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Gene Effects of Quantitative Traits through Six Parameter Model of Generation Mean Analysis in Black Gram [V*igna mungo* (L.) Hepper]

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ABSTRACT

Background: Yellow mosaic disease (YMD) caused by Mungbean Yellow Mosaic Virus (MYMV) is one of the most destructive biotic constraints for production in urdbean. Development and introduction of resistant cultivars with high seed yield is considered as the most economical and eco-friendly option to manage YMD, for which understanding the gene action controlling the inheritance of different traits along with YMD resistance is an important requirement.

Methods: Material comprised of four diverse genotypes (TU 94-2, PU 31, IPU 94-1 and LBG 623), six F_1s, six BC_1s and six BC_2s and six F_2s. These six generations of all the six crosses were evaluated for various yield related traits in *rabi*, 2020-21 and phenotyped for YMD in *summer*, 2021 at Lam, Guntur, Andhra Pradesh which is hotspot for YMD.

Result: Inadequacy of additive-dominant model for all most all traits including YMD except for test weight was observed. It was found that, [*l*] type of non-allelic interaction was observed to be predominant for majority of the traits. Further, the existence of duplicate type of epistasis in the inheritance was evident at least in few crosses for all the traits (except days to maturity). The duplicate epistasis will reduce the variation in F_2 and subsequent generations, thereby hinder the pace of the progress through selection.

Key words: Duplicate epistasis, Generation mean analysis, YMD.

INTRODUCTION

Blackgram is vulnerable to several biotic stresses of which Yellow Mosaic Disease (YMD) is the most destructive one. The YMD caused by Mungbean Yellow Mosaic Virus (MYMV) is a major cause for huge economical losses in the Indian subcontinent (Nene, 1973). Infection of MYMV may cause up to 85-100% yield loss in black gram (Singh *et al*., 2011). For breeding YMD resistance, information regarding gene action controlling the resistance to YMD need to be understood.

The information pertaining to gene action controlling various quantitative characters in any crop helps in selection of appropriate breeding procedure. To provide the information on the relative importance of average effects of the genes, generation mean analysis (Mather and Jinks, 1982) is the best tool that can be employed. The scaling tests (A, B, C and D) as described by Hayman and Mather (1955) check the adequacy of the additive-dominance model for different characters, significance of any one of these scales indicate the presence of non-allelic interaction. The present investigation was carried out to find out the gene action involved in inheritance of resistance to YMD and other yield related traits through generation mean analysis.

MATERIALS AND METHODS

Plant material

A set of four diverse genotypes *viz*., TU 94-2, PU-31, IPU 94-1 and LBG 623 that are selected were crossed in all possible combinations during *rabi*, 2019-20. The F_1s of the above six crosses were backcrossed to their respective parents to obtain six BC_1s (backcross on first/female parent) and six BC_2s (backcross on second/male parent) during *summer*, 2020. During *kharif*, 2020, all the six F_1s were selfed to obtain respective F_2s. Two sets of F_2s for each F_1 were obtained. One hundred and fifty seeds per each F_1, BC_1, BC_2 of all six crosses were obtained.

The generation mean analysis to detect non-allelic interactions for yield attributing characters and YMD were conducted in two separate experiments. During *rabi*, 2020-21, all the six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the six crosses were evaluated and subjected to generation mean analysis to understand the genetic nature of yield and its contributing traits except YMD. While, during *summer*, 2021, the six generations of six crosses were evaluated to understand the nature and magnitude of allelic and non-

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allelic interactions involved in the inheritance of YMD under MYMV hotspot conditions.

Field layout and screening against YMD

The present experiment was carried out at Regional Agricultural Research Station, Lam, Guntur, Andhra Pradesh, which is located at 16.10°N latitude, 28.29°E longitude and 31.5 m altitude. The first experiment (as described above) to estimate the genetic components of variation and to find out the gene action for all the traits except YMD was conducted during *rabi*, 2020-21, for which populations of all the six crosses were grown in randomized complete block design with two replications. The P_1s, P_2s and F_1s were grown in two rows, BC_1s, BC_2s in four rows and F_2s were grown in ten rows of three meter length each such that 60, 60, 120 and 300 plants per parents, backcross, F_1 and F_2 respectively were available for study. Spacing of 30 cm × 10 cm was followed.

