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Inheritance Pattern of Yield and its Components in Brinjal (*Solanum melongena* L.) Through Generation Mean Analysis

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ABSTRACT

Background: Eggplant is a prominent vegetable crop in India, valued for its nutritional and medicinal properties. Improving yield and related traits in brinjal demands a clear insight into the gene-actions governing quantitative traits. The development and cultivation of numerous high-yielding hybrids have further boosted brinjal production across the country. Generation mean analysis offers an effective approach to dissect genetic architecture, including additive, dominance and epistatic effects, that influence trait inheritance.

Methods: The study evaluated six generations (P_1, P_2, F_1, F_2, B_1 and B_2) from four brinjal crosses-JBL-1 × JBR-4, JBR-2 × JBR-5, JBR-1 × JBR-6 and JBR-3 × JBL-3-at the experimental farm of LPU during *Kharif* 2024. Data were recorded on ten traits including fruit yield, its components, earliness and pest infestation. Scaling tests and joint scaling tests were conducted to test model adequacy. A six-parameter model was used to estimate gene effects [m], [d], [h], [i], [j] and [l] to identify the types and magnitudes of gene interactions.

Result: Significant deviations from the additive-dominance model across most traits confirmed the pervasive influence of epistasis. Duplicate epistasis emerged as the predominant form of gene interaction for all traits studied DFF, DP, FL, FG, NFPP (except family 2), NPBP (except family 3), PH, TFYP (except 3 and 4 families) and FBI. Total fruit yield per plant exhibited complex inheritance involving both additive and non-allelic effects. The identification of crosses exhibiting favorable additive and duplicate epistatic effects underscores their potential for genetic enhancement of yield and early maturity in brinjal breeding programs.

Key words: Additive effect, Brinjal, Dominance, Epistasis gene effect, Gene interaction, Generation mean analysis.

INTRODUCTION

Eggplant (*Solanum melongena* L.), a key Solanaceae crop, is widely cultivated year-round in India and globally due to its adaptability to tropical and temperate climates. Primarily valued for its unripe fruits as a vegetable (Rai *et al.*, 1995), brinjal is cultivated during warm seasons in temperate regions. India, being the main center of origin and diversity, ranks second in global production, with 711 lakh hectares yielding 13,558 million tons at an average of 19.1 tons/ha (Gupta *et al.*, 2025). Its growing popularity is attributed to its medicinal and antioxidant benefits (Susmitha *et al.*, 2023).

Brinjal is a major vegetable crop in India, with key producing states including Gujarat, Bihar, Madhya Pradesh, Odisha and West Bengal (Thota and Delvadiya, 2025). It is commercially important due to growing hybrid adoption driven by early maturity, high yield and superior fruit traits (Ginoya *et al.*, 2021). Nutritionally, brinjal provides carbohydrates (6.4%), protein (1.3%), fat (0.3%), minerals like calcium, phosphorus, iron and vitamins such as β-carotene, riboflavin, thiamine, niacin and vitamin C. Crop improvement depends on understanding the genetic control of key traits. Insights into gene action and trait correlations help breeders enhance selection efficiency and predict outcomes in segregating generations (Bhatt *et al.*, 2023; Gunasekar *et al.*, 2018). Variation in gene action across populations stresses the need to assess genetic architecture within specific stocks before breeding (Ginoya *et al.*, 2025). Analyzing gene effects through six basic generations (P_1, P_2, F_1, F_2, B_1 and B_2) helps understand trait expression in both interacting and non-interacting crosses (Kumar *et al.*, 2022).

To accurately assess gene interactions, this study adopted a six-parameter generation mean analysis model, as conventional additive-dominance models often overlook the critical role of inter allelic effects. Incorporating epistatic interactions with additive and dominance effects offers a clearer insight into their impact on eggplant yield and related traits. The six-generation design enables accurate estimation of genotypic values reflected in the average phenotypic performance of each generation.

