



TRIPLE TEST CROSS ANALYSIS FOR YIELD AND ITS COMPONENT TRAITS IN BRINJAL (*SOLANUM MELONGENA* L.)

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Abstract

The success of vegetable breeding operations mainly depends upon the nature and extent of genetic components of variation. Thus it is imperative to have reliable estimates of such components in order to formulate an efficient breeding strategy. In the present study, the components of genetic variation were studied in AN (Arka Nidhi) and SN (Singh Nath) for quantitative characters. The estimates of both additive and dominance components were significant for all the characters except days to 50 per cent flowering, fruit diameter, number of branches per plant, and pedicel length. Epistasis (*i*) and (*j+I*) type was significant in all the traits except days to 50 per cent flowering and fruit diameter (cm). The degree of dominance ($H/D)^{1/2}$ was in the range of over dominance for marketable fruit yield per plant, number of marketable fruits per plant, fruit length (cm), plant height (cm), number of branches per plant and fruit weight (g) where as the presence of partial dominance for days to 50 per cent flowering, days to first picking, fruit diameter (cm) and pedicel length (cm).

Key words : Triple test cross, additive, dominance, epistasis.

Introduction

Brinjal is a well known vegetable crop and it is generally grown in the tropical, sub tropical and warm temperate area of the world. It is a good source of minerals and vitamins in the tropical diets. Brinjal is otherwise called as egg plant and it originates from India. It is an important vegetable in India, china and Japan. The botanical name of brinjal is *Solanum melongena* L. and it has a wide range of varieties. Most of the genetic models have been developed to estimate the component of continuous variation, have as one of their assumption the absence of epistasis. In general, Epistasis causes hidden quantitative genetic variation in natural populations and could be responsible for the small additive effects (Mackay, 2014). In fact a good genetic model, enables the breeder to have precise and unbiased estimates of all the components of genetic variance. The triple test cross biometrical design proposed by Kearsy and Jink (1968), which is an extension of North Carolina Design-III (NCD-

III) of Comstock and Robinson (1952), which envisages the exact nature and magnitude of epistatic interactions viz., additive x additive, additive x dominance and dominance x dominance gene effects. TTC (Triple test cross) analysis provides unambiguous test for the presence of epistasis regardless of gene frequencies, degree of inbreeding and linkage relationships. The design has wide applicability as it can be used to investigate both segregating and non-segregating populations arising from different generations such as F_2 , backcross and homozygous lines. TTC method has many advantages over other multiple mating designs, in this design the number of crosses does not increase tremendously with increase in number of other mating designs. Therefore, the present study was undertaken to get an insight into the genetic factors underlying expression of quantitative traits.

Materials and Methods

The experimental material consisted of (a) AN (Arka Nidhi) and SN (Singh Nath), and their respective F_2 's

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were utilized. Ten plants were randomly taken from each F_2 population, designated as 10Pi lines and crossed to their respective female testers namely L_1 , L_2 and L_3 . L_1 and L_2 are the inbred lines of the respective F_1 and its F_2 , where as L_3 is the F_1 produced from them. The crossing plan thus yielded 3n progenies comprising 30 crosses for each set of experiment in a triple test cross mating design. The 30 families (L_{1i} , L_{2i} and L_{3i}) along with ten Pi lines and three female testers for each set of experiment were grown in a randomised block design (RBD) with three replications during *kharif* season 2015-16 at Vegetable Research Farm, CSKHPKV, Palampur. Each experimental plot comprised two meters long rows/replication with inter and intra plant spacing of 30 and 7.5 cm, respectively. The observations were recorded from the ten competitive plants, taken at random from each entry in each replication for the following traits *viz.*, marketable fruit yield per plant, number of marketable fruits per plant, days to 50 per cent flowering, days to first picking, pedicel length (cm), fruit length (cm), fruit weight (g), fruit diameter (cm), number of branches per plant and plant height. The mean values of each set of experiment for different traits were subjected to the analysis of variance as per randomised block design. Analysis was based on the following model given by Panse and Sukhatme (1984). The data were analysed for (i) the analysis of variance triple test cross design (Kearsey and Jinks, 1968), (ii) analysis of variance to test epistasis and its components (Jinks and Perkins, 1970), (iii) analysis of variance for testing of adequacy of testers (Jinks *et al.*, 1969; Jinks and Virk, 1977; Virk and Jinks, 1977) and (iv) estimation of additive and dominance components of variation (Jinks and Perkins, 1970). Kearsey and Jinks (1968) did not suggest the partitioning of epistasis. This was suggested by Jinks and Perkins (1970). Further the test ($L_{1i} + L_{2i} - - 2L_{3i}$) is non significant, this means that there is no detectable epistasis and the testers are adequate and the estimates of genetic parameters would be unbiased, if the ($L_{1i} + L_{2i} - - 2L_{3i}$) is significant, this indicates that epistasis is present, but we cannot be sure of the adequacy or inadequacy of the testers.