The second experiment of generation mean analysis for YMD (as described above) was conducted in similar lines but without spraying insecticides during the entire cropping period in order to maintain the natural whitefly population in the field. As the experimental study was conducted at Regional Agricultural Research Station, Lam, Guntur, disease incidence was guaranteed, because this area is hotspot for YMD. However, susceptible check LBG 623 was also sown in two rows after each cross (consisting of six generations). Disease reaction was scored on 1 to 9 scale given by Singh *et al*. (1992). Disease scoring was done at 45th day after sowing. Susceptible check had a disease score of '9' by the 45th day *i.e*., the day on which scoring was done on six populations of the six crosses.

Statistical analysis

The data collected on eleven traits *viz*., YMD, days to 50% flowering, plant height, branches per plant, clusters per plant, pods per plant, pod length, seed per pod, test weight, days to maturity and grain yield per plant was subjected to generation mean analysis as per Singh and Chaudhary (2010). The adequacy of simple additive-dominance model was detected using four scaling tests (A, B, C and D) as suggested by Mather (1949).Further, Joint Scaling test of Cavalli (1952) was also employed and additive-dominance model was considered inadequate only when any of the scales was found to deviate significantly from zero. Once the inadequacy of Additive-Dominant model was observed, the six genetic parameters *viz*., [*m*], [*d*], [*h*], [*i*], [*j*] and [*l*] were estimated using six-parameter model of generation mean analysis (Hayman, 1958). Student t-test was used to test the significance of both scaling tests and the genetic parameters. While Chi-square test was used to test the significance of Cavalli's joint scaling test.

RESULTS AND DISCUSSION

Gene effects of yellow mosaic disease (YMD) resistance

There was significant deviation from 'zero' for one or more scaling tests and significant deviation from Chi-square table values in joint scaling test (Table 1) in all the studied six crosses. This indicate the inadequacy of additive-dominant model and suggests the involvement of inter-allelic interactions in the inheritance of YMD resistance. The estimates of dominant x dominant [*l*] gene effects are significant and higher in magnitude than that of both additive x additive [*i*] and additive [*d*] estimates in all the six crosses (Table 2) indicating the operation of dominant x dominant [*l*] type of non allelic interactions in the inheritance of this character. Though, additive and additive x additive gene effects are significant along with additive x dominant effects in some crosses, dominant x dominant gene effects overpower them because of their higher magnitude of estimates. Operation of such dominant x dominant gene action for this character was also reported by Babu (2018). Further all the studied six crosses had significant [*l*] and [*h*] estimates in opposite direction indicating the existence of duplicate type of epistasis. Such duplicate type of epistasis for this trait was earlier indicated by Babu (2018).The duplicate epistasis hinders the improvement through selection and also act as limitation for exploitation of higher magnitudes of dominance and dominance x dominance gene effects. In presence of such dominant x dominant type of inter-allelic interaction with duplicate type of epistasis, population approach in self-pollinated crops proposed by Palmer (1953) which is similar to recurrent selection in cross pollinated crops may be followed or biparental mating followed by conventional selection in the later generations should be adopted for identifying desirable segregants.

Gene effects of yield and yield related traits

Nine out of ten traits *viz.,* days to 50% flowering, plant height, branches per plant, clusters per plant, pods per plant, pod length, seed per pod, days to maturity and grain yield per plant had significance for one or more scaling tests and also had significant Chi-square values of joint scaling tests (Table 1).Hence, the estimates of inter-allelic or non-allelic gene effects were obtained using six parameter model of generation mean analysis.

The trait wise observations of inter-allelic interactions (Table 2) indicate that, dominant x dominant [*l*] type of gene effects found to control the inheritance of days to 50% flowering in three of the crosses, in the remaining three crosses, additive x additive [*i*] type of interaction had control over this trait. In case of plant height in three of the crosses, dominant x dominant [*l*] type of gene effects found to be important, in two crosses, the inheritance was under control of additive x additive [*i*] gene effects and in the remaining one cross additive x dominant [*j*] type of interaction had control over it. The inheritance of branches per plant in four of the six crosses was under the control of [*l*] type of gene effects; one cross under [*j*] type of gene effects and one cross under [*i*] type of gene effects. Inheritance of clusters per plant was under the control of; [*l*] component in three crosses; [*i*] component in one cross and; [*j*] component of non-allelic interactions in another two crosses. In case of pods per plant it is evident that

Table 1: Estimates of scaling tests and joint scaling tests for YMD and yield related traits in blackgram.

