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Role of Digenic and Trigenic Epistasis for Earliness Related Traits in Brinjal (*Solanum melongena* L.)

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Abstract

The present investigation was undertaken with a view to generate genetic information on gene effects for five traits namely, days to first flowering, days to first picking, plant height at final harvest (cm), days to last picking and number of picking in brinjal (*Solanum melongena* L.). The experimental materials composed of twelve generations, namely P_1, P_2, F_1, F_2, B_1, B_2, B_{11}, B_{12}, B_{21}, B_{22}, B_1s and B_2s of four crosses viz., Pant Riturajx GJB-2 (cross-1), Swarna Mani Black x GRB-5 (cross-2), Punjab Sadabahar x ASRB-2 (cross-3) and GBR-2-11 x JBR-3-16 (cross-4). Significance of simple scaling tests and Cavalli's joint scaling test indicated the presence of gene interactions for all the five traits. Based on six-parameter model, significant $^{2}_{(2)}$ value at six degrees of freedom indicated the presence of trigenic or higher order epistasis in all the crosses for all the five traits. In case of trigenic ten-parameter model, non-significant $^{2}_{(3)}$ value was observed for days to first picking in cross Swarna Mani Black x GRB-5 (cross-2); for plant height and days to last picking in cross GBR-2-11 x JBR-3-16 (cross-4) indicating the adequacy of best fitting trigenic interaction model. Hence, trigenic interaction model was found adequate to explain the variation present in the above mentioned traits in particular crosses. On the other hand, the $^{2}_{(3)}$ value at two degrees of freedom was found significant (except for plant height in cross-4) in full trigenic interaction model indicated the presence of higher order epistasis and/or linkage.

Key words *: Brinjal, epistasis, gene effect, additive and non-additive gene action, generation mean analysis.*

Introduction

Brinjal (*Solanum melongena* L.), also known as eggplant is considered as prime vegetable in India and having the chromosome number 2n=2x=24. Brinjal is a popular and principle fruit vegetable grown in India and other parts of tropical and subtropical world but in temperate regions, it is grown mainly during warm season (1). India (Indo-Burma region) is the primary centre of origin of brinjal (*Solanum melongena* L.).

The knowledge of gene effects for different traits in brinjal is basic requirement before starting a rigorous breeding programme. Determination of the most suitable breeding method and selection strategy for genetic improvement of a trait would depend on the knowledge of gene action operating in the breeding population (2). The magnitude and composition of genetic variance are of fundamental importance to a plant breeder, which helps in formulation of an effective and sound breeding programme (3). Information on nature and relative magnitude of genetic component of variation (additive and non-additive) are being generated through generation mean analysis and also provides information on digenic and trigenic non-allelic gene action operating in the inheritance of most of the traits. Hence, experiment was planned to study the gene effects in brinjal using 12 generations.

Materials and Methods

The experimental material was comprised of four crosses *viz*., Pant Rituraj x GJB-2 (cross-1), Swarna Mani Black x GRB-5 (cross-2), Punjab Sadabahar x ASRB-2 (cross-3) and GBR-2-11 x JBR-3-16(cross-4) each with twelve generations namely, P_1, P_2, F_1, F_2, B_1, B_2, B_{11}, B_{12}, B_{21}, B_{22}, B_{1s} and B_{2s}which were sown in Compact Family Block Design with three replications during *Late kharif* 2022-23. The plots of various generations contained different number of rows *i.e.* parents and F_1 in single row; B_1 and B_2 in two rows and F_2, B_{1s}, B_{11}, B_{12}, B_{2s}, B_{21} and B_{22} in four rows. Each row was of 6.0 m in length with 90 cm and 60 cm inter and intra row spacing, respectively. All the recommended agronomical practices and necessary plant protection measures were followed timely to raise good crop of brinjal. The observations were recorded on individual plant basis in each replication on five competitive and randomly selected plants from P_1, P_2 and F_1; ten plants from backcross (B_1 and B_2); and twenty plants from F_2, B_{11}, B_{12}, B_{21}, B_{22}, $B_{1s}$and B_{2s} generations for all the five traits. The inheritance of all the five traits namely, days to first flowering, days to first picking, plant height at final harvest (cm), days to last picking and number of picking was computed through generation mean analysis methods (4, 5, 6, 7). The $^{2}_{(1)}$ of joint scaling

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test under three-parameter model gives idea about fitness of additive-dominance model. In addition to six generations and six-parameter model given by (8) based on weighted least square technique, the data were subjected to ten-parameter model given by (7). He proposed estimation of first order and second order epistasis utilizing twelve generations including double backcross generations. The $^{2}_{(2)}$ and $^{2}_{(3)}$ values were estimated under six-parameter model at six degrees of freedom and for ten-parameter model at two degrees of freedom, respectively. This is an additional advantage of using twelve generations and ten-parameter model as it provides sufficient degree of freedom for testing validity and goodness of fit for different models.

Results and Discussion

The data were initially subjected to simple scaling tests A, B, C and D. Significant estimates of any one or more of these tests indicate the presence of digenic interactions. Further, simple scaling tests *viz*., B_{11}, B_{12}, B_{21}, B_{22}, B_{1s} and B_{2s} given by (Hill, 1966) and special scaling tests namely X and Y given by (9) were also computed. Significant estimate of the test(s) given by (7) shows the contribution of particular generation to higher order epistasis, which is indirectly indicating the presence of epistasis. If any of the Van Der Veen's tests deviate significantly from zero indicates the presence of trigenic or higher order epistasis. The results of simple scaling tests were further confirmed by joint scaling test (8), which effectively combines the whole set of simple scaling tests. Thus, it offers a more general, convenient, adoptable and informative approach for estimating gene effects and also for testing adequacy of additive-dominance model. The $^{2}_{(1)}$ test with nine degrees of freedom; $^{2}_{(2)}$ at six degrees of freedom and $^{2}_{(3)}$ at two degrees of freedom was applied to test the fitness of three-parameter model, six-parameter model and ten-parameter model, respectively. The ten-parameter model was used to estimate higher order epistasis (7). To draw inference on adequacy of ten-parameter model, chi-square test $^{2}_{(3)}$ at two degrees of freedom was applied. The character and cross-wise results of all the traits presented in Table-1 to Table-5.

