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Exploring intra-allelic and inter-allelic gene interactions influencing seed yield and its components in inter-varietal crosses of Mungbean (*Vigna radiata* (L.) Wilczek)

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ABSTRACT

Mungbean (*Vigna radiata* (L.) Wilczek) is a versatile legume widely cultivated for its nutritional value and adaptability. Meeting the increasing global demand for nutritious food requires the development of high-yielding varieties. Therefore, understanding the inheritance of yield and component traits is crucial for defining effective breeding strategies. In the present study, we aimed to investigate the genetic effects and interactions governing inheritance through generation mean analysis. The four crosses *viz.*, IPM409-4×VGG18-002, IPM409-4×WGG42, COGG13-39×VGG16-058 and COGG13-39×VGG18-002 and their five generations (P_1, P_2, F_1, F_2, and F_3) were evaluated for nine yield and yield component traits during 2023 summer season. The significance of additive, dominance, and epistatic components *viz.*,additive×additive [*i*] and dominance×dominance [*l*] of each trait was found to be different among all the crosses. Mungbean is a self-pollinated crop, so only fixable gene effects can be exploited for trait improvement. In the IPM409-4×VGG18-002 cross, all the traits exhibited additive or additive × additive gene action except for plant height and seed yield per plant (dominance). The scaling test was significant in IPM409-4×WGG42 cross for all the traits, except for the number of pods per cluster. Except for the number of branches per plant in which the dominance effect was evident, additive or additive×additive gene effects were observed for the other traits. In COGG13-39×VGG16-058 and COGG13-39×VGG18-002 crosses, all the yield traits recorded fixable (additive and additive×additive) gene effects except for number of pods per plant in COGG13-39×VGG18-002. Considering the results of all four crosses, gene actions that exhibit consistency across crosses revealed that epistatic interaction (additive×additive) significantly influenced the expression of various mung bean traits. Therefore, the

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later generation selection of short-duration segregants with high yield, bold seeds, and resistance to yellow mosaic disease from the above populations can be carried out to develop commercially valuable mung bean varieties.

1 Introduction

Mungbean (*Vigna radiata* (L.) Wilczek) is a dynamic crop in Asia, serving significant roles as a food and economic resource. It is consumed in various forms, including whole or split seeds, flour, or sprouts, and serves as a valuable protein source (24 %). Additionally, mungbean offers substantial amounts of dietary fiber (64%), calcium (13%), magnesium (47%), and other vitamins and minerals (Shanthala et al. 2020). Despite its nutritional and economic value, the yield and productivity of mungbean in India remain unstable and volatile, leading to a broadening gap between demand and supply (Varma and Vishwanath 2023). Consequently, developing high-yielding varieties is crucial to meet the growing demands.

Conventional breeding methods in mungbean primarily involve hybridization followed by selection. Adopting an appropriate breeding strategy to enhance selection efficiency is essential based on understanding the gene action related to the yield and yield component traits. These traits are governed by complex gene actions, *viz.*, intra-allelic (additive and dominance) and inter-allelic interactions (epistasis), which are strongly influenced by environmental factors. Additive gene action resulting from the cumulative effects of many alleles can be effectively fixed through selection (Singh and Mahama 2023). Conversely, exploiting dominant gene action through hybrid development is impractical in mungbean due to the self-pollinating nature of the crop and the challenges in maintaining heterosis. Epistasis, or the interaction between genes at different loci, can significantly influence trait expression and complicate the estimation of additive and dominance effects. Although the epistatic component is of low magnitude, it should not be overlooked, as it can lead to biased estimates of additive and dominance variance. The presence or absence of epistasis can be identified through scaling tests. The application of the biometrical tool, generation mean analysis, is crucial for accurately delineating the nature of gene effects and the types of epistasis involved in the trait expression (Yadav et al. 2017). This method involves evaluating parents, $F_{1,}$ and segregating generations to partition the genetic variance into its constituent components. By doing so, researchers can identify the contributions of additive, dominance, and epistatic effects to the overall phenotype. This approach assists in determining the most appropriate breeding strategy for enhancing various yield-contributing traits in mungbean.