Cross	A	B	C	D	χ^2
Yellow mosaic disease					
Cross1	0.30±0.23	-0.20±0.21	1.44±0.44**	0.67±0.13**	30.14**
Cross2	0.20±0.28	0.08±0.32	4.44±0.55**	2.08±0.11**	354.94**
Cross3	-0.10±0.57	-2.40±0.70**	0.94±1.34	1.72±0.74*	13.06**
Cross4	0.20±0.57	0.52±0.38	7.52±1.28**	3.40±0.65**	34.74**
Cross5	1.00±1.25	-1.50±1.04	7.90±1.72**	4.20±0.97**	31.27**
Cross6	0.30±0.38	-1.90±0.42**	-0.36±0.76	0.62±0.46	21.22**
Days to 50% flowering					
Cross1	5.00±2.03*	10.00±2.51**	23.00±2.79**	4.00±1.60*	70.01**
Cross2	3.50±1.95	6.50±1.87**	9.00±2.49**	-0.50±1.27	17.08**
Cross3	1.50±2.03	3.00±2.45	-4.50±2.73	-4.50±1.60**	8.48*
Cross4	4.50±1.60**	3.00±1.55	12.50±2.01**	2.50±1.22*	39.91**
Cross5	3.00±1.84	6.00±1.92**	16.00±2.57**	3.50±1.46*	40.47**
Cross6	4.50±1.54**	7.00±1.76**	12.50±2.22**	0.50±1.45	45.11**
Plant height					
Cross1	3.84±1.71*	-0.46±2.18	-16.45±1.79**	-9.92±1.60**	92.15**
Cross2	-10.32±2.28**	-11.94±2.04**	-37.79±2.01**	-7.77±1.76**	383.92**
Cross3	-10.64±1.62**	-5.06±1.36**	-15.42±2.08**	0.14±1.40	97.72**
Cross4	-7.30±1.40**	-3.28±1.38*	-14.19±1.39**	-1.81±1.12	120.30**
Cross5	-2.26±1.66	-1.82±1.57	-16.28±2.26**	-6.10±1.40**	52.04**
Cross6	-14.72±1.73**	-17.64±1.81**	-27.07±2.04**	2.64±1.53	296.86**
Branches per plant					
Cross1	2.50±0.39**	2.05±0.40**	4.44±0.60**	-0.06±0.16	58.86**
Cross2	1.25±0.35**	1.00±0.39*	1.38±0.58*	-0.44±0.16**	18.49**
Cross3	1.45±0.36**	1.25±0.34**	2.70±0.55**	0.00±0.14	24.75**
Cross4	-0.22±0.39	-0.10±0.33	0.56±0.57	0.44±0.15**	9.09*
Cross5	-0.20±0.20	-0.30±0.22	-0.90±0.31**	-0.20±0.17	8.72*
Cross6	0.95±0.29**	1.30±0.31**	1.74±0.45**	-0.26±0.14	22.11**
Clusters per plant					
Cross1	5.30±1.07**	-2.75±1.19*	1.32±1.10	-0.62±0.88	31.67**
Cross2	3.05±1.12**	-0.15±0.95	3.46±1.30**	0.28±0.84	13.06**
Cross3	8.90±1.41**	12.35±1.52**	6.36±1.58**	-7.45±1.12**	95.30**
Cross4	-1.34±1.10	-6.14±0.94**	-10.40±1.11**	-1.46±0.74*	102.34**
Cross5	-1.80±1.05	-2.70±0.99**	-2.16±1.46	1.17±0.87	9.97*
Cross6	2.34±1.00*	0.66±1.10	-8.62±1.42**	-5.81±0.95**	48.34**
Pods per plant					
Cross1	17.34±1.71**	11.74±2.19**	9.25±1.81**	-9.92±1.60**	146.47**
Cross2	-7.55±3.80	-7.70±3.27*	-32.80±2.93**	-8.78±2.85**	131.42**
Cross3	-6.40±3.69	-4.06±3.55	-26.56±3.54**	-8.05±3.07**	59.55**
Cross4	-7.20±2.15**	-1.30±2.23	-29.94±2.33**	-10.72±1.84**	169.63**
Cross5	0.90±1.36	-7.90±1.46**	-12.88±1.45**	-2.94±1.14*	101.08**
Cross6	-0.95±2.26	13.55±3.80**	-1.52±3.27	-7.06±2.70**	13.24**
Pod length					
Cross1	0.42±0.10**	-0.06±0.11	0.72±0.16**	0.18±0.07*	34.73**
Cross2	0.09±0.13	-0.77±0.12**	-0.31±0.69	0.18±0.35	40.41**
Cross3	-0.03±0.14	0.36±0.16*	0.37±0.19*	0.02±0.11	8.45*
Cross4	0.26±0.10**	0.05±0.10	-0.31±0.10**	-0.31±0.07**	23.85**
Cross5	-0.07±0.11	0.52±0.15**	0.07±0.15	-0.19±0.11	11.95**
Cross6	-0.27±0.11*	-0.07±0.11	0.07±0.14	0.21±0.09*	8.03*

