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Understanding the Genetic Architecture and Gene Actions Involved in the Inheritance of Yellow Mosaic Disease and Other Yield Related Traits in Mungbean [*Vigna radiata* (L.) Wilczek]

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ABSTRACT

Background: Yellow mosaic disease (YMD) transmitted by white fly, *Bemisia tabaci* is the most persistent and devastating biotic stress worldwide and in India resulting the reduced productivity of mungbean. At the same time the yield levels in mungbean reached a plateau, which emphasizes the importance of varieties with improved productivity.

Methods: In the present investigation, to address this urgent requirement of YMD resistant high yielding varieties, six-parameter model of generation mean analysis was employed for proper understanding of the genetic architecture and gene actions. Susceptible genotype MGG 385 was crossed with four resistant genotypes (LGG 607, LGG 630, WGG 42 and PM 5) to produce respective F_1s (during *rabi,* 2018-19), BC_1s, BC_2s (during *summer*, 2019) and F_2s (during *kharif*, 2019). These generations of the four crosses were evaluated for various yield related traits in *rabi*, 2019-20 and phenotyped for YMD in *summer*, 2020 at Lam, Guntur, Andhra Pradesh which is hotspot for YMD.

Result: The scaling tests and joint scaling test indicated the inadequacy of Additive-dominant model for all most all traits including YMD except for branches per plant and pods per cluster. 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 is predominant. Further, the control of duplicate type of epistasis in the inheritance is evident at least in few crosses for all the traits (except grain yield per plant) 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.

Key words: Additive-Dominant model, Duplicate epistasis, Generation means, Scaling tests, *Vigna radiata.*

INTRODUCTION

Mungbean [*Vigna radiata* (L.) Wilczek] is an easy digestible pulse crop and is considered as a major pulse crop in Asia since ancient times. It occupies an important position as it contains 51% carbohydrate, 24-26% protein, 4% minerals and 3% vitamins. Being rich in nutritional profile, it is an inseparable component in the diets of vast majority of population in the Indian sub-continent. However, several biotic and abiotic stresses are hindering the productivity. Among several constraints for mungbean production, yellow mosaic disease (YMD) is one of the most devastating diseases and an important biotic constraint in mungbean crop, causing 85 to100 per cent yield loss which is transmitted by the white fly, *Bemisia tabaci*. This has become increasingly serious because of the lack of resistance in the existing cultivars. Nariani (1960) first observed the virus at IARI, New Delhi and reported an incidence of 20-30% at the institute area. There is a dire need to identify YMD resistant lines which in turn can be used in various breeding programmes. Various screening methods were devices to screen genotypes against different biotic and abiotic stresses at both gametophytic level (Babu and Ravikumar, 2010) and sporophytic level. However, field screening at sporophytic level in natural hot spots of the disease was proved to be more effective particularly for viral diseases like YMD.

In any crop for improvement programme of productivity, understanding the inheritance of any trait is of major importance. Estimation of gene action is the key in understanding the inheritance of a particular character. Among various approaches, Generation mean analysis (Hayman, 1958; Jinks and Jones, 1958; Mather and Jinks, 1971) is one of the best method to identify the different

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components of gene effects. It checks the adequacy of additive-dominant model using different scaling tests. Inadequacy of additive-dominant model indicate the operation of inter-allelic or non-allelic interactions. The type of non-allelic interaction and its magnitude can be estimated with precision using generation mean analysis. Hence, generation mean analysis was employed in present study to understand the gene actions involved in the inheritance of YMD and other yield related traits threadbare.

MATERIALS AND METHODS

Plant material

The susceptible genotype, MGG 385 was used as female and crossed with four resistant genotypes *viz.,* LGG 607, LGG 630, WGG 42 and PM 5 following keel rupture method of emasculation and hand pollination (Fig 1) during *rabi*, 2018-19. The F_1s of the above four crosses were used as males and back crossed to the respective parents to obtain four BC_1s (back cross on first/female parent) and four BC_2s (back cross on second/male parent) during *summer*, 2019. During *kharif*, 2019 the four F_1s were selfed to obtain the respective F_2s. Three sets of F_2s for each F_1 were obtained.

The generation mean analysis for deciphering the genetic architecture and gene actions involved in the inheritance of yield traits and YMD were conducted in two separate experiments. During *rabi*, 2019-20, the six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the four crosses were employed in generation mean analysis to understand gene actions involved in the inheritance of yield and yield related traits except YMD. While, during *summer*, 2020 the six generations of the four crosses were employed in generation mean analysis to understand gene actions involved in the inheritance of YMD under MYMV hotspot conditions.

Field layout and screening against YMD

Present investigation was taken up at Advanced P.G. Center, Lam, Guntur, Andhra Pradesh which is located at 16°36′ N latitude, 80°43′ E longitude and 31.5 m altitude. The first experiment of generation mean analysis for all the traits except YMD was carried out during *rabi*, 2019-20. Six populations of the four crosses were grown in Completely Randomized Block Design with two replications. The P_1s, P_2s, BC_1s, BC_2s and F_1s were grown in two rows of three meter length, while the F_2s were grown in ten rows of three meter length so that 300 plants per population were available. The seed was sown with a spacing of 30 cm between rows and 10 cm with in rows. The required crop protection practices were followed as per the requirement.