Therefore, the present investigation uses generation mean analysis to estimate the additive, dominance, and epistatic effects of the yield and yield contributing traits in the intra-specific crosses of mungbean. This knowledge will enable the development of mungbean varieties with stable and enhanced yields, ultimately bridging the gap between demand and supply.

2 Materials and Methods

Five mungbean genotypes including IPM 409-4, COGG 13-39, VGG 16-058, VGG 18-002 and WGG 42 were used to generate four segregating populations *viz.*, IPM 409-4 × VGG 18-002, IPM 409-4 × WGG 42, COGG 13-39 × VGG 16-058 and COGG 13-39 ×VGG 18-002. These crosses were decided based on the contrasting nature of the parents for duration and yield attributes. Details of the parental source and characteristics are presented in Table 1. The field experiment was conducted at the Department of Pulses, Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India. The

Table 1 Parent materials involved in the study with their characteristic features

S. No.	Genotypes	Source	Special Characteristics
		Female parents	
1.	IPM 409-4	ICAR-Indian Institute of Pulses Research, Kanpur	Variety: Early duration (<28 days to 50 % flowering), Shiny seeds, short pod (pod length < 8 cm)
2.	COGG 13- 39	Department of Pulses, Tamil Nadu Agricultural University, Coimbatore	Breeding line: Shiny seeds, high yield
		Male parents	
3.	VGG 16-058	National Pulses Research Centre, Vamban, Tamil Nadu Agricultural University, Coimbatore	Breeding line: Shiny, bold seeds (test weight > 5g/100 seeds) and resistant to yellow mosaic disease
4.	VGG 18-002	National Pulses Research Centre, Vamban, Tamil Nadu Agricultural University, Coimbatore	Breeding line: Shiny, bold seeds (test weight > 5g/100 seeds), long pod (pod length > 10 cm)
5.	WGG 42	Regional Agricultural Research Station, Warangal, Professor Jayashankar Telangana State Agricultural University, Hyderabad	Variety: Shiny seeds, bold seeds (test weight > 5g/100 seeds), long pod (pod length > 10 cm)

Table 2 Details of population size of all the generations of four crosses

S. No.	Crosses	Population size				
		P_1	P_2	F_1	F_2	F_3
1.	IPM 409-4 × VGG 18-002	10	10	10	48	89
2.	IPM 409-4 × WGG 42	10	10	10	99	253
3.	COGG 13- 39× VGG 16-058	10	10	10	84	210
4.	COGG 13- 39× VGG 18-002	10	10	10	152	179

crossing program was carried out in 2022 summer to synthesize hybrids of the above four crosses. During *Kharif* 2022, F_1s were raised, and the true hybrids were morphologically confirmed based on contrasting traits between parents. The true hybrid plants of F_1s were harvested individually, and the F_2 populations were raised during *rabi* 2022 to procure the seeds for F_3 generation.

2.1 Evaluation of Genetic Materials

The four crosses' five generations (P1, P2, F1, F2, and F3) were raised during the summer of 2023 in a row length of 4 m at a 30 × 10 cm spacing. Standard cultivation practices were strictly adhered to ensure a healthy crop. Nine biometrical traits, *viz.*, plant height, number of branches, number of clusters, number of pods per cluster, number of pods per plant, pod length, number of seeds per pod, hundred seed weight, and seed yield per plant were recorded in all five generations of four crosses (Table 2). The mean values of five generations were used to derive the gene effects.

2.2 Statistical analysis

The scaling test (Mather 1949) was used to test the adequacy of a simple additive-dominance model. The simple additive-dominance model was considered inadequate when either of the scales, *viz.*, C or D, were significant, indicating the presence of epistasis. The generation means analysis with a five-parameter model (Hayman 1960) was performed to estimate residual effect [*m*], additive [d], dominance [*h*], and epistatic components, *i.e.*, additive × additive [*i*] and dominance × dominance [*l*]. The five-parameter model lacks insights into additive × dominance [*j*] interactions, and data analysis was conducted using the TNAUSTAT statistical package (Manivannan 2014).