Table 1: Continue....

Table 1: Continue....

Seed per pod					
Cross1	-1.65±0.44**	-2.35±0.41**	-4.14±0.67**	-0.07±0.16	40.80**
Cross2	-0.60±0.45	-0.70±0.46	-2.04±0.74**	-0.37±0.21	9.01*
Cross3	0.35±0.36	-0.80±0.39*	-1.24±0.57*	-0.40±0.16*	15.82**
Cross4	-1.70±0.37**	-0.70±0.36	-2.06±0.55**	0.17±0.17	21.73**
Cross5	-1.05±0.45*	-1.25±0.45**	-1.68±0.67*	0.31±0.34	11.36**
Cross6	-0.40±0.43	-0.80±0.35*	0.88±0.62	1.04±0.15**	55.64**
Test weight					
Cross1	-0.51±0.95	-0.29±0.92	1.76±1.08	1.28±0.73	3.99
Cross2	0.16±0.96	-0.37±0.87	-0.31±1.04	-0.05±0.70	0.28
Cross3	-0.55±0.90	-0.08±0.93	0.79±1.18	0.71±0.78	1.05
Cross4	-1.19±1.71	0.60±2.20	0.61±1.82	0.60±1.60	0.70
Cross5	-2.01±1.59	-2.16±1.57	-2.55±1.95	0.81±1.22	3.60
Cross6	0.00±0.97	-0.01±0.92	-1.69±1.31	-0.84±0.83	1.76
Days to maturity					
Cross1	5.50±1.71**	7.50±1.95**	23.00±1.93**	5.00±1.56**	158.76**
Cross2	4.50±1.78*	9.50±1.76**	21.00±1.83**	3.50±1.44*	149.10**
Cross3	4.50±1.83*	-3.00±1.95	12.50±2.16**	5.50±1.48**	44.23**
Cross4	5.50±1.71**	5.00±2.20*	19.50±1.82**	4.50±1.60**	122.95**
Cross5	5.00±1.40**	4.50±1.36**	20.50±1.99**	5.50±1.22**	110.34**
Cross6	13.50±1.30**	10.00±1.39**	38.50±1.71**	7.50±1.12**	542.88**
Grain yield per plant					
Cross1	-4.39±0.88**	-6.68±0.98**	-2.51±1.21*	4.28±0.76**	61.60**
Cross2	-2.32±0.90*	-2.47±0.69**	-3.53±0.91**	0.63±0.58	22.03**
Cross3	2.18±1.13	1.45±1.13	-5.41±1.36**	-4.52±0.99**	23.83**
Cross4	-2.78±1.00**	0.44±1.17	-11.24±1.27**	-4.45±0.95**	85.37**
Cross5	-5.44±1.25**	0.04±1.24	-10.80±1.72**	-2.71±1.03**	52.49**
Cross6	0.96±1.59	0.46±1.66	-4.62±2.08*	-3.02±1.19*	8.32*

* and ** represents 5% and 1% level of significance, respectively.

Cross1=TU94-2 × PU 31, Cross2=TU94-2 × IPU94-1, Cross3=TU94-2 × LBG623, Cross4=PU31 × IP 94-1, Cross5=PU31 × LBG623, Cross6=IPU94-1 × LBG623.

the inheritance of this trait is under influence of; [*l*] type of gene effects in two crosses and; [*i*] type of gene effects in remaining four crosses.