The second experiment of generation mean analysis for YMD was conducted in similar lines but without spraying insecticides during the cropping period in order to maintain the natural whitefly population in the field. Disease incidence was guaranteed at the site of the experiment *i.e*., Advanced, P. G. Center, Lam, Guntur, because this area is hotspot for YMD. However, susceptible genotype LGG 450 was also grown after each five rows of test genotypes. Disease reaction was scored (Fig 2) on 1 to 9 scale given by Singh *et al*. (1992). The 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 four crosses.

Statistical analysis

The data collected on twelve traits *viz.,* yellow mosaic disease, days to 50% flowering, plant height, branches per plant, days to maturity, clusters per plant, pods per cluster, pods per plant, pod length, seeds per pod, test weight and grain yield per plant was subjected to generation mean analysis as per Singh and Chaudhary (2010). The presence or absence of epistasis was detected using four scaling tests (A, B, C and D) given by Mather (1949). Further, Joint Scaling test of Cavalli (1952) was also employed for testing the adequacy of Additive-Dominant model. 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

The mean values with standard errors of YMD scores pertaining to the six generations belonging to the four crosses are presented in the Table 1. None of the F_1s had better disease score than the respective parents and all the four F_1s recorded similar score as that of the resistant parent (P_2) indicating the oligogenic nature of the trait. The oligogenic nature of YMD is in accordance with previously published results [Mahalingam *et al.* (2018) and Sudha *et al.* (2013)]. None of the F_2s are better than the F_1s and had inbreeding depression, indicating the probable operation of dominance type of gene action for YMD inheritance. However, actual gene action will be revealed after performing the generation mean analysis.

It is pertinent from the means of other traits (Table 1) that the F_1s of all the four crosses with respect to seeds per pod, plant height, clusters per plant and pod length were intermediate between the parents. Similarly; one cross (MGG 385 × LGG 607) for branches per plant; one cross (MGG 385 × LGG 630) for days to maturity; three crosses (MGG 385 × LGG 607, MGG 385 × WGG 42 and MGG 385 × PM 5) for pods per plant; three crosses (MGG 385 × LGG 607, MGG 385 × LGG 630 and MGG 385 × WGG 42) for test weight and; two crosses (MGG 385 × LGG 607 and MGG 385 × WGG 42) for days to 50% flowering also had intermediate F_1s values indicating the quantitative nature of inheritance of these traits in the mentioned crosses. The F_1s of three crosses (MGG 385 × LGG 630, MGG 385 × WGG 42 and MGG 385 × PM 5) for branches per plant; three crosses (MGG 385 × LGG 607, MGG 385 × WGG 42 and

Table 1: Mean performance of six generations for YMD and yield related traits in mungbean.