Results and Discussion

The means of fruit yield per plant are presented in table 1 and the analysis of variance is given in table 2, which indicated significant differences among the progenies, Pi lines and testers. The fruit yield per plot ranged from 450.57 ($P_2 \times L_1$) to 725.25 g ($P_6 \times L_1$) in progenies and 498.79 (P_2) to 580.75 g (P_6) in Pi lines. The yield per plant of female testers ranged from 504.80

g (L_2), 560.96 g (L_1) and 545.40 g AN x SN (F_1) L_3 . The cross combination ($P_6 \times L_1$), ($P_6 \times L_3$), ($P_6 \times L_2$), ($P_4 \times L_1$), ($P_3 \times L_1$), ($P_3 \times L_2$), ($P_3 \times L_3$), ($P_7 \times L_2$), ($P_1 \times L_3$) and ($P_1 \times L_2$) were significantly superior to their respective better parent. Eight cross combinations produced significantly higher marketable fruit yield per plant than the cultivar Arka Nidhi (AN), while 21 cross combinations significantly exceeded the cultivar Singh Nath (SN) in marketable fruit yield per plant. The maximum increase in fruit yield was to the extent of 29.28 and 43.67 per cent over AN and SN, respectively. Over the superior Pi line (P_6) and L_3 tester, seven and 11 cross combinations exceeded significantly in marketable fruit yield per plant to the extent of 32.97 and 24.88 per cent, respectively. The result of epistasis and its components are presented in table 3. The mean squares due to epistasis and its additive x additive (i), additive x dominance (j) and dominance x dominance (l) genetic components of variation. The perusal of the table indicates that epistasis and its components i, j and l were significant showing there by the importance of both epistasis and its components *viz.*, additive x additive, additive x dominance and dominance x dominance genic interactions. The analysis of variance of sums and differences for the character were significant, suggesting the presence of both additive and dominance component of genetic variation for the inheritance of the trait. The comparison of D and H components revealed that H component was of greater magnitude than the D component and mean degree of dominance was in over-dominance range.

From the table 1 the mean value of days to 50 per cent flowering ranged from 59.67 (L_1) to 71.00 (L_2) in testers, 57.53 (P_9) to 71.25 (P_3) in Pi lines and 49.11 ($P_9 \times L_1$) to 73.77 ($P_3 \times L_2$) in progenies. Among the progenies, the cross combinations ($P_9 \times L_1$), ($P_9 \times L_3$), ($P_8 \times L_1$), ($P_8 \times L_3$), ($P_4 \times L_1$), ($P_2 \times L_3$), ($P_1 \times L_2$), ($P_{10} \times L_1$), ($P_6 \times L_1$), ($P_6 \times L_3$), ($P_4 \times L_3$), ($P_3 \times L_3$), ($P_4 \times L_2$) and ($P_5 \times L_3$) manifested significantly less number of days to 50 per cent flowering than their respective better parent. The average value of days to 1st picking ranged from 67.22 (L_1) to 77.67 (L_2) in testers, 58.15 ($P_8 \times L_3$) to 78.25 ($P_3 \times L_2$) in progenies and 63.31 (P_9) to 76.15 (P_3) in Pi lines. Among the progenies, the cross combinations ($P_8 \times L_3$), ($P_9 \times L_1$), ($P_9 \times L_3$), ($P_8 \times L_1$), ($P_2 \times L_3$), ($P_4 \times L_1$), ($P_6 \times L_1$), ($P_1 \times L_1$), ($P_{10} \times L_1$), ($P_6 \times L_3$) and ($P_4 \times L_3$) performed significantly better than their respective better parent. The maximum decrease in fruit picking was to the tune of 15.59 and 33.56 per cent over AN and SN, respectively. In relation to number of marketable fruits per plant ranged from 14.51 (L_2) to 21.17 (L_1) in testers, 12.62 (P_5) to 22.35 (P_8) in Pi lines and 10.09 ($P_5 \times L_3$) to

Table 1 : Mean values of the treatments for different characters in TTC progenies of AN (L₁) and SN (L₂).