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MATERIALS AND METHODS

Plant material

The research material comprised six basic generations P_1, P_2, F_1, F_2, B_1 and B_2 developed from four brinjal crosses: JBL-1 × JBR-4, JBR-2 × JBR-5, JBR-1 × JBR-6 and JBR-3 × JBL-3. These generations were evaluated at the experimental farm of Lovely Professional University (LPU) during the *Kharif* season of 2022. Seeds were initially raised in nursery beds measuring 6 m × 1 m × 0.15 m and seedlings were later transplanted at a spacing of 60 cm × 45 cm. The trial was laid out in a Compact Family Block Design (CFBD) with three replications. F_1 seeds were obtained through manual hybridization in 2022, followed by selfing to produce F_2 seeds and backcrossing to generate B_1 and B_2 generations during *Kharif* 2023. All six generations from each cross were again raised in nursery beds and transplanted in the field for evaluation during the *Kharif* season of 2024.

Observations recorded and data analysis

Data was recorded for various traits across different generations. For each parent and F_1 generation, observations were taken from five randomly selected plants per replication. In the F_2 generation, data were recorded from twenty plants per replication, while ten plants were observed from each backcross generation (B_1 and B_2). The traits evaluated included fruit length (FL) (cm), number of fruits per plant (NFPP), number of primary branches per plant (NPBP), plant height (PH) (cm), total fruit yield per plant (TFYP) (g) and fruit borer infestation (FBI) (%). However, for days to 50% flowering (DFF) and days to first picking (DP), observations were recorded on a plot basis.

Scaling tests and genetic model analysis

To evaluate the adequacy of the additive-dominance model, scaling tests proposed by Mather, (1949) and further elaborated by Hayman and Mather, (1955) were applied. These included:

- $A = 2B_1 - P_1 - F_1$
- $B = 2B_2 - P_2 - F_1$
- $C = 4F_2 - 2F_1 - P_1 - P_2$
- $D = 2F_2 - B_1 - B_2$

The joint scaling test (Cavalli, 1952) was employed to evaluate genic effects and the genetic model. It estimates parameters *m*, [*d*] and [*h*] through weighted least squares and compares expected and observed generation means.

For a more comprehensive understanding of gene interactions, a six-parameter model (digenic interaction model) was used to estimate the following genetic components:

- $m = ½ (P_1 + P_2) + 4F_2 - 2B_1 + 2B_2$
- $[d] = ½ (P_1 - P_2)$
- $[h] = 6B_1 + 6B_2 - 8F_2 - F_1 - 3/2P_1 - 3/2P_2$
- $[i] = 2B_1 + 2B_2 - 4F_2$ (Additive × Additive interaction)
- $[j] = 2B_1 - P_1 - 2B_2 + P_2$ (Additive × Dominance interaction)
- $[l] = P_1 + P_2 + 2F_1 + 4F_2 - 4B_1 - 4B_2$ (Dominance × Dominance interaction)

As per Mather and Jinks, (1982), the best-fit genetic model shows the lowest non-significant χ^2 value and the highest number of significant genetic parameters.

RESULTS AND DISCUSSION

The present investigation was undertaken to elucidate the type and magnitude of gene action governing important quantitative traits in brinjal using generation mean analysis. Unlike conventional methods (*e.g.*, diallel, line × tester), this approach captures additive, dominance and epistatic effects, aiding in the identification of fixable genetic components for effective selection.