Out of all the scaling tests such as A, C, D, B_{21}, B_{22} and X were significant in cross-1; A, B, C, D, B_{11}, B_{12}, B_{21}, B_{22}, $B_{1s,}$ X and Yin cross-2; A, B, D, B_{11}, B_{21}, B_{22}, B_{1s}, X and Y in cross-3 and A, B, B_{12} and X in cross-4 for days to first flowering; scaling tests such as A, B, D, B_{11}, B_{12}, B_{21}, B_{22}, B_{2s} and X were significant in cross-1; A, B, D, B_{11}, B_{21}, B_{22}, $B1_s$, X and Y in cross-2; A, B_{11}, B_{21}, B_{22}, B_{1s}, X and Y in cross-3 and B, B_{12}, B_{22} and B_{2s}in cross-4 for days to first picking; scaling tests namely A, B, C, D, B_{11}, B_{12}, B_{21}, B_{22}, B_{1s}, B_{2s},X and Y were significant for cross-1; B_{12}, B_{21}, B_{22}, B_{1s}, B_{2s},X and Y in cross-2; A, B, D, B_{11}, B_{12}, B_{1s}, B_{2s} and Y in cross-3 and A, B_{11}, B_{21}, B_{22}, B_{1s}, X and Y in cross-4 for plant height at final harvest; scaling tests such as C, B_{11}, B_{12}, B_{21}, B_{22} and X were significant in cross-1; B_{12}, B_{21} and Y in cross-2; C, D, B_{12}, B_{21} and B_{2s} in cross-3 and B_{21}, B_{1s} and B_{2s} in cross-4 for days to last picking and scaling tests namely, C, B_{11}, B_{12}, B_{21}, B_{22} and X were significant in cross-1; B_{11}, B_{12}, B_{21} and Y in cross-2; C, D, B_{12}, B_{21} and B_{2s} in cross-3 and B_{21} and B_{1s} in cross-4 for number of picking advocating the presence of digenic and trigenic epistasis.

Under additive-dominance model, the estimates of 'm' and [d] gene effects were significant in cross-1 and all the three gene effects *viz*., 'm', [d] and [h] were found significant in cross-2, cross-3 and cross-4 for days to first flowering; all the three gene effects *viz*., 'm', [d] and [h] were found significant in cross-2 and cross-3; 'm' and [d] gene effects were significant in cross-1 and 'm' and [h] gene effects were significant in cross-4 for days to first picking; all the three gene effects *viz*., 'm', [d] and [h] were found significant in cross-1, cross-2 and cross-3 and 'm' and [d] gene effects were significant in cross-4 for plant height at final harvest. All the three gene effects *viz*., 'm', [d] and [h] were found significant in cross-1; 'm' and [d] gene effects were significant in cross-2; 'm' and [h] gene effects were significant in cross-3 and only 'm' gene effect was found significant in cross-4 for days to last picking and number of picking. The $^{2}_{(1)}$ value with nine degrees of freedom of joint scaling test was significant in all the four crosses in all the five traits resulting to the failure of additive-dominance model which indirectly pointed out the presence of epistasis. (10) postulated that the epistatic gene action is common in the inheritance of quantitative traits and there is no sound biological reason why this type of gene action should be less common for these traits.

When the simple additive-dominance model failed to explain the variation among generation means, a six-parameter perfect fit model involving three digenic interactions ([i], [j] and [l]) proposed by (8) was applied. This model utilized only six basic generations *viz*., P_1, P_2, F_1, F_2, B_1 and B_2which had provision of testing the adequacy of model with six degrees of freedom besides being utilizing means of all the twelve generations. According to the six-parameter model of (8), all the gene effects *viz*., 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j] and dominance x dominance [l] were found significant in cross-1; 'm', additive [d], dominance [h], additive x dominance [j] and dominance x dominance [l] were found significant in cross-2; 'm', additive [d], dominance [h] and additive x additive [i] were observed significant in cross-3 and 'm', additive x dominance [j] and dominance x dominance [l] were found significant in cross-4 for days to first flowering;

Table-1 : Scaling tests and estimation of gene effects for days to first flowering in four crosses of brinjal.