Treatments	Marketable fruit yield/plant (g)	Days to 50 per cent flowering	Days to first picking	Number of marketable fruits per plant	Fruit length (cm)	Fruit diameter (cm)	Plant height (cm)	Number of branches per plant	Fruit weight (g)	Pedicel length (cm)
P ₁ xL ₁	530.71	55.71	63.51	24.70	15.75	2.20	76.29	7.11	30.57	5.79
P ₁ xL ₃	565.77	57.71	65.51	21.37	16.32	2.28	80.71	6.99	26.26	5.66
P ₁ xL ₂	525.25	66.61	72.87	18.27	18.74	1.90	72.58	7.25	32.59	6.86
P ₂ xL ₁	450.57	65.79	74.18	17.99	19.78	2.59	82.71	5.97	30.96	6.91
P ₂ xL ₃	472.19	54.78	60.11	18.34	18.56	2.44	78.75	6.13	28.91	7.05
P ₂ xL ₂	494.19	66.36	71.54	17.95	21.82	2.58	94.72	5.17	24.70	7.18
P ₃ xL ₁	620.19	65.21	73.29	12.73	20.51	2.82	82.19	5.99	33.93	5.41
P ₃ xL ₃	592.92	59.74	69.38	15.72	17.12	2.99	101.22	6.92	35.79	4.94
P ₃ xL ₂	612.72	73.77	78.25	13.75	22.50	2.64	96.74	5.16	32.54	5.23
P ₄ xL ₁	640.45	52.71	60.71	21.48	14.74	3.02	90.25	5.50	31.12	6.87
P ₄ xL ₃	522.43	59.54	66.73	20.31	16.81	3.45	97.77	4.18	37.98	6.15
P ₄ xL ₂	490.69	62.79	75.11	18.01	19.13	2.35	108.70	3.76	38.71	7.71
P ₅ xL ₁	556.30	67.62	74.57	11.75	18.91	2.48	83.31	8.11	27.07	4.70
P ₅ xL ₃	527.66	63.31	68.77	10.09	20.88	2.95	79.59	6.21	24.23	4.81
P ₅ xL ₂	512.21	70.21	77.56	13.19	21.93	2.45	93.38	6.67	23.71	5.25
P ₆ xL ₁	725.25	56.64	62.59	14.35	17.01	2.86	75.11	6.25	38.88	5.61
P ₆ xL ₃	685.50	58.78	64.07	16.51	21.98	2.22	76.95	5.05	33.51	7.21
P ₆ xL ₂	640.77	68.92	76.18	16.01	22.27	1.95	87.67	4.71	39.61	6.62
P ₇ xL ₁	514.56	63.34	71.44	22.64	20.15	2.36	80.48	5.91	38.10	5.86
P ₇ xL ₃	495.95	63.48	68.71	22.94	23.97	2.59	85.33	5.46	37.18	5.07
P ₇ xL ₂	575.70	67.91	75.41	20.20	24.62	2.47	99.29	5.98	40.15	5.37
P ₈ xL ₁	536.20	50.63	59.71	25.30	16.95	2.91	81.24	6.93	28.11	6.01
P ₈ xL ₃	550.19	52.39	58.15	24.96	19.21	2.60	79.22	5.68	23.64	5.71
P ₈ xL ₂	558.85	60.91	67.73	19.48	18.51	2.18	74.07	5.57	24.47	5.02
P ₉ xL ₁	529.36	49.11	58.47	19.37	14.75	3.11	82.59	5.43	31.71	6.81
P ₉ xL ₃	502.47	50.47	59.12	17.31	15.85	2.97	75.31	5.69	29.15	7.37
P ₉ xL ₂	482.25	64.31	70.55	16.41	15.03	2.35	79.17	5.96	27.71	7.96
P ₁₀ xL ₁	536.36	55.87	63.79	16.76	17.32	2.90	86.78	8.75	33.61	7.49
P ₁₀ xL ₃	522.22	62.51	71.84	14.27	18.14	2.98	73.56	8.21	35.61	6.95
P ₁₀ xL ₂	508.78	67.43	76.77	15.97	16.86	2.03	85.62	6.03	38.19	7.20
P ₁	509.64	58.32	66.91	19.01	16.96	2.15	68.62	6.31	29.62	6.19