The joint scaling test and generation mean analysis indicated significant deviations from the additive-dominance model for most traits, revealing the presence of epistatic. Traits as DFF, DP, FG and PH exhibited strong epistasis across most families, with all scales and χ^2 values being significant (Table 1). For FL, significant epistasis was observed in Families 3 and 4, while Families 1 and 2 showed a mix of significant and non-significant scales but still recorded significant χ^2 values. In AFW, Family 3 followed the additive-dominance model, whereas Families 1, 2 and 4 exhibited epistasis; Family 2 also displayed a positive dominance component. Non-allelic interactions were evident in NFPP (Families 1, 3 and 4), while Family 2 showed mixed gene interactions. In NBPP, only Family 3 fit the additive-dominance model; others, especially Family 2, suggested complementary gene action. For TFYP, Family 3 showed model adequacy, while others revealed epistasis. For FBI, only Family 4 showed significant epistasis, indicating non-allelic gene action, while other families displayed non-significant X^2 values, suggesting a partial fit to the additive-dominance model.

Earliness is crucial for market value in vegetables with DFF and DP serving as key indicators. In the present study, all brinjal families showed significant gene interactions for DFF, particularly additive × additive [i] and dominance × dominance [l], indicating duplicate epistasis favoring early flowering. Families 2 and 4 showed opposing [h] and [l] signs, confirming this interaction. For DP, dominance was notable in Family 1, while Families 2, 3 and 4 showed duplicate epistatic effects, suggesting gene interactions contribute to early maturity.

Duplicate gene action was prominent in Families 1, 3 and 4 through significant [i] and negative [l] effects. Family 3 expressed all gene parameters, indicating strong improvement potential. In AFW, favorable [h], [i] and [l] were noted in Family 1, whereas Families 2 and 3 had negative additive and dominance effects. Family 4 showed negative [j] and [l], limiting its use for this trait. For FG, Families 1 and 3 exhibited favorable dominance and [i] effects, while Families 2 and 4 also indicated improvement scope through positive interactions.

Different gene actions governed yield and plant architecture traits, with duplicate epistasis observed in Families 1, 2 and 4 for NFPP, NPBP and PH. Family 4

Table 1: Estimates of additive, dominance and epistatic effects for yield traits in Brinjal.