Scaling tests / gene effects	Pant Rituraj x GJB-2 (cross 1)	Swarna Mani Black x GRB-5 (cross 2)	Panjab Sadabahar x ASRB-2 (cross 3)	GBR-2-11 x JBR-3-16 (cross 4)
A	3.47** ± 1.28	10.87** ± 1.46	-11.20** ± 1.46	4.13** ± 1.44
B	0.67 ± 1.18	4.27** ± 1.44	3.47* ± 1.66	3.40* ± 1.39
C	-7.40** ± 2.15	5.27* ± 2.44	-0.13 ± 3.17	4.00 ± 2.84
D	-5.77** ± 0.97	-4.93** ± 1.26	3.80* ± 1.56	-1.77 ± 1.22
B11	-0.80 ± 2.60	-10.20** ± 2.67	11.73** ± 2.86	0.87 ± 3.14
B12	-2.00 ± 2.37	-7.20* ± 2.96	-1.87 ± 3.08	-10.60** ± 2.94
B21	-7.47** ± 2.40	-13.73** ± 2.98	-17.93** ± 2.52	2.47 ± 3.07
B22	-11.67** ± 2.37	6.80* ± 2.91	-6.20* ± 2.56	-3.20 ± 2.77
B1S	7.13 ± 4.90	-22.40** ± 5.08	65.73** ± 4.65	2.47 ± 5.90
B2S	4.47 ± 4.12	-2.53 ± 5.15	-4.00 ± 4.77	-9.80 ± 5.06
X	4.08** ± 0.84	-2.62* ± 1.14	8.50** ± 0.93	-2.25* ± 1.00
oY	0.75 ± 1.03	-4.38** ± 1.31	-6.33** ± 1.19	-1.45 ± 1.28
Three parameter model (Cavalli, 1952)				
m	45.51** ± 0.23	47.64** ± 0.28	46.75** ± 0.24	50.22** ± 0.28
(d)	-1.09** ± 0.21	-1.40** ± 0.27	-3.57** ± 0.23	-0.96** ± 0.26
(h)	-0.77 ± 0.47	-1.56** ± 0.57	5.63** ± 0.48	-2.01** ± 0.56
2(1) (9 df)	139.82**	81.06**	600.18**	47.32**
Six parameter full digenic interaction model (Cavalli, 1952)				
m	38.50** ± 0.87	44.81** ± 1.25	39.34** ± 0.99	48.33** ± 1.14
(d)	-2.04** ± 0.37	-2.64** ± 0.39	-3.73** ± 0.40	-0.09 ± 0.43
(h)	16.90** ± 2.65	11.06** ± 3.55	18.45** ± 3.10	5.77 ± 3.30
(i)	7.72** ± 0.87	1.62 ± 1.25	10.29** ± 0.99	1.14 ± 1.15
(j)	3.30** ± 1.21	6.40** ± 1.43	1.80 ± 1.34	-3.56** ± 1.32
(l)	-11.46** ± 2.18	-11.81** ± 2.69	-4.85 ± 2.60	-7.35** ± 2.69
2(2)(6 df)	52.93**	33.41**	460.97**	31.09**
Ten parameter full trigenic interaction model (Cavalli, 1952)				
m	42.09** ± 1.17	46.76** ± 1.64	34.65** ± 1.38	48.80** ± 1.57
(d)	2.17 ± 1.64	-3.44 ± 2.39	-15.32** ± 1.71	-4.41* ± 2.18
(h)	-0.38 ± 4.66	0.24 ± 6.22	50.17** ± 6.47	2.13 ± 6.31
(i)	3.51** ± 1.30	0.01 ± 1.71	16.99** ± 1.50	0.80 ± 1.69
(j)	-15.50** ± 4.42	13.67* ± 6.24	4.54 ± 4.75	10.76 ± 5.67
(l)	4.76 ± 4.22	0.17 ± 5.52	-37.69** ± 6.20	-3.43 ± 5.73
(w)	-2.81 ± 1.62	0.37 ± 2.38	16.03** ± 1.70	3.76 ± 2.18
(x)	19.45** ± 4.80	13.93* ± 6.09	-48.56** ± 7.38	6.37 ± 6.32
(y)	25.17** ± 4.33	-11.63 ± 6.10	25.43** ± 4.69	-14.22** ± 5.34
(z)	-2.25** ± 0.75	-4.07** ± 1.00	1.31 ± 1.07	-1.32 ± 0.98
2(3) (2 df)	7.28*	7.73*	80.98**	19.20**
Final trigenic interaction model after removing non-significant digenic and trigenic interaction parameters (Cavalli, 1952)				
m	40.75** ± 0.57	46.70** ± 0.36	35.49** ± 1.23	49.39** ± 0.44
(d)	-0.57 ± 0.47	-2.68** ± 0.39	-13.93** ± 0.71	-0.37 ± 0.31
(h)	5.01** ± 0.86	0.49 ± 0.65	44.85** ± 4.86	3.35 ± 2.06
(i)	4.88** ± 0.79	- ± -	16.18** ± 1.37	- ± -
(j)	-9.21** ± 2.66	6.93** ± 1.43	- ± -	- ± -
(l)	- ± -	- ± -	-32.18** ± 4.29	-5.96** ± 2.11
(w)	- ± -	- ± -	14.82** ± 1.02	- ± -
(x)	15.16** ± 2.53	13.87** ± 2.96	-41.71** ± 4.39	- ± -
(y)	20.98** ± 3.73	- ± -	29.67** ± 2.50	-6.58** ± 1.89
(z)	-1.70** ± 0.60	-4.18** ± 0.68	- ± -	- ± -
2(4)	10.98* (4 d.f.)	12.73* (6 d.f.)		27.07** (7 d.f.)
Overall type of epistasis	- -	-	Duplicate	Duplicate

*, ** Significant at 5 and 1 per cent levels, respectively.

Table-2 : Scaling tests and estimation of gene effects for days to first picking in four crosses of brinjal.