The inheritance of pod length was determined by dominant x dominant [*l*] type of epistasis in three crosses; additive x additive [*i*] type of epistasis in one cross and additive x dominant [*j*] type of epistasis in remaining two crosses. The trait, seed per pod was found to be under control of; dominant x dominant [*l*] type of gene effects in four crosses; additive x dominant [*j*] type of gene effects in one cross and additive x additive [*i*] type of gene effects in one cross. The inheritance of days to maturity was under the influence of additive x additive [*i*] type of non-allelic interactions in all the six crosses studied. With respect to grain yield per plant, in three of the crosses, inheritance was under the control of dominant x dominant [*l*] type of non-allelic interaction while in the remaining three crosses it was under control of additive x additive [*i*] type of non allelic component. The inheritance of disease reaction of YMD was observed to be influenced by dominant x dominant [*l*] type of non-allelic interactions in all the six crosses studied. Inadequacy of additive-dominant model for explaining the inheritance of the ten out of eleven traits emphasizes the complex nature of gene effects suggesting that simple selection procedures may not be sufficient to improve the yield and its contributing traits. Further, significant magnitudes with opposite signs of [*h*] and [*l*] gene effects indicate the operation of duplicate type of epistasis. This control of duplicate type of epistasis in the inheritance was evident at least in few crosses for all the traits (except days to maturity) that had inadequacy for additive-dominant model. This duplicate type of epistasis was earlier indicated for various traits by different scientists [Babu (2018), Bharathi (2019) and Panigrahi *et al*. (2020)]. 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 in presence of non-allelic interactions is to go for inter-mating in early segregating generations and postpone the selections to the later generations.

Table 2: Estimates of components of gene effects and type of epistasis for YMD and yield related traits in blackgram.

