	-
DKU 87 × LBG 787	7.57±0.22**	-0.60±1.31	0.26±1.31	0.07±1.31	-0.09±0.49	4.36±2.16*	-
LBG 623 × LBG 787	6.74±0.17**	-0.31±1.89**	5.07±1.85*	4.52±1.85*	1.17±0.86	-4.38±3.59	-

*and** represents 5% and 1% level of significance, respectively, D= Duplicate epistasism= Mean; d= Additive; h= Dominant; i= Additive × Additive; j= Additive x Dominant; l = Dominant × Dominant.

in one cross (DKU 87 × LBG 623), dominant × dominant gene effects overpower (because of their higher magnitude of estimates, Fig 2) them in the above crosses. In presence of such dominant × dominant type of inter-allelic interaction population approach in self-pollinated crops proposed by Palmer (1953) which is similar to recurrent selection in cross pollinated crops or biparental mating followed by conventional selection in the later generations should be adopted for identifying desirable segregants.

Estimates of inter-allelic interactions for yield and yield components

The trait wise observations of inter-allelic interactions divulged that days to 50% flowering is under control of dominant × dominant [*l*] type of inter-allelic interaction in two crosses; additive × dominant [*j*] kind in one cross and additive × additive [*i*] type of interaction in three crosses. In four of the six crosses, dominant × dominant [*l*] interaction appeared to be important in the inheritance of days to maturity and in the remaining two crosses additive × dominant [*j*] kind of interaction was significant. The inheritance of plant height is determined by dominant × dominant [*l*] type of epistasis in four crosses; and additive × additive [*i*] type of inter-allelic interaction in two crosses (Table 1; Fig 2).

Inheritance of branches per plant is under the control of [*l*] component in one cross; and [*i*] component of inter-