Cross no.	Cross	P_1	P_2	F_1	BC_1	BC_2	F_2
			Yellow mosaic disease				
1	MGG 385 × LGG 607	8.90±0.10	1.80±0.10	1.80±0.13	4.10±0.13	1.90±0.10	3.34±0.33
2	MGG 385 × LGG 630	8.90±0.10	2.00±0.10	2.10±0.13	4.40±0.10	2.10±0.13	3.60±0.31
3	MGG 385 × WGG 42	8.90±0.10	3.20±0.13	3.60±0.13	5.90±0.10	3.40±0.10	5.45±0.33
4	MGG 385 × PM 5	8.80±0.13	1.80±0.10	2.00±0.13	4.60±0.10	2.00±0.13	3.90±0.33
			Days to 50% flowering				
1	MGG 385 × LGG 607	32.00±0.16	29.50±0.24	30.00±0.16	33.00±0.42	33.00±0.43	30.50±0.19
2	MGG 385 × LGG 630	32.00±0.20	33.00±0.14	30.50±0.22	33.50±0.23	33.50±0.24	33.00±0.20
3	MGG 385 × WGG 42	35.50±0.16	29.50±0.15	33.50±0.19	35.00±0.29	34.00±0.28	34.00±0.20
4	MGG 385 × PM 5	36.00±0.16	30.50±0.20	30.00±0.22	34.00±0.28	32.50±0.30	32.50±0.22
			Plant height (cm)				
1	MGG 385 × LGG 607	52.30±1.04	45.80±0.92	48.60±0.95	48.50±1.19	43.20±1.12	48.00±0.37
2	MGG 385 × LGG 630	51.60±1.01	52.80±0.70	52.00±1.13	50.20±0.87	51.00±1.14	47.00±0.38
3	MGG 385 × WGG 42	55.10±0.87	46.40±1.23	50.20±1.22	48.90±1.21	45.00±1.24	47.80±0.51
4	MGG 385 × PM 5	54.90±1.30	47.70±1.36	49.90±1.30	53.61±1.15	47.40±1.26	47.00±0.35
			Branches per plant				
1	MGG 385 × LGG 607	6.40±0.35	4.90±0.36	5.50±0.41	5.80±0.39	4.80±0.32	5.37±0.38
2	MGG 385 × LGG 630	6.10±0.40	6.20±0.34	6.80±0.39	6.00±0.29	6.60±0.22	6.00±0.15
3	MGG 385 × WGG 42	5.90±0.39	5.90±0.43	6.20±0.43	5.89±0.39	5.90±0.29	5.37±0.23
4	MGG 385 × PM 5	6.00±0.38	6.00±0.47	6.12±0.42	6.00±0.26	5.87±0.45	5.82±0.38
			Days to maturity				
1	MGG 385 × LGG 607	67.50±0.23	66.50±0.22	65.00±0.23	67.40±0.35	66.00±0.45	66.00±0.22
2	MGG 385 × LGG 630	65.00±0.20	67.50±0.18	66.00±0.20	67.50±0.27	67.00±0.26	62.50±0.37
3	MGG 385 × WGG 42	67.50±0.24	62.00±0.22	60.50±0.23	64.00±0.28	62.50±0.28	62.50±0.38
4	MGG 385 × PM 5	69.50±0.21	61.00±0.08	60.50±0.07	66.00±0.29	62.50±0.28	62.50±0.38
			Clusters per plant				
1	MGG 385 × LGG 607	9.40±0.27	5.10±0.24	6.50±0.26	7.40±0.29	7.30±0.35	5.37±0.38
2	MGG 385 × LGG 630	10.20±0.50	8.10±0.36	9.30±0.47	9.80±0.37	7.90±0.29	7.08±0.22
3	MGG 385 × WGG 42	11.00±0.44	5.30±0.45	9.20±0.44	9.80±0.39	5.70±0.39	6.74±0.19
4	MGG 385 × PM 5	11.00±0.14	5.50±0.07	10.10±0.39	10.40±0.50	6.90±0.47	9.32±0.18
			Pods per cluster				
1	MGG 385 × LGG 607	3.60±0.22	4.40±0.32	4.62±0.22	3.74±0.17	4.54±0.24	3.97±0.38
2	MGG 385 × LGG 630	3.40±0.27	3.70±0.32	4.40±0.32	3.90±0.24	4.30±0.32	3.50±0.35
3	MGG 385 × WGG 42	3.30±0.22	4.10±0.29	4.30±0.30	3.37±0.35	4.00±0.35	4.24±0.25
4	MGG 385 × PM 5	3.90±0.39	3.00±0.35	4.01±0.35	3.90±0.33	2.93±0.43	3.52±0.32
			Pods per plant				
1	MGG 385 × LGG 607	32.40±0.71	17.80±0.66	29.00±0.78	30.60±0.88	16.40±0.57	29.00±0.38
2	MGG 385 × LGG 630	34.30±0.85	32.60±0.64	35.70±0.87	25.10±0.93	31.20±0.90	33.00±0.45
3	MGG 385 × WGG 42	34.70±0.80	25.80±0.78	32.60±0.94	31.70±0.85	25.00±0.65	28.00±0.47
4	MGG 385 × PM 5	35.10±1.09	16.00±1.20	34.82±1.40	31.30±1.16	13.86±1.01	28.30±0.58
			Pod length (cm)				
1	MGG 385 × LGG 607	7.22±0.13	6.09±0.06	7.00±0.13	8.07±0.19	7.94±0.17	6.74±0.38
2	MGG 385 × LGG 630	8.32±0.12	7.30±0.09	7.99±0.09	8.01±0.12	7.95±0.10	6.52±0.05
3	MGG 385 × WGG 42	8.38±0.10	8.97±0.10	8.96±0.09	8.41±0.11	8.82±0.11	8.31±0.13
4	MGG 385 × PM 5	8.42±0.12	9.04±0.08	8.94±0.09	8.00±0.12	8.56±0.14	8.57±0.13
			Seeds per pod				
1	MGG 385 × LGG 607	12.80±0.32	10.80±0.45	11.20±0.36	12.34±0.59	10.56±0.47	10.06±0.38
2	MGG 385 × LGG 630	13.10±0.37	11.10±0.46	12.20±0.41	11.50±0.47	12.30±0.39	11.00±0.15
3	MGG 385 × WGG 42	13.90±0.40	11.90±0.52	12.70±0.34	11.50±0.69	11.90±0.71	10.30±0.31
4	MGG 385 × PM 5	13.80±0.46	11.80±0.58	13.50±0.57	12.30±0.97	11.63±0.75	10.56±0.28

Table 1: Continue...