Scaling tests / gene effects	Pant Rituraj x GJB-2 (cross 1)	Swarna Mani Black x GRB-5 (cross 2)	Panjab Sadabahar x ASRB-2 (cross 3)	GBR-2-11 x JBR-3-16 (cross 4)
A	3.93** ± 1.17	11.00** ± 1.73	-10.73** ± 1.91	2.80 ± 1.45
B	4.60** ± 1.24	4.20* ± 1.61	3.00 ± 1.90	3.60* ± 1.48
C	-2.20 ± 2.10	4.07 ± 2.71	-1.13 ± 3.64	5.20 ± 2.77
D	-5.37** ± 1.16	-5.57** ± 1.37	3.30 ± 1.69	-0.60 ± 1.40
B11	-6.13** ± 2.10	-9.67** ± 3.28	10.73** ± 3.58	0.27 ± 2.56
B12	-7.67** ± 2.50	-6.67 ± 3.46	-0.67 ± 3.81	-9.73** ± 3.01
B21	-11.80** ± 2.40	-13.53** ± 3.30	-18.00** ± 3.41	3.67 ± 2.79
B22	-17.60** ± 1.78	9.20** ± 3.12	-7.13* ± 3.42	-10.73** ± 2.55
B1S	-1.93 ± 4.10	-23.67** ± 6.30	62.87** ± 6.10	-1.60 ± 5.18
B2S	-10.07** ± 3.24	-0.73 ± 5.59	-5.80 ± 6.23	-19.20** ± 4.83
X	3.90** ± 0.90	-3.00* ± 1.27	8.80** ± 1.17	-0.60 ± 1.02
Y	1.07 ± 1.05	-4.93** ± 1.47	-5.57** ± 1.51	1.10 ± 1.26
Three parameter model (Cavalli, 1952)				
m	56.64** ± 0.16	59.56** ± 0.32	58.79** ± 0.31	61.55** ± 0.24
(d)	-0.66** ± 0.16	-1.40** ± 0.30	-3.66** ± 0.29	-0.11 ± 0.23
(h)	0.64 ± 0.39	-1.57* ± 0.66	4.54** ± 0.64	-1.60** ± 0.50
$\chi^2_{(1)}$ (9 df)	136.42**	69.25**	336.23**	53.16**
Six parameter full digenic interaction model (Cavalli, 1952)				
m	49.50** ± 1.04	57.11** ± 1.38	51.68** ± 1.26	61.15** ± 1.33
(d)	-0.50** ± 0.19	-2.85** ± 0.46	-4.08** ± 0.51	0.74* ± 0.29
(h)	24.06** ± 2.91	9.30* ± 3.98	17.38** ± 3.94	3.74 ± 3.67
(i)	6.78** ± 1.04	1.23 ± 1.38	9.76** ± 1.26	-0.27 ± 1.33
(j)	-2.27* ± 0.98	6.79** ± 1.66	2.31 ± 1.68	-5.74** ± 1.21
(l)	-18.77** ± 2.19	-10.23** ± 3.06	-5.18 ± 3.32	-6.44* ± 2.82
$\chi^2_{(2)}$ (6 df)	57.00**	38.76**	259.37**	15.47*
Ten parameter full trigenic interaction model (Cavalli, 1952)				
m	54.01** ± 1.40	59.29** ± 1.83	47.65** ± 1.69	62.33** ± 1.79
(d)	1.69 ± 1.99	-3.55 ± 2.65	-15.76** ± 2.20	-1.89 ± 2.55
(h)	2.00 ± 5.47	-2.69 ± 6.86	43.65** ± 7.41	-2.32 ± 7.00
(i)	2.14 ± 1.42	-0.56 ± 1.93	15.65** ± 1.85	-1.57 ± 1.83
(j)	-16.14** ± 5.05	15.12* ± 6.88	5.64 ± 6.10	0.82 ± 6.38
(l)	1.67 ± 4.91	3.12 ± 6.05	-31.81** ± 6.98	-0.96 ± 6.29
(w)	-1.97 ± 1.98	0.08 ± 2.64	16.33** ± 2.18	2.60 ± 2.55
(x)	22.82** ± 5.40	16.42* ± 6.63	-39.50** ± 8.16	7.35 ± 6.88
(y)	24.84** ± 4.86	-14.46* ± 6.67	25.52** ± 5.97	-4.21 ± 5.74
(z)	-2.40** ± 0.88	-4.73** ± 1.10	1.03 ± 1.22	-0.09 ± 1.07
$\chi^2_{(3)}$ (2 df)	9.24**	8.95*	52.07**	12.05**
Final trigenic interaction model after removing non-significant digenic and trigenic interaction parameters (Cavalli, 1952)				
m	55.93** ± 0.18	58.66** ± 0.43	48.23** ± 1.55	60.89** ± 0.29
(d)	-0.31 ± 0.19	-3.49** ± 0.52	-13.99** ± 0.92	0.74* ± 0.29
(h)	0.47 ± 0.44	0.49 ± 0.75	39.97** ± 6.06	4.40** ± 1.61
(i)	- ± -	- ± -	15.10** ± 1.75	- ± -
(j)	-10.89** ± 2.01	15.13** ± 3.44	- ± -	-5.75** ± 1.21
(l)	- ± -	- ± -	-27.97** ± 5.35	-6.87** ± 1.80
(w)	- ± -	- ± -	14.82** ± 1.32	- ± -
(x)	17.48** ± 2.22	13.38** ± 3.40	-34.71** ± 5.50	- ± -
(y)	21.02** ± 3.81	-14.84** ± 5.52	30.64** ± 3.07	- ± -
(z)	-1.12** ± 0.57	-4.28** ± 0.77	- ± -	- ± -
$\chi^2_{(4)}$	23.63** (5 d.f.)	9.28 (5 d.f.)	53.50** (4 d.f.)	15.51* (7 d.f.)
Overall type of epistasis	-	-	Duplicate	Duplicate

*, ** Significant at 5 and 1 per cent levels, respectively.

Table-3 : Scaling tests and estimation of gene effects for plant height at final harvest (cm) in four crosses of brinjal.