3 Results and Discussion

The precise knowledge of gene effects governing the expression of yield and yield-contributing traits is essential for formulating an efficient breeding and selection strategy. The generation mean analysis was carried out in the four inter-varietal crosses *viz.*, IPM 409-4 × VGG 18-002, IPM 409-4 × WGG 42, COGG 13-39 × VGG 16-058 and COGG 13-39 × VGG 18-002 to estimate the additive, dominant and epistatic effects influencing yield and yield components. Each parent exhibited distinctive characteristics, such as IPM 409-4 with early duration (<28 days for 50 % flowering), COGG 13-39 being high-yielding (>20 g/singe plant), and male parents *viz.*, VGG 18-002, VGG 16-058 and WGG 42 with bold seeds (test weight >5 g/100 seeds) (Table 3). This indicates that variability in mean performance exists for yield components, suggesting the potential for further improvement.

Among the parents, COGG 13-39 outperformed for traits such as number of branches (2.70), number of clusters (15.70), number of pods per cluster (5.00), number of pods per plant (49.90), and seed yield per plant (23.09 g) (Table 3). The male parent, VGG 18-002 was found to be superior for pod length (10.15 cm), number of seeds per pod (12.40), and hundred seed weight (5.54 g) (Table 3). In F_1 generation, mean performance surpassed that of the parental mean value in IPM 409-4 × VGG 18-002 cross for seed yield per plant (18.85 g) and in IPM 409-4 × WGG 42 cross for number of branches (3.50) indicating potential vigor for yield and branching (Table 3). However, major yield components *viz.*, number of clusters, number of pods per plant, pod length and hundred seed weight in all the four crosses (IPM 409-4 × VGG 18-002, IPM 409-4 × WGG 42, COGG 13-39 × VGG 16-058 and COGG 13-39 × VGG 18-002) exhibited intermittent values within the range of parental values (Table 3). In F_2 to F_3 generations, an upward trend was observed in the expression of all traits in IPM 409-4 × VGG 18-002 and COGG 13-39 × VGG 18-002 populations except for number of clusters in IPM 409-4 × VGG 18-002 and number of branches, pod length and number of seeds per pod in COGG 13-39 × VGG 18-002 (Table 3).

In all the four inter-varietal crosses evaluated for nine biometrical traits through scaling tests, at least one of the two scales (C and D) consistently exhibited statistical significance except the number of pods per cluster in IPM 409-4 × WGG 42 and the number of pods per plant in COGG 13-39 × VGG 16-058 (Table 4). The significant deviation of scales from zero indicated the presence of epistasis (non-allelic interaction). The presence of epistatic interactions in mungbean for yield and yield-related traits has been substantiated through various studies and research findings. In mungbean, Lenka et al. (2022) and Nainu et al. (2023) have observed complex genetic interactions influencing traits such as yield per plant, number of pods per plant, seed weight, and other productivity-related parameters. These interactions play a significant role in shaping the phenotypic expression of traits and are critical considerations in breeding programs aimed at enhancing yield in mungbean varieties.

Table 3 Mean and standard errors for yield and yield component traits in various generations of mungbean crosses