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				Test weight (g)			
1	MGG 385 × LGG 607	4.07±0.09	3.37±0.08	3.94±0.11	4.00±0.10	3.37±0.06	3.90±0.38
2	MGG 385 × LGG 630	4.17±0.11	3.28±0.06	3.88±0.09	4.02±0.11	3.43±0.07	3.26±0.05
3	MGG 385 × WGG 42	4.26±0.08	5.02±0.08	4.93±0.08	4.00±0.12	4.98±0.26	4.61±0.11
4	MGG 385 × PM 5	4.32±0.14	5.79±0.18	5.94±0.14	4.20±0.09	5.73±0.14	5.07±0.13
				Yield per plant (g)			
1	MGG 385 × LGG 607	6.70±0.48	6.82±0.45	6.62±0.46	6.80±0.54	6.23±0.55	5.37±0.28
2	MGG 385 × LGG 630	6.82±0.47	6.79±0.45	6.93±0.56	6.76±0.71	6.30±0.71	5.20±0.34
3	MGG 385 × WGG 42	6.83±0.38	6.83±0.37	6.93±0.43	6.81±0.54	6.98±0.46	6.02±0.22
4	MGG 385 × PM 5	6.53±0.35	6.83±0.45	6.72±0.46	6.53±0.56	6.57±0.60	5.37±0.29

MGG 385 × PM 5) for days to maturity; all four crosses for pods per plant; one cross (MGG 385 × PM 5) for test weight and; two crosses (MGG 385 × LGG 630 and MGG 385 × WGG 42) for yield per plant had superior F_1s than the respective parent with less F_2 means indicating the probable operation of dominance for these traits in these crosses. However, exact gene action can be understood only after examining the results of generation mean analysis.

Gene effects of yellow mosaic disease (YMD)

There was significant deviation from 'zero' for at least one of the scaling tests and significantly deviated from Chi-square table values in joint scaling test (Table 2) in all the four crosses for YMD. This indicate the inadequacy of additive-dominant model and suggests the involvement of inter-allelic interactions *viz.,* [*i*], [*j*] and [*l*] in the inheritance of this trait. The component means (Table 3) derived from generation mean analysis revealed; positive and significant [*m*] component, [*d*] components and [*h*] components for all the four crosses.

The estimates of dominant × dominant [*l*] gene effects are significant and higher in magnitude than that of both additive × additive [*i*] and additive [*d*] estimates in all the four crosses indicating the operation of dominant × dominant [*l*] type of non-allelic interactions in the inheritance of this character. Though, additive and additive × additive gene (in one cross) effects are significant along with additive × dominant effects, dominant × dominant gene effects overpower them because of their higher magnitude of estimates. Operation of such dominant × dominant gene action for this character was reported by Narasimhulu *et al*. (2018). Further these crosses also had significant [*l*] and [*h*] estimates with opposite signs (Table 3) indicating the operation of duplicate type of epistasis. Such duplicate type of epistasis for this trait was earlier observed by Narasimhulu *et al*. (2018). This duplicate epistasis hinders the improvement through selection and also act as limitation for exploitation of higher magnitudes of dominance and dominance × dominance gene effects. In presence of such dominant × 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 or biparental mating followed by conventional selection in the later generations should be adopted for identifying desirable segregants.

Gene effects of other yield related traits

Generation mean analysis of yield and yield related traits except YMD, indicate that additive-dominant model is adequate only for two traits *viz.,* number of branches per plant and pods per cluster. All other nine traits *viz.,* days to 50% flowering, plant height, days to maturity, clusters per plant, pods per plant, pod length, seeds per pod, test weight 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 2). This clearly indicate the inadequacy of additive-dominant model in explaining the inheritance in these traits. Hence, the estimates of inter-allelic or non-allelic gene effects were obtained (Table 3) using six parameter model of generation mean analysis. In spite of having significant additive [*d*] and dominance [*h*] components, the non-allelic interaction overpowered them due to their higher estimates hence, had a great role in the inheritance of these twelve traits.

The trait wise observations of inter-allelic interactions (Table 3) indicate that, dominant × dominant [*l*] type of gene effects are found to control the inheritance of days to maturity in all the four crosses. In case of plant height, two (MGG 385 × LGG 607 and MGG 385 × WGG 42) of the crosses, dominant × dominant [*l*] type of gene effects are found to be important and in the remaining two crosses (MGG 385 × LGG 630 and MGG 385 × WGG PM 5), the inheritance is under control of additive × additive [*i*] gene effects. The inheritance of days to maturity in all the four crosses is under the control of [*l*] type of inter-allelic interactions. Inheritance of clusters per plant is under the control of [*l*] component in two crosses (MGG 385 × LGG 607 and MGG 385 × WGG PM 5) and [*i*] component of non-allelic interactions in another two crosses (MGG 385 × LGG 630 and MGG 385 × WGG 42). In case of pods per plant it is evident that the inheritance is under influence of [*l*] type of gene effects in all the four crosses.

The inheritance of pod length is determined by dominant × dominant [*l*] type of epistasis in three crosses (MGG 385 × LGG 607, MGG 385 × LGG 630 and MGG 385 × PM 5) and

Table 2: Estimates of scaling tests and joint scaling tests of YMD and yield related traits in mungbean.