Scaling tests / gene effects	Pant Rituraj x GJB-2 (cross 1)	Swarna Mani Black x GRB-5 (cross 2)	Panjab Sadabahar x ASRB-2 (cross 3)	GBR-2-11 x JBR-3-16 (cross 4)
A	11.67** ± 3.55	-6.40 ± 5.15	-16.33** ± 5.81	9.73* ± 3.78
B	-8.40* ± 3.32	-0.40 ± 5.53	-8.73* ± 4.19	4.07 ± 4.32
C	-19.87** ± 5.42	-12.00 ± 9.20	15.53 ± 7.98	3.20 ± 6.73
D	-11.57** ± 2.62	-2.60 ± 4.90	20.30** ± 4.02	-5.30 ± 3.14
B11	-37.13** ± 7.62	11.20 ± 6.99	68.27** ± 9.65	-34.80** ± 7.50
B12	31.73** ± 6.37	93.93** ± 8.84	-89.33** ± 10.01	6.80 ± 8.08
B21	33.00** ± 6.23	52.93** ± 8.59	-7.40 ± 9.42	24.00** ± 7.39
B22	43.73** ± 6.00	89.13** ± 7.27	9.73 ± 5.93	-19.13* ± 8.17
B1S	-25.20* ± 12.43	-43.40** ± 12.75	112.00** ± 15.74	48.80** ± 13.60
B2S	-47.47** ± 12.41	67.40** ± 13.36	68.67** ± 14.24	-32.13 ± 16.60
X	-20.53** ± 2.39	-9.23** ± 2.56	-5.85 ± 3.11	-8.22** ± 2.72
Y	14.53** ± 2.89	11.63** ± 3.50	-43.68** ± 3.91	21.18** ± 3.38
Three parameter model (Cavalli, 1952)				
m	82.56** ± 0.66	78.46** ± 0.70	73.51** ± 0.71	80.87** ± 0.76
(d)	1.71** ± 0.63	8.74** ± 0.66	4.28** ± 0.67	4.42** ± 0.72
(h)	-11.74** ± 1.26	-6.88** ± 1.51	22.59** ± 1.67	-1.82 ± 1.48
$^{2}_{(1)}$ (9 df)	218.98**	343.04**	249.23**	159.49**
Six parameter full digenic interaction model (Cavalli, 1952)				
m	95.29** ± 2.81	112.66** ± 3.12	74.09** ± 3.19	57.74** ± 3.14
(d)	-0.43 ± 0.94	3.21** ± 1.03	9.10** ± 1.18	5.70** ± 1.12
(h)	-46.67** ± 8.17	-107.91** ± 9.67	2.38 ± 9.84	65.67** ± 9.22
(i)	-13.10** ± 2.81	-32.95** ± 3.08	5.43 ± 3.19	22.22** ± 3.12
(j)	7.76* ± 3.04	25.89** ± 3.84	-17.16** ± 4.39	-6.72 ± 3.67
(l)	24.53** ± 6.44	75.38** ± 8.03	26.66** ± 8.12	-50.02** ± 7.39
$^{2}_{(2)}$ (6 df)	190.02**	175.75**	209.53**	99.67**
Ten parameter full trigenic interaction model (Cavalli, 1952)				
m	106.74** ± 3.77	107.49** ± 4.24	46.51** ± 4.34	64.70** ± 4.50
(d)	-49.64** ± 5.51	6.08 ± 5.29	23.53** ± 5.93	-34.73** ± 6.55
(h)	-99.66** ± 13.86	-74.87** ± 19.19	128.09** ± 17.38	51.86** ± 16.67
(i)	-27.43** ± 3.99	-27.64** ± 4.46	40.03** ± 4.62	12.05* ± 4.75
(j)	157.51** ± 14.22	47.76** ± 14.10	-50.25** ± 15.35	95.46** ± 16.41
(l)	70.08** ± 12.09	40.73* ± 18.19	-80.91** ± 15.83	-47.63** ± 14.57
(w)	45.67** ± 5.50	-6.17 ± 5.25	-10.65 ± 5.89	38.74** ± 6.54
(x)	81.26** ± 12.73	-45.45* ± 21.49	-132.53** ± 18.03	-2.80 ± 15.58
(y)	-130.09** ± 12.71	-58.28** ± 13.68	-1.35 ± 14.94	-73.38** ± 14.64
(z)	0.64 ± 2.11	10.21** ± 3.15	-4.03 ± 2.91	13.28** ± 2.45
$^{2}_{(3)}$ (2 df)	16.48**	136.91**	72.83**	4.48
Final trigenic interaction model after removing non-significant trigenic interaction parameters (Cavalli, 1952)				
m	107.24** ± 3.39	107.17** ± 4.23	47.88** ± 3.94	65.25** ± 3.33
(d)	-49.50** ± 5.49	0.02 ± 1.20	13.87** ± 1.25	-34.96** ± 6.43
(h)	-101.95** ± 11.60	-73.94** ± 19.17	130.01** ± 14.93	49.41** ± 9.58
(i)	-27.90** ± 3.66	-27.33** ± 4.45	39.07** ± 4.35	11.44** ± 3.36
(j)	156.80** ± 14.03	61.76** ± 7.56	-34.62** ± 4.65	95.77** ± 16.32
(l)	72.31** ± 9.56	39.97* ± 18.18	-86.73** ± 12.87	-45.39** ± 7.54
(w)	45.55** ± 5.49	- ± -	- ± -	38.97** ± 6.41
(x)	83.75** ± 9.72	-45.15* ± 21.48	-150.31** ± 12.95	- ± -
(y)	-129.10** ± 12.28	-66.50** ± 11.76	- ± -	-73.19** ± 14.61
(z)	- ± -	10.41** ± 3.14	- ± -	12.99** ± 1.82
$^{2}_{(4)}$	16.53** (3 d.f.)	138.29** (3 d.f.)	80.46** (5 d.f.)	4.51 (3 d.f.)
Overall type of epistasis	Duplicate	Duplicate	Duplicate	Duplicate

*, ** Significant at 5 and 1 per cent levels, respectively.

Table-4 : Scaling tests and estimation of gene effects for days to last picking in four crosses of brinjal.