Trait/cross	Gene Effect											
	A	B	C	D	χ^2	M	[d]	[h]	[i]	[j]	[l]	Epistasis
DFF												
Family-1	*	*	*	*	166.50**	45.2**± 0.33	0.03±0.73	10.76**±2.09	11.8**±1.99	-0.33±0.88	-36.73**±3.47	D
Family-2	*	*	*	*	72.19**	40.5**±0.35	-2.4**±0.73	12.56**±2.21	10.66**±2.04	-2.36**±0.84	-27.66**±3.69	D
Family-3	*	*	*	*	167.07**	43.01**±0.33	0.4±0.75	8.7**±2.12	8.6**±2.01	0.23±0.88	-33.73**±3.57	D
Family-4	*	*	-	*	87.53**	41.15**±0.23	-2.3**±0.46	13.03**±1.50	11.6**±1.30	-1.26*±0.60	-21.86**±2.55	D
DP												
Family-1	*	*	-	*	74.91**	64.85**±0.66	0.6±0.48	-7.23*±2.91	-5.8*±2.82	6.23**±0.82	7.06±3.60	D
Family-2	*	*	*	-	48.63**	62.93**±0.19	-0.13±0.41	1.5±1.27	-1.86±1.12	-2.76**±0.66	-6.2**±2.18	D
Family-3	*	-	*	-	21.58**	63.1**±0.231	0.76±0.48	2.56±1.41	0.33±1.33	1.93**±0.54	-7.13**±2.32	D
Family-4	*	*	*	-	62.14**	62.5**±0.25	0.2±0.50	5.43**±1.53	0.8±1.44	-1.63*±0.62	-11.00**±2.49	D
FL												
Family-1	-	*	-	-	6.11	6.88**±0.12	0.67**±0.21	2.12**±0.76	0.98±0.67	-0.42±0.26	-2.05±1.23	D
Family-2	-	*	*	*	51.33*	8.09**±0.20	-1.23**±0.32	-2.43*±1.08	-3.39**±1.04	-1.01**±0.34	0.17±1.63	D
Family-3	*	*	*	*	95.35**	6.45**±0.07	0.18±0.14	3.1**±0.43	2.09**±.41	0.21±0.16	-6.84**±0.71	D
Family-4	*	*	*	-	142.18**	6.33**±0.10	-0.35*±0.17	1.17*±0.55	0.78±0.53	-0.37±0.19	-5.64**±0.84	D
AFW												
Family-1	*	*	*	*	108.39**	177.47**±1.92	0.37± 2.20	66.16**±9.93	24.05**±8.88	4.51±4.21	-120.19** ± 14.69	D
Family-2	-	-	*	*	20.93**	189.76**±1.94	-8.49**±2.62	-36.7**±9.77	-35.34**±9.38	2.82±3.05	29.18*±14.14	D
Family-3	-	-	-	-	1.06	184.57**±2.02	-8.15*±3.15	-22.15±11.56	-5.47±10.83	2.43±3.51	3.06±17.37	D
Family-4	-	*	-	-	42.24**	185.63**±1.53	-5.84*±2.56	10.01±8.48	14.48±7.99	-18.17**±3.07	-31.62*±13.24	D
FG												
Family-1	-	*	-	*	80.43**	11.32**±0.26	-1.10±0.60	8.22**±1.76	7.70**±1.60	-5.75**±0.75	-16.58**±3.02	D
Family-2	*	*	*	-	71.43**	13.7**±0.40	-0.99*±0.44	-1.48±1.93	-3.11±1.86	-0.81±0.49	-6.71*±2.62	D
Family-3	*	*	*	-	109.22**	13.80**±0.34	1.93**±0.60	2.86±1.87	1.42±1.81	2.93**±0.64	-13.51**±2.91	D
Family-4	*	*	*	-	101.65**	14.84**±0.32	0.165±0.61	1.26±1.83	-1.61±1.79	1.19±0.63	-9.60**±2.90	D
NFPP												
Family-1	*	*	*	-	50.40**	4.9*±0.17	0.26±0.33	-2.5*±1.01	-1.73±.96	1.16**±0.35	7.00**±1.65	D
Family-2	*	-	*	-	25.52*	5.46**±0.23	-0.73±0.37	-3.36 **±1.23	-2.26±1.21	0.63±0.40	-0.2±1.84	C
Family-3	*	-	*	-	48.10**	4.76**±0.16	-0.13±0.34	-1.3±0.97	-0.13±0.95	-1.9**±0.36	2.46±1.58	D
Family-4	*	*	*	-	103.42**	5.25**±0.18	0.16±0.35	0.66±1.07	0.53±1.04	0.43±0.38	-8.2**±1.71	D
NPBP												
FAM-1	*	-	-	-	16.228**	3.1**±0.70	-0.05±0.10	3.01±2.00	1.2±0.70	2.7**±0.8	2.9**±0.5	D
FAM-2	-	*	*	*	22.798**	4.36**±0.13	-0.4±0.28	2.83**±0.82	2.66**±0.79	-1.03**±0.31	-3.4*±1.34	D
FAM-3	-	-	-	-	4.1458	5.00**±0.16	-0.23±0.26	2.83**±0.91	0.73±0.85	-0.26±0.29	0.2±1.41	C
FAM-4	*	*	*	*	56.788**	5.18**±0.11	-0.03±0.26	4.46**±0.72	2.66**±0.69	0.16±0.29	-7.53**±1.21	D

Table 1: Continue.....

Table 1: Continue.....