Cross no.	Cross	A	B	C	D	χ^2
		Yellow mosaic disease				
1	MGG 385 × LGG 607	-2.50±0.31**	0.20±0.26	-0.94±1.34	0.68±0.67	69.75**
2	MGG 385 × LGG 630	-2.20±0.26**	0.10±0.31	-0.70±1.27	0.70±0.64	76.46**
3	MGG 385 × WGG 42	-0.70±0.26*	0.00±0.27	2.50±1.37	1.60±0.68*	12.22**
4	MGG 385 × PM 5	-1.60±0.27**	0.20±0.31	1.00±1.37	1.20±0.69*	39.44**
		Days to 50% flowering				
1	MGG 385 × LGG 607	4.00±0.87**	6.50±0.90**	0.50±0.86	-5.00±0.71**	71.92**
2	MGG 385 × LGG 630	4.50±0.54**	3.50±0.56**	6.00±0.94**	-1.00±0.52	105.06**
3	MGG 385 × WGG 42	1.00±0.63	-3.00±0.61**	0.00±0.91	1.00±0.56	28.57**
4	MGG 385 × PM 5	2.00±0.63**	4.50±0.66**	1.50±1.00	-2.50±0.60**	51.65**
		Plant height				
1	MGG 385 × LGG 607	-3.90±2.76	-8.00±2.61**	-3.30±2.79	4.30±1.79*	10.59*
2	MGG 385 × LGG 630	-3.20±2.30	-2.80±2.63	-20.40±2.98**	-7.20±1.62**	56.17**
3	MGG 385 × WGG 42	-7.50±2.85*	-6.60±3.03*	-10.70±3.52**	1.70±2.02	12.76**
4	MGG 385 × PM 5	2.42±2.95	-2.80±3.14	-14.40±3.51**	-7.01±1.85**	29.44**
		Branches per plant				
1	MGG 385 × LGG 607	-0.30±0.95	-0.80±0.84	-0.82±1.79	0.14±0.90	0.95
2	MGG 385 × LGG 630	-0.90±0.81	0.20±0.68	-1.90±1.12	-0.60±0.48	5.05
3	MGG 385 × WGG 42	-0.32±0.97	-0.30±0.84	-2.73±1.38	-1.05±0.67	4.49
4	MGG 385 × PM 5	-0.12±0.77	-0.38±1.10	-0.96±1.83	-0.23±0.92	0.32
		Days to maturity				
1	MGG 385 × LGG 607	2.30±0.78**	0.50±0.95	0.00±1.03	-1.40±0.71	9.32*
2	MGG 385 × LGG 630	4.00±0.61**	0.50±0.59	-14.50±1.54**	-9.50±0.82**	152.09**
3	MGG 385 × WGG 42	0.00±0.66	2.50±0.65**	-0.50±1.61	-1.50±0.85	15.92**
4	MGG 385 × PM 5	2.00±0.62**	3.50±0.57**	-1.50±1.55	-3.50±0.86**	49.36**
		Clusters per plant				
1	MGG 385 × LGG 607	-1.10±0.70	3.00±0.78**	-6.03±1.64**	-3.96±0.88**	35.35**
2	MGG 385 × LGG 630	0.10±1.02	-1.60±0.83	-8.58±1.43**	-3.54±0.65**	48.37**
3	MGG 385 × WGG 42	-0.60±0.99	-3.10±0.99**	-7.74±1.31**	-2.02±0.67**	39.97**
4	MGG 385 × PM 5	-0.30±1.08	4.20±1.03**	0.58±1.06	-1.66±0.77*	17.60**
		Pods per cluster				
1	MGG 385 × LGG 607	-0.74±0.47	0.06±0.62	-1.36±1.62	-0.34±0.81	3.00
2	MGG 385 × LGG 630	0.00±0.64	0.50±0.77	-1.90±1.59	-1.20±0.80	2.41
3	MGG 385 × WGG 42	-0.86±0.79	-0.40±0.81	0.96±1.21	1.11±0.69	2.78
4	MGG 385 × PM 5	-0.11±0.85	-1.15±0.99	-0.84±1.54	0.21±0.83	1.43
		Pods per plant				
1	MGG 385 × LGG 607	-0.20±2.05	-14.00±1.53**	7.80±2.38**	11.00±1.29**	153.84**
2	MGG 385 × LGG 630	-19.80±2.23**	-5.90±2.11**	-6.30±2.73*	9.70±1.58**	82.95**
3	MGG 385 × WGG 42	-3.90±2.10	-8.40±1.79**	-13.70±2.88**	-0.70±1.42	30.62**
4	MGG 385 × PM 5	-7.32±2.92*	-23.10±2.73**	-7.54±3.99	11.44±1.93**	80.28**
		Pod length				
1	MGG 385 × LGG 607	4.00±0.42**	2.79±0.37**	-0.35±1.54	-2.53±0.80**	72.10**
2	MGG 385 × LGG 630	4.50±0.28	0.61±0.24*	-5.52±0.30**	-2.92±0.18**	459.10**
3	MGG 385 × WGG 42	1.00±0.27	-0.31±0.26	-2.07±0.57**	-0.61±0.31*	15.41**
4	MGG 385 × PM 5	2.00±0.28**	-0.86±0.30**	-1.06±0.58	0.58±0.32	30.77**
		Seeds per pod				
1	MGG 385 × LGG 607	0.68±1.28	-0.88±1.10	-5.76±1.76**	-2.78±1.07**	11.88**
2	MGG 385 × LGG 630	-2.30±1.09*	1.30±0.99	-4.60±1.18**	-1.80±0.68**	28.28**
3	MGG 385 × WGG 42	-3.60±1.48*	-0.80±1.55	-10.00±1.55**	-2.80±1.16*	44.36**
4	MGG 385 × PM 5	-2.70±2.08	-2.04±1.72	-10.36±1.77**	-2.81±1.36*	34.85**