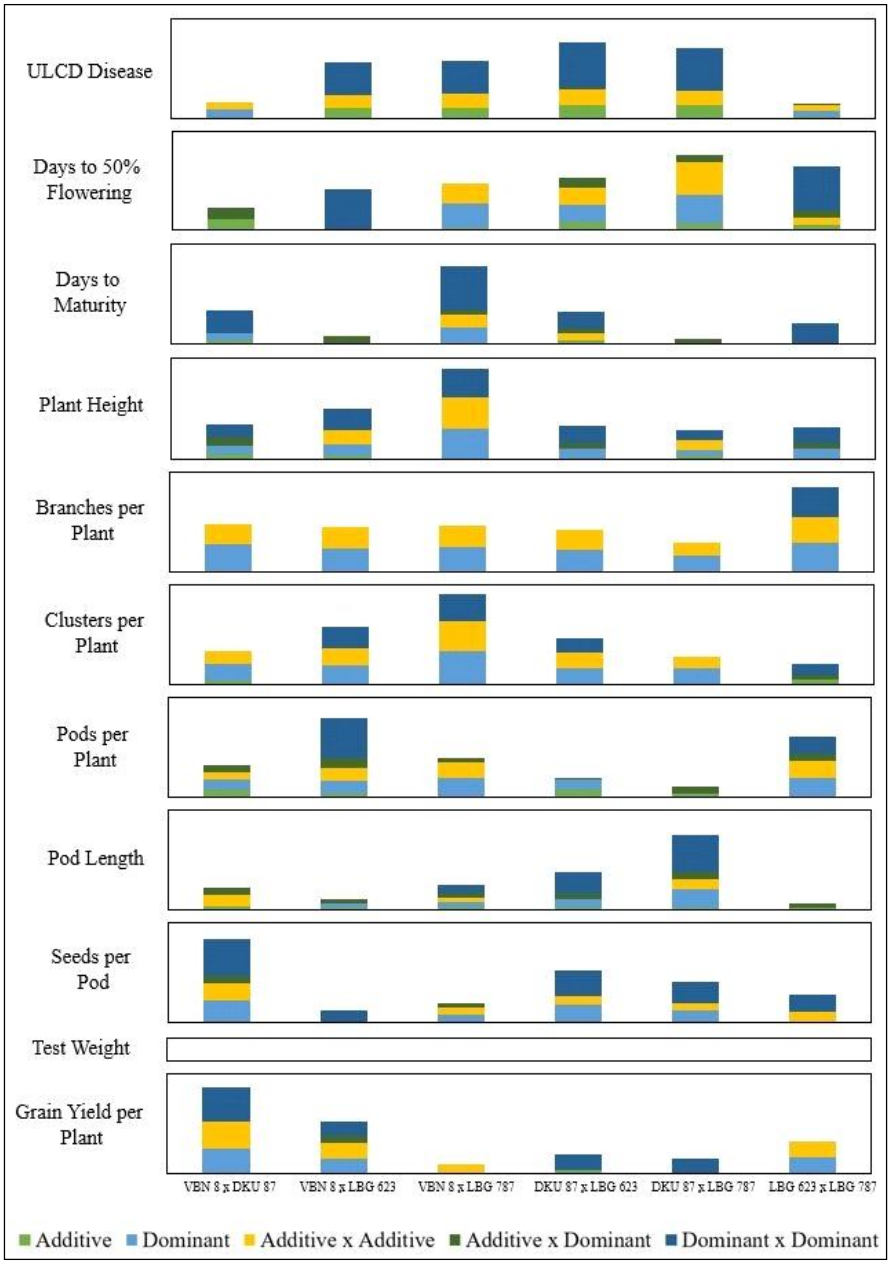

Fig 2: Estimates of gene effects of ULCD and yield components for six crosses.

allelic interactions in five crosses. The inheritance of clusters per plant in two of the six crosses is under the control of [*l*] type of inter-allelic interactions; and four crosses under [*i*] type of gene effects. The inheritance of pods per plant is determined by dominant × dominant [*l*] type of epistasis in two crosses; additive × additive [*i*] type of epistasis in two other crosses and additive × dominant [*j*] type of epistasis in remaining two crosses. Pod length is under control of dominant × dominant [*l*] type of interaction in three crosses; additive × dominant [*j*] type of interaction in two crosses and additive × additive [*i*] type of interaction in one cross (Table 1; Fig 2).

The inheritance of seeds per pod is determined by dominant × dominant [*l*] type of epistasis in five crosses; and additive × additive [*i*] kind of interaction in one cross. The trait grain yield per plant is inherited by dominant × dominant [*l*] type of inter-allelic interaction in three crosses and additive × additive [*i*] type of non-allelic component in the remaining three crosses (Table 1; Fig 2).

In spite of having significant additive [*d*] and dominance [*h*] components, epistatic gene effects were predominant (due to their higher estimates) and hence had a great role in the inheritance of these ten traits. The existing dominant × dominant type of inter-allelic interaction [*l*] in few of the crosses for various traits can be exploited by breeding methods like biparental mating followed by conventional selection or population approach as applicable in self-pollinated crops (Palmer, 1953). For exploiting additive × dominant [*j*] type of interactions, the successful breeding method would be recurrent selection. Hence, Diallel Selective Mating Scheme (DSMS) proposed by Jensen (1970) might prove to be an effective approach. The additive × additive [*i*] gene effects which are fixable, can be exploited using breeding methods like pedigree, bulk, single seed descent method, *etc*., where hybridization followed by selection and transgressive segregants are targeted.

Detection of type of epistasis

Significant estimates of dominant [*h*] and dominant × dominant [*l*] components with opposite signs indicates the presence of duplicate type of epistasis, whereas similar signs of [*h*] and [*l*] indicate the presence of complementary gene action. In the present study, two crosses for days to maturity; all the six crosses for plant height; one cross for branches per plant; three crosses for clusters per plant; two crosses for pods per plant; three crosses for pod length; three crosses for seeds per pod; and two crosses for grain yield per plant had significant [*l*] and [*h*] estimates with contrasting signs revealing the existence of duplicate type of epistasis (Table 1).

The control of duplicate type of epistasis in the inheritance is evident at least in few crosses for eight different traits that had inadequacy for additive-dominant model. This duplicate type of epistasis will reduce the variation in F_2 and subsequent generations, consequently hinders the pace of the progress through selection. Therefore, the best strategy to counter this duplicate epistasis is to go for intermating in early segregating generations (for breaking undesirable linkages) and postpone the selections to the later generations. The observed differences in the crosses in terms of gene action for the same trait could be attributed to change in gene frequencies and proportion of dominant and recessive genes possessed by the parents involved in the crosses (Viana *et al*., 1999). Similar utilization of generation mean analysis to estimate gene effects were earlier reported in balck gram (Ayesha and Babu, 2023; Soharu *et al*., 2023; Bindra *et al*., 2017).

CONCLUSION

The significance of scaling and Joint Scaling tests indicated the inadequacy of Additive-Dominant model for all most all traits including ULCD, which reveals the importance of non-allelic interactions in the inheritance of majority of traits. Finally, from the results of six parameter model of generation mean analysis it can be culminated that gene interactions varied cross wise as well as trait wise. The observed differences in the crosses in terms of gene action for the same trait could be attributed to change in gene frequencies and proportion of dominant and recessive genes possessed by the parents involved in the crosses. Hence, specific breeding strategy has to be adopted in particular cross for a particular trait depending up on the kind of gene effects operating, for overall improvement of yield and its contributing traits.

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Conflict of interest

All authors declared that there is no conflict of interest.

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