Cross	Traits	Generation				
		P_1	P_2	F_1	F_2	F_3
IPM 409-4 × VGG 18-002	Plant height (cm)	60.69±0.97	58.39±0.80	52.16±1.31	32.33±0.72	40.68±0.98
	Number of branches	2.20 ± 0.13	2.40 ± 0.16	2.40 ± 0.24	2.71 ± 0.12	2.88 ± 0.09
	Number of clusters	14.90 ± 0.72	8.40 ± 0.62	11.60 ± 0.93	10.04 ± 0.42	8.38 ± 0.34
	Number of pods per clusters	4.10 ± 0.28	4.20 ± 0.25	3.60 ± 0.24	3.25 ± 0.08	4.07 ± 0.10
	Number of pods per plant	50.50 ± 4.01	29.80 ± 1.05	31.80 ± 1.11	27.31 ± 1.22	31.78 ± 1.54
	Pod length (cm)	7.05 ± 0.11	10.15 ± 0.13	7.88 ± 0.11	7.65 ± 0.12	7.95 ± 0.08
	Number of seeds per pod	11.50 ± 0.29	12.40 ± 0.29	12.20 ± 0.27	10.74 ± 0.12	10.95 ± 0.10
	Hundred seed weight (g)	3.53 ± 0.11	5.54 ± 0.09	4.71 ± 0.07	4.17 ± 0.07	4.25 ± 0.05
	Seed yield per plant (g)	16.48 ± 1.13	15.97 ± 0.84	18.85 ± 0.86	12.55 ± 0.41	14.39 ± 0.42
IPM 409-4 × WGG 42	Plant height (cm)	60.69 ± 0.97	66.76 ± 2.46	48.67 ± 2.32	30.32 ± 0.60	39.11 ± 0.35
	Number of branches	2.20 ± 0.13	2.10 ± 0.10	3.50 ± 0.22	2.33 ± 0.06	2.29 ± 0.03
	Number of clusters	14.90 ± 0.72	12.90 ± 0.5	14.83 ± 1.62	11.01 ± 0.30	9.28 ± 0.2
	Number of pods per clusters	4.10 ± 0.28	4.40 ± 0.37	4.00 ± 0.37	3.79 ± 0.09	3.92 ± 0.05
	Number of pods per plant	50.50 ± 4.01	30.60 ± 0.69	38.00 ± 4.18	35.61 ± 1.18	29.78 ± 0.81
	Pod length (cm)	7.05 ± 0.11	9.56 ± 0.14	7.18 ± 0.16	7.75 ± 0.07	6.80 ± 0.03
	Number of seeds per pod	11.50 ± 0.29	12.73 ± 0.24	10.06 ± 0.23	10.67 ± 0.09	11.26 ± 0.05
	Hundred seed weight (g)	3.53 ± 0.11	5.02 ± 0.17	4.27 ± 0.10	4.09 ± 0.05	3.44 ± 0.02
	Seed yield per plant (g)	16.48 ± 1.13	15.96 ± 0.75	11.30 ± 2.34	15.42 ± 0.53	13.95 ± 0.22
COGG 13-39 × VGG 16-058	Plant height (cm)	66.54 ± 1.60	58.10 ± 0.74	52.34 ± 1.15	54.99 ± 0.63	54.51 ± 0.51
	Number of branches	2.70 ± 0.26	1.70 ± 0.26	2.10 ± 0.10	3.17 ± 0.09	2.76 ± 0.07
	Number of clusters	15.70 ± 0.98	9.00 ± 0.47	8.10 ± 0.60	9.99 ± 0.48	8.44 ± 0.21
	Number of pods per clusters	5.00 ± 0.15	4.00 ± 0.26	5.00 ± 0.26	4.08 ± 0.09	4.03 ± 0.06
	Number of pods per plant	49.90 ± 2.51	28.80 ± 0.71	29.20 ± 1.70	33.95 ± 2.14	33.88 ± 0.96
	Pod length (cm)	8.04 ± 0.1331	8.84 ± 0.147	8.07 ± 0.22	8.55 ± 0.06	8.41 ± 0.05
	Number of seeds per pod	11.63 ± 0.3	11.53 ± 0.14	11.12 ± 0.29	11.37 ± 0.10	11.19 ± 0.06
	Hundred seed weight (g)	4.13 ± 0.03	5.03 ± 0.05	4.28 ± 0.14	4.51 ± 0.05	4.37 ± 0.04
	Seed yield per plant (g)	23.09 ± 0.9	14.24 ± 0.35	15.47 ± 1.22	15.79 ± 0.38	14.32 ± 0.28
COGG 13-39 × VGG 18-002	Plant height (cm)	66.54 ± 1.6	58.39 ± 0.77	53.50 ± 1.79	64.29 ± 1.02	65.13 ± 0.81
	Number of branches	2.70 ± 0.26	2.40 ± 0.16	2.60 ± 0.22	3.11 ± 0.08	3.42 ± 0.08
	Number of clusters	15.70 ± 0.98	8.40 ± 0.62	14.00 ± 0.63	10.55 ± 0.37	12.14 ± 0.38
	Number of pods per clusters	5.00 ± 0.15	4.20 ± 0.25	3.60 ± 0.22	4.15 ± 0.07	4.96 ± 0.07
	Number of pods per plant	49.90 ± 2.51	29.80 ± 1.05	45.30 ± 3.12	37.45 ± 1.31	45.56 ± 1.25
	Pod length (cm)	8.04 ± 0.13	10.15 ± 0.13	8.60 ± 0.12	8.24 ± 0.04	7.85 ± 0.04
	Number of seeds per pod	11.63 ± 0.30	12.40 ± 0.29	11.87 ± 0.16	11.40 ± 0.06	11.24 ± 0.05
	Hundred seed weight (g)	4.13 ± 0.030	5.54 ± 0.09	4.66 ± 0.09	4.21 ± 0.03	3.96 ± 0.02
	Seed yield per plant (g)	23.09 ± 0.90	15.97 ± 0.48	20.97 ± 0.77	16.35 ± 0.53	16.50 ± 0.39