Scaling tests / gene effects	Pant Rituraj x GJB-2 (cross 1)	Swarna Mani Black x GRB-5 (cross 2)	Panjab Sadabahar x ASRB-2 (cross 3)	GBR-2-11 x JBR-3-16 (cross 4)
A	-2.67 ± 3.37	-0.13 ± 3.44	1.07 ± 3.62	-2.60 ± 2.99
B	-6.00 ± 3.88	-2.60 ± 3.92	-0.33 ± 2.30	-0.80 ± 3.46
C	-15.87** ± 5.32	-2.47 ± 5.44	-9.47* ± 4.54	-9.73 ± 5.41
D	-3.60 ± 2.38	0.13 ± 2.59	-5.10* ± 2.22	-3.17 ± 2.17
B11	14.40* ± 6.93	14.20 ± 7.31	8.20 ± 8.82	9.53 ± 5.34
B12	18.73** ± 6.65	16.53** ± 5.85	8.73* ± 3.70	6.67 ± 6.38
B21	25.00** ± 6.83	28.93** ± 5.90	21.60** ± 5.74	20.53** ± 6.43
B22	31.40** ± 7.12	5.13 ± 7.40	4.93 ± 5.14	-2.67 ± 7.93
B1S	19.07 ± 11.53	23.47 ± 13.56	16.07 ± 15.00	23.60* ± 10.30
B2S	7.60 ± 13.10	20.53 ± 13.94	22.87** ± 8.06	31.47* ± 14.35
X	-5.82* ± 2.33	-0.83 ± 2.28	-2.40 ± 2.39	-0.42 ± 2.15
Y	-0.52 ± 2.92	6.53* ± 2.68	4.30 ± 2.54	5.08 ± 2.69
Three parameter model (Cavalli, 1952)				
m	129.64** ± 0.63	127.16** ± 0.63	125.51** ± 0.53	128.66** ± 0.54
(d)	1.77** ± 0.58	-2.29** ± 0.58	-0.04 ± 0.54	-0.26 ± 0.48
(h)	-3.14* ± 1.27	-1.05 ± 1.21	4.84** ± 0.94	-1.01 ± 1.17
$^{2}_{(1)}$(9 df)	49.99**	43.13**	28.11**	32.75**
Six parameter full digenic interaction model (Cavalli, 1952)				
m	138.84** ± 2.45	129.58** ± 2.54	123.88** ± 2.18	122.86** ± 2.17
(d)	1.53 ± 1.02	-1.48 ± 1.07	0.96 ± 0.97	1.00 ± 0.94
(h)	-33.37** ± 7.68	-8.95 ± 7.61	4.52 ± 6.42	10.56 ± 6.66
(i)	-7.88** ± 2.39	-1.88 ± 2.46	3.64 ± 2.21	7.03** ± 2.08
(j)	0.12 ± 3.32	-2.93 ± 3.39	-2.31 ± 3.06	-4.87 ± 3.07
(l)	24.52** ± 6.36	6.29 ± 6.06	2.80 ± 4.81	-5.40 ± 5.55
$^{2}_{(2)}$ (6 df)	33.93**	41.19**	20.31**	15.79*
Ten parameter full trigenic interaction model (Cavalli, 1952)				
m	140.22** ± 3.12	126.25** ± 3.32	123.99** ± 2.83	122.50** ± 2.88
(d)	-13.72** ± 4.46	-1.29 ± 4.80	2.46 ± 4.34	8.55* ± 3.98
(h)	-40.22** ± 11.57	8.09 ± 12.38	5.88 ± 10.63	14.01 ± 11.10
(i)	-8.96* ± 3.50	0.09 ± 3.72	1.58 ± 3.20	6.66* ± 3.35
(j)	46.12** ± 12.32	1.94 ± 12.60	1.84 ± 12.45	-20.03 ± 10.82
(l)	30.74** ± 10.15	-11.63 ± 10.84	-1.00 ± 9.38	-10.00 ± 9.90
(w)	13.82** ± 4.42	-1.23 ± 4.74	-3.40 ± 4.32	-7.70* ± 3.91
(x)	11.96 ± 10.81	-18.89 ± 12.29	4.09 ± 10.90	-7.19 ± 11.22
(y)	-41.60** ± 12.07	-10.53 ± 11.71	-12.27 ± 12.25	5.50 ± 10.90
(z)	-1.19 ± 1.89	6.31** ± 1.86	2.97 ± 1.74	3.08 ± 1.77
$^{2}_{(3)}$ (2 df)	16.77**	28.71**	13.36**	8.01*
Final trigenic interaction model after removing non-significant digenic and/or trigenic interaction parameters (Cavalli, 1952)				
m	138.12** ± 2.46	126.64** ± 0.66	125.51** ± 0.53	124.44** ± 1.28
(d)	-13.55** ± 4.42	-2.33** ± 0.58	-0.04 ± 0.54	7.16* ± 3.22
(h)	-30.71** ± 7.72	-1.34 ± 1.22	4.84** ± 0.94	4.42* ± 1.92
(i)	-6.33** ± 2.44	- ± -	- ± -	6.22** ± 1.73
(j)	46.59** ± 12.15	- ± -	- ± -	-14.23* ± 5.63
(l)	22.01** ± 6.40	- ± -	- ± -	- ± -
(w)	13.54** ± 4.38	- ± -	- ± -	-7.30* ± 3.55
(x)	- ± -	- ± -	- ± -	- ± -
(y)	-43.52** ± 11.71	- ± -	- ± -	- ± -
(z)	- ± -	3.42** ± 1.24	- ± -	- ± -
$^{2}_{(4)}$	18.00** (4 d.f.)	35.59** (8 d.f.)	28.11** (9 d.f.)	12.52 (6 d.f.)
Overall type of epistasis	Duplicate	-	-	-

*, ** Significant at 5 and 1 per cent levels, respectively.

Table-5 : Scaling tests and estimation of gene effects for number of picking in four crosses of brinjal.