Cross	m	d	h	i	j	l	Epistasis
Yellow mosaic disease							
Cross1	2.06±0.06**	0.65±0.05**	-1.54±0.32**	-1.14±0.26**	0.25±0.12*	1.24±0.48*	D
Cross2	3.07±0.05**	-0.06±0.06	-4.08±0.34**	-3.16±0.22**	0.06±0.15	3.88±0.60**	D
Cross3	3.91±0.31**	-2.30±0.41**	-6.79±1.50**	-3.44±1.48*	1.15±0.42**	5.94±2.11**	D
Cross4	3.40±0.29**	-0.60±0.28*	-7.04±1.33**	-6.01±1.30**	-0.16±0.30	6.08±1.69**	D
Cross5	5.45±0.34**	-2.50±0.69**	-11.75±2.01**	-8.40±1.94**	1.25±0.75	8.90±3.26**	D
Cross6	3.61±0.18**	-2.20±0.27**	-4.44±0.92**	-1.24±0.91	1.10±0.28**	2.84±1.32*	D
Days to 50% flowering							
Cross1	47.00±0.42**	0.00±1.36	-5.50±3.39	-8.00±3.21*	-2.50±1.46	-7.00±6.12	-
Cross2	44.00±0.33**	0.50±1.09	4.50±2.75	1.00±2.54	-1.50±1.16	-11.00±5.01*	-
Cross3	40.50±0.42**	0.50±1.36	9.75±3.38**	9.00±3.21**	-0.75±1.43	-13.50±6.09*	D
Cross4	44.00±0.37**	-0.50±0.96	-2.75±2.53	-5.00±2.43*	0.75±1.05	-2.50±4.35	-
Cross5	45.00±0.46**	-2.50±1.12*	-4.00±3.05	-7.00±2.92*	-1.50±1.22	-2.00±5.17	-
Cross6	44.00±0.48**	-0.50±1.08	-0.75±2.96	-1.00±2.91	-1.25±1.13	-10.50±4.87*	-
Plant height							
Cross1	38.29±0.42**	5.75±1.36**	24.43±3.22**	19.83±3.21**	2.15±1.38	-23.21±5.74**	D
Cross2	32.23±0.46**	6.66±1.50**	23.19±3.55**	15.54±3.53**	0.81±1.52	6.72±6.33	-
Cross3	41.62±0.48**	-4.54±1.01**	-0.23±2.83	-0.28±2.80	-2.79±1.03**	15.98±4.56**	-
Cross4	31.67±0.30**	0.07±0.94	4.93±2.26*	3.61±2.23	-2.01±0.96*	6.96±4.02	-
Cross5	38.00±0.47**	-5.30±1.04**	14.00±2.86**	12.20±2.79**	-0.22±1.07	-8.12±4.72	-
Cross6	34.61±0.47**	-5.57±1.21**	-0.76±3.08	-5.28±3.05	1.46±1.22	37.64±5.25**	-
Branches per plant							
Cross1	3.89±0.04**	0.07±0.14	0.56±0.43	0.11±0.32	0.23±0.23	-4.66±0.81**	-
Cross2	3.55±0.05**	-0.18±0.12	1.87±0.41**	0.87±0.31**	0.13±0.22	-3.12±0.75**	D
Cross3	3.55±0.04**	-0.05±0.12	0.65±0.38	0.00±0.27	0.10±0.20	-2.70±0.72**	-
Cross4	3.09±0.04**	-0.06±0.13	-0.78±0.40	-0.88±0.30**	-0.06±0.20	1.20±0.76	-
Cross5	2.80±0.06**	0.20±0.12	0.95±0.35**	0.40±0.34	0.05±0.14	0.10±0.59	-
Cross6	3.51±0.04**	-0.13±0.11	0.96±0.34**	0.51±0.27	-0.18±0.18	-2.76±0.64**	D
Clusters per plant							
Cross1	10.81±0.22**	2.38±0.76**	5.68±1.79**	1.23±1.76	4.03±0.78**	-3.78±3.23	-
Cross2	9.99±0.25**	2.05±0.66**	5.39±1.72**	-0.56±1.67	1.60±0.69*	-2.34±2.95	-
Cross3	11.59±0.29**	-2.73±0.96**	19.69±2.30**	14.89±2.24**	-1.73±0.97	-36.14±4.14**	D
Cross4	7.23±0.18**	4.65±0.64**	6.47±1.53**	2.92±1.47*	2.40±0.67**	4.56±2.81	-
Cross5	9.01±0.30**	1.15±0.63	-2.04±1.79	-2.34±1.75	0.45±0.69	6.84±2.91*	-
Cross6	5.47±0.32**	-0.61±0.70	12.37±1.92**	11.62±1.90**	0.84±0.72	-14.62±3.14**	D
Pods per plant							
Cross1	38.29±0.42**	5.75±1.36**	22.88±3.22**	19.83±3.21**	2.80±1.38*	-48.91±5.74**	D
Cross2	27.48±0.70**	2.83±2.48	19.40±5.72**	17.55±5.70**	0.07±2.49	-2.30±10.35	-
Cross3	28.44±0.86**	4.28±2.54	22.15±6.15**	16.10±6.13**	-1.17±2.55	-5.64±10.75	-
Cross4	23.04±0.53**	-3.20±1.51*	18.59±3.72**	21.44±3.68**	-2.95±1.52	-12.94±6.46*	D
Cross5	24.88±0.32**	7.30±0.95**	5.88±2.31*	5.88±2.29*	4.40±0.97**	1.12±4.08	-
Cross6	28.02±0.79**	-4.25±2.19	12.92±5.41*	14.12±5.40**	-7.25±2.19**	-26.72±9.34**	D
Pod length							
Cross1	4.55±0.02**	0.08±0.05	-0.46±0.16**	-0.36±0.14*	0.24±0.06**	0.00±0.27	-
Cross2	4.32±0.17**	0.36±0.08**	-0.26±0.70	-0.37±0.70	0.43±0.09**	1.04±0.76	-
Cross3	4.59±0.03**	-0.21±0.09*	0.40±0.23	-0.04±0.22	-0.20±0.09*	-0.29±0.41	-
Cross4	4.32±0.02**	0.26±0.06**	0.62±0.15**	0.62±0.15**	0.11±0.07	-0.93±0.27**	D
Cross5	4.51±0.03**	-0.15±0.09	0.47±0.23*	0.38±0.22	-0.29±0.09**	-0.83±0.39*	D
Cross6	4.45±0.03**	-0.11±0.07	-0.35±0.18*	-0.41±0.17*	-0.10±0.07	0.75±0.31*	D

Table 2: Continue....

Table 2: Continue....