Mean ± Standard error

Table 4 Scaling test and estimates of genetic parameters for yield and yield contributing traits of mungbean crosses

Cross	Trait	Scale		Parameter				
		C	D	*m*	[*d*]	[*h*]	[*i*]	[*l*]
IPM 409-4 × VGG 18-002	Plant height	-94.39** ± 4.09	-21.32** ± 4.38	32.33** ± 0.72	1.00 ± 0.63	-9.05** ± 3.12	0.48 ± 2.97	97.42** ± 8.53
	Number of branches	1.43* ± 0.72	1.49** ± 0.49	2.71** ± 0.12	-0.10 ± 0.11	-0.65 ± 0.38	-0.95* ± 0.42	0.07 ± 1.26
	Number of clusters	-6.33* ± 2.68	-9.86** ± 1.87	10.04** ± 0.42	3.25** ± 0.48	5.46** ± 1.39	12.01** ± 1.65	-4.70 ± 4.56
	Number of pods per clusters	-2.50** ± 0.70	1.47** ± 0.56	3.25** ± 0.08	-0.05 ± 0.19	-1.95** ± 0.34	-1.50** ± 0.47	5.29** ± 1.05
	Number of pods per plant	-34.65** ± 6.78	-7.82 ± 7.82	27.31** ± 1.22	10.35** ± 2.08	-8.91 ± 4.84	20.14** ± 6.2	35.77** ± 13.10
	Pod length	-2.35** ± 0.54	-0.70 ± 0.44	7.65** ± 0.12	-1.55** ± 0.08	-0.65 ± 0.33	-3.03** ± 0.36	2.20* ± 1.07
	Number of seeds per pod	-5.32** ± 0.85	-1.60* ± 0.63	10.74** ± 0.12	-0.45* ± 0.21	0.42 ± 0.41	-0.72 ± 0.55	4.97** ± 1.34
	Hundred seed weight	-1.82** ± 0.35	-0.39 ± 0.30	4.17** ± 0.07	-1.01** ± 0.07	0.14 ± 0.21	-2.06** ± 0.25	1.90** ± 0.66
	Seed yield per plant	-21.44** ± 2.77	-1.49 ± 2.35	12.55** ± 0.41	-0.5 ± 0.70	-0.71 ± 1.51	-3.57 ± 1.96	26.59** ± 4.62
IPM 409-4 × WGG 42	Plant height	-103.53** ± 5.85	-31.64** ± 3.23	30.32** ± 0.6	-3.04* ± 1.32	-11.22** ± 2.17	-2.23 ± 2.88	95.84** ± 8.04
	Number of branches	-1.97** ± 0.53	0.19 ± 0.24	2.33** ± 0.06	0.05 ± 0.08	0.90** ± 0.21	-0.35 ± 0.28	2.87** ± 0.77
	Number of clusters	-13.43** ± 3.57	-12.71** ± 1.33	11.01** ± 0.3	1.00* ± 0.44	7.17** ± 1.34	8.24** ± 1.69	0.95 ± 5.05
	Number of pods per clusters	-1.35 ± 0.94	-0.39 ± 0.54	3.79** ± 0.09	-1.15* ± 0.23	-0.21 ± 0.34	-	-
	Number of pods per plant	-14.68 ± 10.43	-33.18** ± 5.71	35.61** ± 1.18	9.95** ± 2.04	17.13** ± 4.24	39.58** ± 6.37	-24.67 ± 15.23
	Pod length	0.02 ± 0.48	-4.88** ± 0.27	7.75** ± 0.07	-1.26** ± 0.09	2.13** ± 0.20	0.74** ± 0.27	-6.54** ± 0.75
	Number of seeds per pod	-1.65* ± 0.71	-0.54 ± 0.48	10.67** ± 0.09	-0.62** ± 0.19	-1.98** ± 0.28	-1.15* ± 0.46	1.48 ± 1.01
	Hundred seed weight	-0.73* ± 0.34	-2.97** ± 0.23	4.09** ± 0.05	-0.75** ± 0.10	1.85** ± 0.13	0.36 ± 0.21	-2.99** ± 0.48
	Seed yield per plant	4.61 ± 5.31	-9.55** ± 1.94	15.42** ± 0.53	-0.77 ± 0.68	1.19 ± 1.98	5.60* ± 2.58	-18.88* ± 7.64