PH													
FAM-1	-	*	-	*	67.284**	63.1**±0.61	-3.55**±0.86	5.31±3.08	7.38*±3.02	-3.48**±0.92	-19.54**±4.42	D
FAM-2	*	*	*	-	54.234**	64.18**±0.33	0.08±0.69	9.99**±2.23	2.66±1.92	-0.42±0.93	-28.26**±3.83	D
FAM-3	*	-	*	-	69.301**	65.23**±0.43	-1.08±0.61	5.06*±2.22	-3.04±2.14	3.35**±0.71	-6.75*±3.24	D
FAM-4	*	*	*	*	108.985**	63.78**±0.36	1.40±0.70	9.56**±2.17	5.01*±2.02	3.00**±0.84	-26.42**±3.55	D
TFYP													
FAM-1	*	*	*	-	14.47**	434.51**±3.54	5.6±7.18	32.4±21.68	3.8±20.20	8.86±7.50	-74.33*±35.72	D
FAM-2	*	-	*	*	55.79**	435.75**±3.48	62.66**±10.24	112.4** ±26.04	96.6**±24.78	66.6**±10.79	-257.4**±46.15	D
FAM-3	-	-	-	-	6.492	435.4**±3.38	10.9±6.55	18.8±19.84	-15.4±18.85	13.16±7.07	0.53±32.00	C
FAM-4	-	*	*	-	66.26**	445.9**±6.51	65.66**±7.15	98.13**±30.81	28.93±29.74	51.46**±8.07	22.26±41.93	C
FBI													
FAM-1	*	-	*	-	11.873**	2.65**±0.13	0.36±0.23	-1.00±0.78	-1.33±0.72	0.43±0.26	0.20±1.24	D
FAM-2	-	-	-	-	1.148	2.81**±0.18	-0.53±0.32	-0.06±0.99	-0.33±0.98	0.26±0.33	0.86±1.52	D
FAM-3	*	-	*	-	6.182	2.71**±0.16	-0.30±0.31	-1.00±1.00	-0.13±0.92	-0.16±0.32	2.33±1.63	D
FAM-4	*	-	-	-	20.885**	3.06**±0.17	0.43±0.31	0.66±1.00	0.33±0.94	1.23**±0.34	-2.40±1.59	D

consistently showed favorable gene effects, making it ideal for developing taller plants. Traits like TFYP and FBI exhibited complex inheritance, with Family 4 again showing clear signs of duplicate epistasis.

Significant epistatic interactions reveal the complex genetic control of earliness in brinjal. For DFF, dominant × dominant [l] interactions were evident across all families *via* scale C significance. Family 1 showed only the mean effect (m), suggesting higher-order interactions or linkage. Negative additive effects [d] in Families 2 and 4 indicate potential for early-generation selection. The consistent negative [l] effects, opposing positive dominance [h], confirm duplicate epistasis, endorsing biparental mating and heterosis breeding to improve earliness traits. Similar findings of duplicate epistasis were documented by Ansari *et al.* (2017), Sharma *et al.* (2024), Raju *et al.* (2019) and Dinesh *et al.* (2019). For DP, Family 1 showed significant positive [l] effects, indicating potential for transgressive segregants. High [h] and significant [i] effects further suggest the importance of late-generation selection. Duplicate epistasis across all families, evident from opposing signs of [h] and [l], supports a breeding approach combining inter-mating and early selection. These results align with Sharma *et al.* (2024), Raju *et al.* (2019) and Dinesh *et al.* (2019).

For FL, opposite signs of [h] and [l] across all families indicated duplicate gene action. Family 2 showed significant negative additive and dominance effects, limiting its potential for direct selection. In contrast, significant positive [i] effects in Families 3 and 4 suggest promise for heterosis breeding and later-generation selection. These findings align with Sharma *et al.* (2024), Raju *et al.* (2019), Dinesh *et al.* (2019) and Barik *et al.* (2022). For FG, gene action was mainly non-additive, with duplicate epistasis confirmed by contrasting [h] and [l] values in all families. Families 3 and 4 showed favorable [i] effects, indicating suitability for heterosis breeding and pedigree selection in late generations. Similar patterns of duplicate epistasis have been observed by Sharma *et al.* (2024), Raju *et al.* (2019), Dinesh *et al.* (2019) and Sidhu *et al.* (2022) and Anvesh *et al.* (2025), who demonstrated asymmetrical allele distribution and overdominance through Wr-Vr analysis reflecting the complexity of non-additive gene interactions in brinjal.