Table 2: Continue...

Table 2: Continue...

		Test weight				
1	MGG 385 × LGG 607	-0.01±0.24	-0.55±0.18**	0.28±1.53	0.42±0.76	10.58*
2	MGG 385 × LGG 630	-0.01±0.26	-0.30±0.18	-2.17±0.30**	-0.93±0.17**	60.17**
3	MGG 385 × WGG 42	-1.19±0.27**	0.01±0.53	-0.70±0.49	0.24±0.36	19.57**
4	MGG 385 × PM 5	-1.86±0.27**	-0.27±0.37	-1.71±0.63**	0.21±0.31	47.68**
		Grain yield per plant				
1	MGG 385 × LGG 607	0.28±1.27	-0.98±1.27	-5.29±1.60**	-2.29±0.95*	12.88**
2	MGG 385 × LGG 630	-0.23±1.60	-1.12±1.59	-6.67±1.89**	-2.66±1.22*	13.22**
3	MGG 385 × WGG 42	-0.14±1.22	0.20±1.07	-3.44±1.33*	-1.75±0.83*	8.53*
4	MGG 385 × PM 5	-0.17±1.25	-0.41±1.36	-5.33±1.60**	-2.37±1.00*	12.19**
5	LGG 607 × LGG 630	0.14±1.25	0.08±1.25	-3.56±1.39*	-1.89±0.89*	8.52*

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



Fig 1: Crossing technique a. Emasculation, b. Pollination, c. Tagging and d. Developed pod from crossed flower.

by additive × additive [*i*] type of epistasis in the remaining one crosses (MGG 385 × WGG 42). The trait, seeds per pod is under control of additive × additive [*i*] type of gene effects in all the four crosses. Test weight's inheritance is under influence of; dominant × dominant [*l*] gene effects in one cross (MGG 385 × PM 5); additive × additive [*i*] gene effects in one cross (MGG 385 × LGG 630) and; additive × dominant [*j*] gene effects in the remaining two crosses (MGG 385 × LGG 607 and MGG 385 × WGG 42). With respect to grain yield per plant, all the four crosses, inheritance is under the control of additive × additive [*i*] type of non-allelic interactions. In spite of having significant magnitudes of other gene effects for various traits of different crosses, the above-mentioned gene effects overpowered them due to their higher magnitudes of effects.

Similar results of involvement of non-allelic or inter-allelic interactions in the inheritance of various traits were reported by many scientists [Khattak *et al*. (2004), Singh *et al*. (2006), Alam *et al*. (2014), Pathak *et al*. (2015), Singh *et al*. (2016), Narasimhulu *et al*. (2018), Yadav *et al*. (2017) and Sinha *et al*. (2020)] in mungbean. 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

Table 3. Estimates of components of gene effects and type of epistasis for YMD and yield related traits of mungbean.