Cross	Trait	Scale		Parameter				
		C	D	*m*	[*d*]	[*h*]	[*i*]	[*l*]
COGG 13-39 × VGG 16-058	Plant height	-9.36* ± 3.84	-16.59** ± 2.97	54.99** ± 0.63	4.22** ± 0.88	-0.48 ± 2.00	17.94** ± 2.71	-9.64 ± 6.49
	Number of branches	4.07** ± 0.54	0.31 ± 0.50	3.17** ± 0.09	0.50* ± 0.18	0.37 ± 0.27	1.47** ± 0.41	-5.00** ± 0.83
	Number of clusters	-0.95 ± 2.5	-10.92** ± 1.67	9.99** ± 0.48	3.35** ± 0.54	2.87* ± 1.18	13.82** ± 1.72	-13.30** ± 4.29
	Number of pods per clusters	-2.67** ± 0.71	-1.03* ± 0.43	4.08** ± 0.09	0.50** ± 0.15	0.74* ± 0.31	1.24** ± 0.39	2.18* ± 1.08
	Number of pods per plant	-1.29 ± 9.59	-11.10 ± 6.32	33.95** ± 2.14	10.55** ± 1.30	-2.97 ± 5.12	-	-
	Pod length	1.17* ± 0.55	-0.33 ± 0.31	8.55** ± 0.06	-0.40** ± 0.10	0.05 ± 0.23	-0.39 ± 0.30	-2.00* ± 0.82
	Number of seeds per pod	0.10 ± 0.78	-1.17* ± 0.46	11.37** ± 0.10	0.05 ± 0.17	0.33 ± 0.32	1.89* ± 0.49	-1.68 ± 1.16
	Hundred seed weight	0.32 ± 0.34	-0.70** ± -0.19	4.51** ± 0.05	-0.45** ± 0.03	0.22 ± 0.17	-0.37* ± 0.18	-1.36* ± 0.56
	Seed yield per plant	-5.12 ± 3.03	-11.60** ± 1.67	15.79** ± 0.38	4.43** ± 0.48	3.69** ± 1.35	15.73** ± 1.74	-8.64 ± 4.70
COGG 13-39 × VGG 18-002	Plant height	25.24** ± 5.71	7.01 ± 4.22	64.29** ± 1.02	4.08** ± 0.89	-9.43** ± 3.2	7.68* ± 3.70	-24.31* ± 10.39
	Number of branches	2.15** ± 0.63	2.37** ± 0.46	3.11** ± 0.08	0.15 ± 0.15	-1.18** ± 0.3	-0.93* ± 0.42	0.30 ± 0.97
	Number of clusters	-9.89** ± 2.27	3.35 ± 2.04	10.55** ± 0.37	3.65** ± 0.58	-1.93 ± 1.32	3.42* ± 1.69	17.66** ± 3.97
	Number of pods per clusters	0.21 ± 0.60	2.34** ± 0.42	4.15** ± 0.07	0.4* ± 0.15	-2.53** ± 0.27	-0.73* ± 0.34	2.85** ± 0.90
	Number of pods per plant	-20.51* ± 8.59	27.66** ± 6.27	37.45** ± 1.31	10.05** ± 1.36	-16.41** ± 4.72	-1.76 ± 5.42	64.23** ± 14.95
	Pod length	-2.42** ± 0.36	-3.29** ± 0.25	8.24** ± 0.04	-1.06** ± 0.09	1.3** ± 0.16	-0.32 ± 0.23	-1.16* ± 0.53
	Number of seeds per pod	-2.18** ± 0.58	-1.87** ± 0.48	11.4** ± 0.06	-0.38 ± 0.21	0.73** ± 0.21	0.12 ± 0.42	0.41 ± 0.71
	Hundred seed weight	-2.17** ± 0.24	-2.25** ± 0.16	4.21** ± 0.03	-0.7** ± 0.05	0.96** ± 0.11	-0.27* ± 0.13	-0.10 ± 0.39
	Seed yield per plant	-15.59** ± 2.82	-5.76** ± 2.15	16.35** ± 0.53	3.56** ± 0.51	2.69 ± 1.58	8.36** ± 1.91	13.11* ± 5.16