Scaling tests / gene effects	Pant Rituraj x GJB-2 (cross 1)			Swarna Mani Black x GRB-5 (cross 2)			Panjab Sadabahar x ASRB-2 (cross 3)			GBR-2-11 x JBR-3-16 (cross 4)		
A	-0.73	±	0.97	0.01	±	0.95	0.20	±	1.00	-0.67	±	0.85
B	-1.67	±	1.10	-0.73	±	1.09	-0.07	±	0.66	0.13	±	1.01
C	-4.47**	±	1.51	-0.60	±	1.51	-2.73*	±	1.27	-2.33	±	1.54
D	-1.03	±	0.67	0.07	±	0.72	-1.43*	±	0.62	-0.90	±	0.61
B11	3.93*	±	1.95	4.00*	±	2.00	2.47	±	2.42	2.73	±	1.49
B12	5.27**	±	1.90	4.60**	±	1.64	2.47*	±	1.07	1.47	±	1.82
B21	6.67**	±	1.94	8.00**	±	1.64	6.00**	±	1.59	5.53**	±	1.80
B22	8.87**	±	2.01	1.47	±	2.06	1.20	±	1.30	-1.67	±	2.40
B1S	5.33	±	3.27	6.73	±	3.74	4.80	±	4.12	6.20*	±	2.89
B2S	2.27	±	3.71	5.67	±	3.86	6.27**	±	2.28	7.13	±	4.28
X	-1.58*	±	0.65	-0.22	±	0.63	-0.57	±	0.64	0.08	±	0.62
Y	-0.22	±	0.82	1.78*	±	0.74	1.20	±	0.69	1.48	±	0.77
Three parameter model (Cavalli, 1952)												
m	16.40**	±	0.18	15.73**	±	0.17	15.26**	±	0.15	16.10**	±	0.15
(d)	0.52**	±	0.16	-0.66**	±	0.16	0.02	±	0.15	-0.06	±	0.13
(h)	-0.85*	±	0.36	-0.32	±	0.34	1.33**	±	0.27	-0.25	±	0.33
$^{2}_{(1)}$(9 df)		48.84**			44.47**			27.38**			32.12**	
Six parameter full digenic interaction model (Cavalli, 1952)												
m	18.99**	±	0.69	16.37**	±	0.70	14.80**	±	0.60	14.49**	±	0.61
(d)	0.44	±	0.29	-0.43	±	0.30	0.31	±	0.27	0.34	±	0.27
(h)	-9.36**	±	2.17	-2.36	±	2.11	1.27	±	1.78	3.14	±	1.88
(i)	-2.21**	±	0.67	-0.52	±	0.68	1.02	±	0.61	1.90**	±	0.58
(j)	0.07	±	0.93	-0.81	±	0.93	-0.74	±	0.85	-1.55	±	0.87
(l)	6.91**	±	1.80	1.60	±	1.68	0.75	±	1.34	-1.73	±	1.57
$^{2}_{(2)}$(6 df)		32.92**			42.67**			19.82**			15.55*	
Ten parameter full trigenic interaction model (Cavalli, 1952)												
m	19.35**	±	0.88	15.44**	±	0.92	14.86**	±	0.78	14.47**	±	0.80
(d)	-3.81**	±	1.25	-0.44	±	1.32	0.67	±	1.17	2.52*	±	1.11
(h)	-11.16**	±	3.25	2.46	±	3.43	1.49	±	2.95	3.78	±	3.09
(i)	-2.47*	±	0.98	0.07	±	1.03	0.43	±	0.88	1.65	±	0.95
(j)	12.79**	±	3.44	0.61	±	3.48	0.49	±	3.31	-6.39*	±	3.08
(l)	8.56**	±	2.85	-3.43	±	3.00	-0.12	±	2.61	-2.73	±	2.76
(w)	3.84**	±	1.24	-0.28	±	1.31	-0.85	±	1.17	-2.12	±	1.09
(x)	3.26	±	3.03	-5.48	±	3.40	1.14	±	3.03	-1.57	±	3.15
(y)	-11.38**	±	3.35	-2.90	±	3.23	-3.31	±	3.24	2.47	±	3.13
(z)	-0.38	±	0.53	1.75**	±	0.51	0.79	±	0.48	0.84	±	0.49
$^{2}_{(3)}$(2 df)		16.00**			30.27**			13.34**			7.77*	
Final trigenic interaction model after removing non-significant digenic and trigenic interaction parameters (Cavalli, 1952)												
m	-	±	-	15.59**	±	0.18	15.26**	±	0.15	14.97**	±	0.35
(d)	-	±	-	-0.67**	±	0.16	0.02	±	0.15	-0.09	±	0.14
(h)	-	±	-	-0.38**	±	0.34	1.33**	±	0.27	1.24*	±	0.53
(i)	-	±	-	-	±	-	-	±	-	1.69**	±	0.48
(j)	-	±	-	-	±	-	-	±	-	-	±	-
(l)	-	±	-	-	±	-	-	±	-	-	±	-
(w)	-	±	-	-	±	-	-	±	-	-	±	-
(x)	-	±	-	-	±	-	-	±	-	-	±	-
(y)	-	±	-	-	±	-	-	±	-	-	±	-
(z)	-	±	-	0.92**	±	0.35	-	±	-	-	±	-
$^{2}_{(4)}$		-			37.34** (8 d.f.)			27.38** (9 d.f.)			19.47* (8 d.f.)	
Overall type of epistasis		Duplicate			-			-			-	

*, ** Significant at 5 and 1 per cent levels, respectively.

Table-6 : Absolute totals of epistatic effects and fixable v/s non-fixable gene effects for different traits in four crosses of brinjal.

Sr. No.	Characters	Cross	Main effects		Absolute totals of epistatic interactions		Absolute totals of gene effects	
			[d]	[h]	I order	II order	Fixable	Non-fixable
1.	Days to first flowering	1	2.17	0.38	23.77	49.68	8.49	67.51
		2	3.44	0.24	13.85	30.00	3.82	43.71
		3	15.32	50.17	59.22	91.33	48.34	167.70
		4	4.41	2.13	14.99	25.67	8.97	38.23
2.	Days to first picking	1	1.69	2.00	19.95	52.03	5.80	69.87
		2	3.55	2.69	18.80	35.69	4.19	56.54
		3	15.76	43.65	53.10	82.38	47.74	147.15
		4	1.89	2.32	3.35	14.25	6.06	15.75
3.	Plant height at final harvest (cm)	1	49.64	99.66	255.02	257.66	122.74	539.24
		2	6.08	74.87	91.13	120.11	39.89	277.30
		3	23.53	128.09	171.19	148.56	74.21	397.16
		4	34.73	51.86	155.14	128.10	85.52	284.21
4.	Days to last picking	1	13.72	40.22	85.82	68.57	36.50	171.83
		2	1.29	8.09	13.66	36.96	2.61	57.39
		3	2.46	5.88	4.42	22.73	7.44	28.05
		4	8.55	14.01	36.69	23.47	22.91	59.81
5.	Number of picking	1	3.81	11.16	23.82	18.86	10.12	47.53
		2	0.44	2.46	4.11	10.41	0.79	16.60
		3	0.67	1.49	1.04	6.09	1.95	7.34
		4	2.52	3.78	10.77	7.00	6.29	17.78