For AFW, Family 1 showed a combination of additive, dominance and duplicate epistatic effects, with highly significant and positive [h] and [i] values, supporting its use in heterosis breeding. Families 2 and 3 had negative additive and dominance effects, suggesting limited early selection potential but suitability for recurrent selection. These observations are consistent with previous studies by Sharma *et al.* (2024), Raju *et al.* (2019), Dinesh *et al.* (2019) and Sidhu *et al.* (2022).

For NFPP, Family 1 showed significant positive [j] and [l] effects, indicating good potential for heterosis breeding. Family 3 showed negative [j] and Family 2 showed

complementary epistasis, highlighting the need for cross-specific strategies. Duplicate epistasis observed aligns with earlier studies Ansari *et al.* (2017); Raju *et al.* (2019); Dinesh *et al.* (2019); Barik *et al.* (2022) and Sidhu *et al.* (2022). For NPBP, significant additive effects [d] in all families support early generation selection. Family 4, with strong duplicate epistasis and positive [i], is suitable for pedigree breeding after inter-mating. Family 2 also showed promising gene effects, but negative [l] suggests improved selection efficiency in later generations. These findings are consistent with Ansari *et al.* (2017); Dinesh *et al.* (2019); Barik *et al.* (2022) and Sharma *et al.* (2024).

For PH, all families showed negative [l] effects, indicating duplicate epistasis. Families 1 and 4 also had significant positive [i] effects, supporting biparental mating followed by selection. Family 4 showed favorable additive, dominance and epistatic effects, making it promising for genetic improvement. Duplicate epistasis for plant height has also been documented by Ansari *et al.* (2017), Dinesh *et al.* (2019), Barik *et al.* (2022) and Sharma *et al.* (2024). For TFYP, Families 2 and 4 exhibited complex inheritance with significant additive and non-additive effects and strong duplicate epistasis through [i], [j] and [l] interactions. Families 1 and 3 showed fewer significant effects, suggesting simpler inheritance or environmental influence. These results agree with Ansari *et al.* (2017); Dinesh *et al.* (2019); Gunasekar *et al.* (2018) and Raju *et al.* (2019), who also documented duplicate epistasis for yield-related traits. Complementary epistasis reported by Afful *et al.* (2020) further supports the role of allelic combinations in yield enhancement.

For FBI, most families showed limited significant effects, indicating strong environmental influence. However, Families 1 and 4 had significant mean and additive [d] effects with duplicate epistasis supported by contrasting [h] and [l] values. Family 3 showed a significant positive [l] effect, suggesting potential for hybrid breeding. These findings align with Dinesh *et al.* (2019) and Raju *et al.* (2019).

In summary, the dominance of duplicate epistasis across most traits indicates complex genetic architecture in brinjal. Significant non-allelic interactions suggest simple selection is inadequate. Effective improvement will require a mix of heterosis breeding, biparental mating and recurrent selection to harness both additive and non-additive gene effects.

CONCLUSION

Generation mean analysis in four brinjal families showed complex inheritance of key traits. Significant duplicate epistasis suggested that the additive-dominance model was inadequate. Both additive and non-additive gene actions influenced DFF, DP, TFYP, FL, FG and NPBP. Families 2 and 4 showed promise for improvement through biparental mating, heterosis and selection. Trait- and family-specific gene effects highlight the need for tailored breeding strategies. Additive effects favor early selection, while epistasis supports later generation selection and recombination. These results guide targeted breeding for yield enhancement in brinjal.

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Disclaimers

The views expressed in this article are solely those of the authors and may not reflect their institutions. The authors have ensured accuracy but are not liable for any losses resulting from the use of this content.

Conflict of interest

No conflicts.

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