* & ** Significance at 0.05 and 0.01 probability levels, respectively; C- Scale C; D- Scale D; m- Residual; [d]- Additive; [h]- Dominance; [i]- Additive × Additive; [l]- Dominance × Dominance; (-)- Absence of epistasis

3.1 Gene action

On dissection of the generation mean into five different genetic components, the effect of residual mean was highly significant, indicating variation across the generations in all crosses. For each trait, the significance and relative strength of additive, dominance, and epistatic components *viz.*, additive × additive [*i*] and dominance × dominance [*l*] were different from each other in all four crosses (Table 4). The observed disparity can be attributed to the involvement of genes with varying frequencies and contrasting or synergistic effects in the parental genotypes. Therefore, a targeted selection strategy tailored to specific crosses could be developed for trait improvement, followed by a more generalized strategy. However, as a highly self-pollinated crop, mungbean, only the fixable gene effects, *viz.*, additive and additive × additive, could be exploited for trait improvement. Therefore, in the present study, for deciding the selection criteria, the non-fixable gene effects (dominance and dominance × dominance) were ignored when the fixable gene effects for the traits were significant.

In IPM 409-4 × VGG 18-002 population, various traits such as number of clusters, number of pods per plant, pod length, and hundred seed weight displayed additive and additive × additive gene actions (Table 4). This indicates that the expression of these traits is influenced by individual gene effects (additive) and interactions between genes (epistasis), specifically additive × additive interactions. In contrast, traits like the number of seeds per pod exhibited additive gene action, and the number of branches and pods per cluster exhibited additive × additive gene action (Table 4). These findings suggest that selection strategies for traits exhibiting epistatic interactions should be deferred to later generations to harness these interactions for trait improvement effectively. Previous studies by Latha et al. (2018) and Kanwade et al. (2019) have reported similar genetic findings in mungbean, corroborating the presence of fixable gene effects for traits such as number of branches, number of clusters, number of pods per cluster, number of pods per plant and hundred seed weight. This implies that these traits can be improved through selective breeding efforts targeting additive and epistatic gene interactions. Conversely, plant height and seed yield per plant displayed nonfixable gene effects (dominance and dominance × dominance) (Table 4). Latha et al. (2019) and Lenka et al. (2022) have also reported the predominance of dominance × dominance gene interaction for plant height and Kanwade et al. (2019) and Patel et al. (2012) for seed yield per plant in mungbean. However, in mungbean, non-fixable gene effects cannot be exploited through selection.

The outcomes of the scaling test in the IPM 409-4 × WGG 42 population revealed that epistasis was significant for all the traits except for the number of pods per cluster (Table 4). Notably, additive gene action was observed for the number of pods per cluster, indicating the feasibility of early-generation selection for trait improvement. The additive gene action for the number of pods per cluster corroborates with the findings of Pathak et al. (2014) in mungbean, validating the role of additive effects in shaping this trait. Simultaneously, additive and additive × additive gene effects influenced the inheritance of the number of clusters, number of pods per plant, pod length, number of seeds per pod, and hundred seed weight, while the predominance of additive gene effect for plant height and additive × additive gene effects for seed yield per plant were observed (Table 4) underscoring their complex genetic inheritance. With fixable gene effects and epistasis, the above traits can be improved through selection in later generations. The results of fixable gene effects were reported for plant height, number of clusters, and number of pods per plant by Latha et al. (2018), for pod length by Lenka et al. (2022), and number of seeds per pod and hundred seed weight by Yadav et al. (2017) and Narasimhulu et al. (2018) in mungbean. On the other hand, the absence of significant fixable gene effects for the number of branches indicated that trait improvement through selection is not feasible in this population.