Seed per pod							
Cross1	5.12±0.04**	-0.15±0.14	0.84±0.46	0.14±0.33	0.35±0.23	3.86±0.88**	-
Cross2	4.92±0.07**	0.10±0.16	1.09±0.54*	0.74±0.42	0.05±0.25	0.56±0.99	-
Cross3	5.29±0.05**	0.08±0.13	0.39±0.42	0.79±0.33*	0.58±0.23*	-0.34±0.77	-
Cross4	5.36±0.04**	0.15±0.15	-0.49±0.42	-0.34±0.33	-0.50±0.20*	2.74±0.80**	-
Cross5	5.71±0.11**	0.05±0.25	-1.07±0.72	-0.62±0.67	0.10±0.28	2.92±1.21*	-
Cross6	5.77±0.03**	-0.50±0.13**	-2.38±0.42**	-2.08±0.29**	0.20±0.21	3.28±0.82**	D
Test weight							
Cross1	4.92±0.21**	0.04±0.60	-2.58±1.49	-2.56±1.45	-0.11±0.63	3.36±2.62	-
Cross2	4.12±0.20**	0.67±0.58	0.03±1.45	0.10±1.41	0.27±0.62	0.11±2.55	-
Cross3	4.63±0.25**	-0.07±0.59	-1.51±1.58	-1.42±1.55	-0.23±0.62	2.05±2.65	-
Cross4	4.10±0.42**	-0.64±1.36	-1.46±3.22	-1.20±3.21	-0.90±1.38	1.79±5.74	-
Cross5	3.97±0.36**	0.09±0.99	-1.06±2.52	-1.62±2.44	0.07±1.05	5.79±4.39	-
Cross6	3.70±0.28**	-0.24±0.61	1.84±1.69	1.68±1.65	0.00±0.64	-1.67±2.76	-
Days to maturity							
Cross1	80.50±0.45**	0.00±1.27	-9.50±3.14**	-10.00±3.12**	-1.00±1.28	-3.00±5.43	-
Cross2	82.00±0.40**	-1.50±1.19	-2.50±2.90	-7.00±2.87*	-2.50±1.24*	-7.00±5.09	-
Cross3	82.00±0.42**	0.50±1.22	-10.75±3.04**	-11.00±2.97**	3.75±1.28**	9.50±5.33	-
Cross4	79.50±0.42**	0.50±1.36	-8.25±3.22*	-9.00±3.21**	0.25±1.38	-1.50±5.74	-
Cross5	84.00±0.42**	-3.50±0.88**	-8.75±2.49**	-11.00±2.44**	0.25±0.93	1.50±4.03	-
Cross6	88.50±0.35**	-1.50±0.87	-12.75±2.29**	-15.00±2.23**	1.75±0.90	-8.50±3.87*	C
Grain yield per plant							
Cross1	7.46±0.23**	-0.40±0.60	-8.09±1.57**	-8.57±1.53**	1.14±0.60	19.64±2.70**	D
Cross2	5.78±0.15**	1.05±0.50*	1.40±1.22	-1.25±1.17	0.07±0.53	6.04±2.19**	-
Cross3	6.04±0.31**	-0.11±0.77	10.27±2.00**	9.04±1.98**	0.36±0.78	-12.67±3.38**	D
Cross4	4.72±0.29**	0.91±0.75	10.25±1.92**	8.90±1.90**	-1.61±0.76*	-6.56±3.24*	D
Cross5	5.25±0.34**	-1.53±0.77	4.89±2.12*	5.41±2.06**	-2.74±0.82**	-0.02±3.53	-
Cross6	4.59±0.35**	-1.00±0.96	6.07±2.50*	6.04±2.38*	0.25±1.06	-7.46±4.38	-

*and ** represents 5% and 1% level of significance, respectively. C = Complementary and D = Duplicate.

Cross 1=TU94-2 × PU 31, Cross 2=TU94-2 × IPU94-1, Cross 3=TU94-2 × LBG623, Cross 4=PU31 × IP 94-1, Cross 5=PU31 × LBG623, Cross 6=IPU94-1 × LBG623.

CONCLUSION

The study revealed the importance of non-allelic interactions in the inheritance of majority of traits including YMD. Among the non-allelic interactions, [*l*] type of interaction was predominant. Further, the control of duplicate type of epistasis in the inheritance was evident at least in few crosses for all the traits (except days to maturity) that had inadequacy for additive-dominant model, which hinders the pace of the progress through selection. In presence of inter-allelic interaction with such duplicate type of epistasis, population approach in self-pollinated crops, 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. It can be concluded that gene interactions varied cross wise as well as trait wise. Hence, specific breeding strategy has to be adopted in particular cross for a particular trait depending up on the type of gene effects operating, for overall improvement of yield and its contributing traits.

Conflict of interest: None.

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