all the gene effects *viz*., 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j] and dominance x dominance [l] were found significant in cross-1; 'm', additive [d], dominance [h], additive x dominance [j] and dominance x dominance [l] were found significant in cross-2; 'm', additive [d], dominance [h] and additive x additive [i] were observed significant in cross-3 and 'm', additive [d], additive x dominance [j] and dominance x dominance [l] were found significant in cross-4 for days to first picking; 'm', dominance [h], additive x additive [i], additive x dominance [j] and dominance x dominance [l] were found significant in cross-1; all the gene effects *viz*., 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j] and dominance x dominance [l] were found significant in cross-2; 'm', additive [d], additive x dominance [j] and dominance x dominance [l] were found significant in cross-3 and 'm', additive [d], dominance [h], additive x additive [i] and dominance x dominance [l] were found significant in cross-4for plant height at final harvest; 'm', dominance [h], additive x additive [i] and dominance x dominance [l] were found significant in cross-1; only 'm' gene effect was found significant in cross-2 and cross-3 and 'm' and additive x additive [i] gene effects were found significant in cross-4 for days to last picking and only 'm' gene effect was found significant in cross-1, cross-2and cross-3 and 'm' and additive x additive [i] gene effects were found significant in cross-4for number of picking. The $^{2}_{(2)}$ value with six degrees of freedom of joint scaling test was significant in all the four crosses in all the five traits supporting the presence of epistasis. Similar results were obtained for days to first picking by (11, 12, 13).

In ten-parameter model, 'm', additive x additive [i], additive x dominance [j], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] were found significant in cross-1; 'm', additive x dominance [j], additive x additive x dominance [x] and dominance x dominance x dominance [z] were found significant in cross-2; 'm', additive [d], dominance [h], additive x additive [i], dominance x dominance [l], additive x additive x additive [w], additive x additive x dominance [x] and additive x dominance x dominance [y] were found significant in cross-3 and 'm', additive [d] and additive x dominance x dominance [y] were found significant in cross-4 for days to first flowering; 'm', additive x dominance [j], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] were found significant in cross-1; 'm', additive x dominance [j], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] were found significant in cross-2; 'm', additive [d], dominance [h], additive x additive [i], dominance x dominance [l], additive x additive x additive [w], additive x additive x dominance [x], and additive x dominance x dominance [y] were found significant in cross-3 and only 'm' gene effect was found significant in cross-4 for days to first picking; 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x additive [w], additive x additive x dominance [x] and additive x dominance x dominance [y] were found significant in cross-1; 'm', dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x dominance [x], additive x dominance x dominance [y] and dominance x dominance x dominance [z] were found significant in cross-2; 'm', additive [d], dominance [h] and additive x additive [i], additive x dominance [j], dominance x dominance [l] and additive x additive x dominance [x] were found significant in cross-3 and 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x additive [w], additive x dominance x dominance [y] and dominance x dominance x dominance [z] were found significant in cross-4for plant height at final harvest; 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x additive [w] and additive x dominance x dominance [y] were found significant in cross-1; 'm' and dominance x dominance x dominance [z] were found significant in cross-2; only 'm' gene effect was found significant in cross-3 and cross-4 for days to last picking and 'm', additive [d], dominance [h], additive x additive [i], additive x dominance [j], dominance x dominance [l], additive x additive x additive [w] and additive x dominance x dominance [y] were found significant in cross-1; 'm' and dominance x dominance x dominance [z] were found significant in cross-2; only 'm' gene effect was found significant in cross-3 and 'm', additive [d] and additive x dominance [j] were found significant in cross-4for number of picking. The $^{2}_{(3)}$ value was significant at two degrees of freedom in all the four crosses (except for plant height at final harvest in cross-4) in all the five traits indicating the presence of higher order epistasis and/or linkage.

In case of trigenic ten-parameter model, non-significant $^{2}_{(3)}$ value was observed for days to first picking (after removing non-significant components [i], [l] and [w]) in cross Swarna Mani Black x GRB-5 (cross-2); for plant height at final harvest (after removing non-significant component [x]) in cross GBR-2-11 x JBR-3-16 (cross-4) indicating the adequacy of best fitting trigenic interaction model. Hence, trigenic interaction model was found adequate to explain the variation present in the above mentioned traits in particular crosses.

The opposite sign of two or all the three gene effects *viz.*, dominance [h], dominance x dominance [l] and dominance x dominance x dominance [z] suggest the presence of duplicate type of epistasis. In the present study, duplicate type of epistasis were observed in most of the crosses for all the five traits. Duplicate type of epistasis for fruit yield per plant and its component traits in brinjal was reported by (13, 14, 15, 16, 17, 18).

In the present study of trigenic interaction model, the 12 generation mean analysis (Table-6) further revealed that absolute totals of epistatic effects were higher than the main effects in all the five traits in all the four crosses. The second order interactions (absolute totals) were much higher than the first order interactions for all the five traits in four crosses [except plant height at final harvestin Panjab Sadabahar x ASRB-2 (cross-3) and GBR-2-11 x JBR-3-16 (cross-4) and for days to last picking and number of picking in Pant Rituraj x GJB-2 (cross-1) and GBR-2-11 x JBR-3-16 (cross-4)]. The higher value of second order interactions (absolute totals) indicating its important role in controlling inheritance of the traits.While, comparing absolute totals of fixable v/s non-fixable gene effects (Table-6), it was found that absolute totals of non-fixable gene effects were higher than fixable gene effects for all the five traits in all the four crosses indicating the greater role of non-additive gene effects in the inheritance of all the five traits studied in all the four crosses. Overall, the study revealed that non-additive gene action was more important than additive gene action in the expression of these five traits in four crosses of brinjal.

Conclusion

It can be concluded from the present study that days to first flowering, days to first picking, plant height at final harvest, days to last picking and number of picking recorded in four brinjal crosses were governed by additive, dominance and digenic and/or trigenic epistasis gene effects along with duplicate type of gene action. When additive as well as non-additive effects are involved, a breeding scheme efficient in exploiting both types of gene effects should be employed. Reciprocal recurrent selection and biparental mating could be followed which would facilitate exploitation of both additive and non-additive gene effects simultaneously for genetic improvement in brinjal.

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