Cross no.	Cross	*m*	*d*	*h*	*i*	*j*	*l*	Epistasis
				Yellow mosaic disease				
1	MGG 385 × LGG 607	3.34±0.33**	2.20±0.17**	-4.91±1.35**	-1.36±1.35	-1.35±0.18**	3.66±1.50*	D
2	MGG 385 × LGG 630	3.60±0.31**	2.30±0.17**	-4.75±1.29**	-1.40±1.28	-1.15±0.18**	3.50±1.44*	D
3	MGG 385 × WGG 42	5.45±0.33**	2.50±0.14**	-5.65±1.37**	-3.20±1.36*	-0.35±0.16*	3.90±1.48**	D
4	MGG 385 × PM 5	3.90±0.33**	2.60±0.17**	-5.70±1.38**	-2.40±1.37	-0.90±0.19**	3.80±1.52*	D
				Days to 50% flowering				
1	MGG 385 × LGG 607	30.50±0.19**	0.00±0.60	9.25±1.43**	10.00±1.41**	-1.25±0.62	-20.50±2.55**	D
2	MGG 385 × LGG 630	33.00±0.20**	0.00±0.33	0.00±1.06	2.00±1.03	0.50±0.35	-10.00±1.63**	-
3	MGG 385 × WGG 42	33.00±0.20**	5.00±0.40**	-1.00±1.15	-2.00±1.13	2.00±0.42**	4.00±1.85*	-
4	MGG 385 × PM 5	32.00±0.22**	1.50±0.41**	1.75±1.22	5.00±1.19**	-1.25±0.43**	-11.50±1.93**	-
				Plant height				
1	MGG 385 × LGG 607	48.00±0.37**	5.30±1.63**	-9.05±3.78*	-8.60±3.59*	2.05±1.78	20.50±7.11**	D
2	MGG 385 × LGG 630	47.00±0.38**	-0.80±1.43	14.20±3.48**	14.40±3.23**	-0.20±1.56	-8.40±6.44	-
3	MGG 385 × WGG 42	47.80±0.51**	3.90±1.74*	-3.95±4.28	-3.40±4.04	-0.45±1.89	17.50±7.80*	-
4	MGG 385 × PM 5	47.00±0.35**	6.21±1.71**	12.62±4.03**	14.02±3.69**	2.61±1.95	-13.64±7.67	-
				Branches per plant				
1	MGG 385 × LGG 607	5.37±0.38**	1.00±0.50	-0.42±1.87	-0.27±1.81	0.25±0.56	1.38±2.68	No non-allelic
2	MGG 385 × LGG 630	6.00±0.15**	-0.60±0.37	1.85±1.07	1.20±0.96	-0.55±0.45	-0.50±1.85	interactions
3	MGG 385 × WGG 42	5.37±0.23**	-0.01±0.49	2.41±1.44	2.11±1.34	-0.01±0.57	-1.49±2.40	
4	MGG 385 × PM 5	5.82±0.38**	0.13±0.52	0.58±1.91	0.46±1.84	0.13±0.61	0.04±2.78	
				Days to maturity				
1	MGG 385 × LGG 607	66.00±0.22**	1.40±0.57*	0.80±1.45	2.80±1.43	0.90±0.59	-5.60±2.50*	-
2	MGG 385 × LGG 630	62.50±0.37**	0.50±0.37	18.75±1.66**	19.00±1.64**	1.75±0.40**	-23.50±2.15**	D
3	MGG 385 × WGG 42	62.50±0.38**	1.50±0.40**	-1.25±1.73	3.00±1.70	-1.25±0.43**	-5.50±2.27*	-
4	MGG 385 × PM 5	62.50±0.38**	3.50±0.40**	2.25±1.73	7.00±1.73**	-0.75±0.42	-12.50±2.23**	-
				Clusters per plant				
1	MGG 385 × LGG 607	5.37±0.38**	0.10±0.45	7.18±1.79**	7.93±1.76**	-2.05±0.49**	-9.83±2.44**	D
2	MGG 385 × LGG 630	7.08±0.22**	1.90±0.47**	7.23±1.41**	7.08±1.29**	0.85±0.57	-5.58±2.38*	D
3	MGG 385 × WGG 42	6.74±0.19**	4.10±0.55**	5.09±1.43**	4.04±1.33**	1.25±0.63	-0.34±2.55	-
4	MGG 385 × PM 5	9.32±0.18**	0.50±0.69	5.17±1.60**	3.32±1.55*	-2.25±0.69**	-7.22±2.95*	D
				Pods per cluster				
1	MGG 385 × LGG 607	3.97±0.38**	-0.80±0.30	1.30±1.65	0.68±1.62	-0.40±0.36	0.00±2.02	No non-allelic
2	MGG 385 × LGG 630	3.50±0.35**	-0.40±0.40	3.25±1.65	2.40±1.61	-0.25±0.45	-2.90±2.25	interactions
3	MGG 385 × WGG 42	4.24±0.25**	-0.63±0.49	-1.62±1.43	-2.22±1.39	-0.23±0.52	3.48±2.30	
4	MGG 385 × PM 5	3.52±0.32**	0.97±0.54	0.14±1.72	-0.42±1.67	0.52±0.60	1.68±2.66	

Table 3: Continue...

Table 3: Continue...