In this study, COGG 13-39 × VGG 16-058 population of mungbean, we investigated the genetic effects influencing various agronomic traits (Table 4). Epistasis was notably present in all traits except for the number of pods per plant, which displayed primarily additive gene action, suggesting its suitability for early-generation selection. This finding is consistent with previous research by Kumar et al. (2015), further supporting the role of additive genetic effects in influencing the number of pods per plant. Whereas, for most traits *viz.*, plant height, number of branches, number of clusters, number of pods per cluster, hundred seed weight, and seed yield per plant were recorded as additive and additive × additive gene effects (Table 4). Further, pod length and number of seeds per pod exhibited additive and additive × additive gene actions, respectively (Table 4). Consequently, the above traits with fixable epistatic gene effects can be effectively improved by postponing the selection process to later generations. This indicates a complex genetic architecture where trait expression is influenced by interactions between alleles at different loci, highlighting the need for strategic breeding approaches. The findings of Pathak et al. (2014) suggested a selection procedure involving delayed selection that fixes the additive × additive genetic effect for the above traits in later generations. The selection procedure of delayed selection, which fixes the additive × additive genetic effect for the number of branches, number of clusters, number of pods per cluster, and hundred seed weight, was also reported by Narasimhulu et al. (2018) and for pod length and number of seeds per pod by Lenka et al. (2022) in mungbean. Kumar et al. (2015) have also reported additive and additive × additive gene actions for seed yield per plant in mungbean. These studies advocate for a delayed selection strategy that stabilizes additive × additive genetic effects in subsequent generations, providing insights for optimizing breeding programs to improve mungbean productivity traits through genetic manipulation and selection strategies tailored to trait-specific genetic architectures.

In COGG 13-39 × VGG 18-002 population, additive, and additive × additive gene effects were reported for plant height, number of clusters, number of pods per cluster, hundred seed weight, and seed yield per plant (Table 4). The findings of significant fixable genetic components for the above traits in mungbean were in accordance with Latha et al. (2018), Narasimhulu et al. (2018), and Nainu et al. (2023). Whereas, additive gene action was prevalent for expressing the number of pods per plant and pod length, and additive × additive gene action was prevalent for the number of branches (Table 4). Additive × additive gene action for the number of branches (Kumar et al. 2015; Narasimhulu et al. 2018) and additive gene effects for the number of pods per plant and pod length (Alam et al. 2014) were reported in mungbean. The presence of significant additive and additive × additive gene actions suggests that selecting for these traits should be deferred to later generations to exploit their genetic potential fully. This strategic selection delay aligns with current literature recommendations, ensuring stabilization and enhancement of desired traits through cumulative genetic effects over generations. On the contrary, the predominance of dominance gene action in the expression of the number of seeds per pod indicates that trait improvement is not achievable through selection. This finding is corroborated by recent studies of Narasimhulu et al. (2018) and Latha et al. (2019), highlighting the challenge of improving number of seeds per pod through traditional selection approaches due to the nature of non-fixable genetic effects. The complex interplay of additive, additive × additive, and dominance gene actions in trait inheritance is evident. These insights underscore the importance of tailored breeding strategies that leverage genetic interactions to optimize mungbean cultivars for enhanced productivity.

Conclusion

For formulating a selection program for mungbean, emphasis was placed on identifying gene actions that exhibit consistency in most of the crosses. Epistatic interactions played a crucial role in the inheritance of the number of branches, number of clusters, number of pods per cluster, hundred seed weight, and seed yield per plant. However, these traits were under the influence of additive × additive (fixable) gene effects, and hence, improvement through selection in later generations is feasible when desirable recombinants become available. As these populations were derived from early-maturing, bold-seeded, and high-yielding parents, selecting high-yielding segregants, combined with traits such as early maturity and bold seeds, becomes feasible in subsequent generations. In addition, due to the involvement of MYMV-resistant male parents (VGG 16-058), the selection strategy coupled with MYMV screening will be rewarding.

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Conflict of Interest

The authors declare no conflict of interest

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