			Pods per plant					
1	MGG 385 × LGG 607	29.00±0.38**	14.20±1.05**	-18.10±2.74**	-22.00±2.58**	6.90±1.16**	36.20±4.82**	D
2	MGG 385 × LGG 630	33.00±0.45**	-6.10±1.30**	-17.15±3.33**	-19.40±3.17**	-6.95±1.40**	45.10±5.87**	D
3	MGG 385 × WGG 42	28.00±0.47**	6.70±1.07**	3.75±3.04	1.40±2.84	2.25±1.21	10.90±5.16*	-
4	MGG 385 × PM 5	28.30±0.58**	17.44±1.54**	-13.61±4.19**	-22.88±3.87**	7.89±1.74**	53.30±7.33**	D
			Pod length					
1	MGG 385 × LGG 607	6.74±0.38**	0.13±0.25	5.41±1.60**	5.06±1.59**	-0.44±0.26	-9.77±1.84**	D
2	MGG 385 × LGG 630	6.52±0.05**	0.06±0.16	6.02±0.38**	5.84±0.36**	-0.45±0.17*	-6.16±0.69**	D
3	MGG 385 × WGG 42	8.31±0.13**	-0.41±0.16*	1.53±0.63*	1.22±0.61*	-0.12±0.18	-0.37±0.86	-
4	MGG 385 × PM 5	8.57±0.13**	-0.56±0.18**	-0.95±0.65	-1.16±0.64	-0.25±0.19	3.38±0.92**	-
			Seeds per pod					
1	MGG 385 × LGG 607	10.06±0.38**	1.78±0.75*	4.96±2.18*	5.56±2.13**	0.78±0.80	-5.36±3.49	-
2	MGG 385 × LGG 630	11.00±0.15**	-0.80±0.61	3.70±1.45*	3.60±1.36**	-1.80±0.68*	-2.60±2.70	-
3	MGG 385 × WGG 42	10.30±0.31**	-0.40±0.99	5.40±2.38*	5.60±2.33*	-1.40±1.04	-1.20±4.25	-
4	MGG 385 × PM 5	10.56±0.28**	0.67±1.23	6.32±2.80*	5.62±2.71*	-0.33±1.29	-0.88±5.24	D
			Test weight					
1	MGG 385 × LGG 607	3.90±0.38**	0.62±0.11**	-0.62±1.53	-0.84±1.52	0.27±0.13*	1.40±1.59	-
2	MGG 385 × LGG 630	3.26±0.05**	0.59±0.13**	2.02±0.36**	1.86±0.34**	0.15±0.15	-1.55±0.61*	D
3	MGG 385 × WGG 42	4.61±0.11**	-0.98±0.29**	-0.19±0.73	-0.48±0.73	-0.60±0.29*	1.66±1.25	-
4	MGG 385 × PM 5	5.07±0.13**	-1.53±0.17**	0.47±0.65	-0.42±0.63	-0.80±0.21**	2.55±0.93**	-
			Grain yield per plant					
1	MGG 385 × LGG 607	5.37±0.28**	0.57±0.77	4.45±1.99*	4.59±1.91*	0.63±0.84	-3.89±3.47	-
2	MGG 385 × LGG 630	5.20±0.34**	0.46±1.01	5.45±2.52*	5.32±2.44*	0.44±1.06	-3.97±4.45	-
3	MGG 385 × WGG 42	6.02±0.22**	-0.17±0.71	3.60±1.74*	3.50±1.66*	-0.17±0.75	-3.56±3.12	-
4	MGG 385 × PM 5	5.37±0.29**	-0.03±0.82	4.79±2.08*	4.75±2.01*	0.12±0.87	-4.17±3.63	-

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

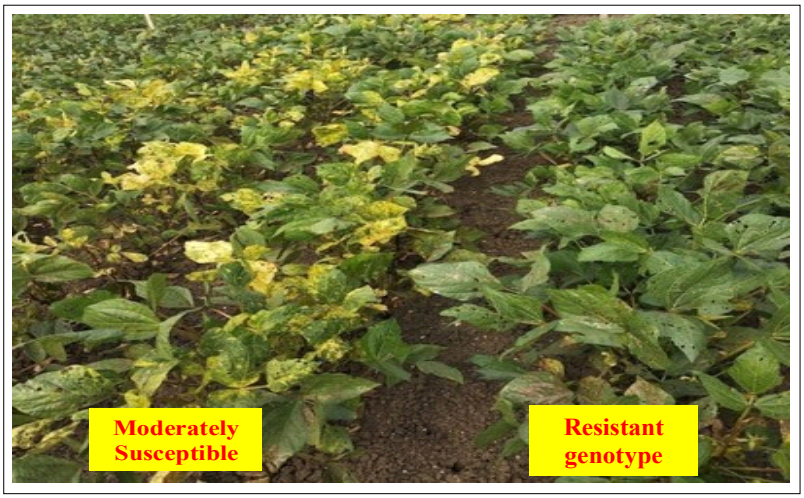


Fig 2: Screening of greengram genotypes against yellow mosaic disease.

the parents involved in the crosses (Viana *et al*., 1999). Inadequacy of additive-dominant model for explaining the inheritance of the ten out of twelve 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 is evident at least in few crosses for all the traits (except grain yield per plant) that had inadequacy for additive-dominant model. This duplicate type of epistasis was earlier indicated for various traits by different scientists [Khattak *et al*. (2004), Singh *et al*. (2006), Pathak *et al*. (2015), Singh *et al*. (2016), Narasimhulu *et al*. (2018), Yadav *et al*. (2017) and Sinha *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-matings in early segregating generations and postpone the selections to the later generations.

CONCLUSION

The scaling tests and Joint Scaling test indicated the inadequacy of Additive-dominant model for all most all traits including YMD except for branches per plant and pods per cluster. 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 is predominant. Further, the control of duplicate type of epistasis in the inheritance is evident at least in few crosses for all the traits (except grain yield per plant) 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. Finally, from the results of six parameter model of generation mean analysis 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

The authors of manuscript are having no conflict of interest.

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