Table 1 continued...

Table 1 continued...

P ₂	498.79	63.67	70.22	16.50	17.87	2.32	74.18	5.99	27.04	6.65
P ₃	525.72	71.25	76.15	14.15	18.05	2.61	87.74	6.12	31.55	5.10
P ₄	555.12	65.49	73.15	18.34	16.56	2.69	89.45	4.19	33.36	6.38
P ₅	536.14	68.21	74.62	12.62	17.07	2.57	81.12	6.40	28.11	4.95
P ₆	580.75	64.98	69.34	15.56	19.00	2.35	74.45	5.48	30.85	6.63
P ₇	542.30	62.84	70.11	20.37	19.70	2.28	86.47	5.19	35.68	5.25
P ₈	562.17	58.63	64.89	22.35	17.15	2.44	78.82	4.79	28.02	5.86
P ₉	537.21	57.53	63.31	17.50	13.02	2.52	75.40	5.10	26.59	6.90
P ₁₀	517.42	59.87	65.19	15.80	15.33	2.21	83.27	6.81	31.63	6.52
L ₁	560.96	59.67	67.22	21.17	16.61	2.65	80.84	6.75	28.72	5.28
L ₃	545.40	63.62	69.51	19.58	18.94	2.75	88.94	6.15	32.38	6.62
L ₂	504.80	71.00	77.67	14.51	20.06	2.10	91.25	5.34	34.82	7.02
SE(m)±	0.23	0.39	0.11	0.14	0.34	0.15	0.36	0.29	0.18	0.64
CD at 5%	10.24	2.74	3.14	0.16	1.47	0.12	3.84	0.13	2.28	0.14

25.30 (P₈ x L₁) in progenies. The cross combinations (P₈ x L₁), (P₈ x L₃), (P₁ x L₁), (P₇ x L₃), (P₇ x L₁), (P₄ x L₁), (P₁ x L₃), (P₄ x L₃), (P₂ x L₂), (P₆ x L₂) and (P₁₀ x L₂) produced significantly more number of marketable fruits per plant than their respective better parent. Eight cross combinations significantly surpassed the cultivar Arka Nidhi (AN), *vis-a-vis* 21 cross combinations out yielded in number of marketable fruits per plant over Singh Nath (SN) giving an increase in number of marketable fruits per plant to the extent of 19.50 and 74.36 per cent over AN and SN, respectively. Over the superior Pi line (P₈) five crosses (P₁ x L₁), (P₇ x L₁), (P₇ x L₃), (P₈ x L₁) and (P₈ x L₃) exceeded in number of marketable fruits per plant and the increase was to the extent of 29.21 and 24.32 per cent over L₃ and best Pi line (P₈), respectively. The fruit length ranged from 16.61 cm (L₁) to 20.06 cm (L₂) in testers, 13.02 cm (P₉) to 19.70 cm (P₇) in Pi lines and 14.74 (P₄ x L₁) to 24.62 (P₇ x L₂) in progenies. Combinations (P₇ x L₂) excelled the superior Pi line (P₇) in fruit length significantly. With the respect of fruit diameter, the mean value of Pi lines was in the range of 2.15 cm (P₁) to 2.69 cm (P₄) and in progenies it ranged from 1.90 cm (P₁ x L₂) to 3.45 cm (P₄ x L₃). Among the progenies, the cross combinations (P₄ x L₃), (P₉ x L₁), (P₄ x L₁), (P₃ x L₃), (P₁₀ x L₃), (P₉ x L₃), (P₅ x L₃), (P₈ x L₁), (P₁₀ x L₁), (P₆ x L₁) and (P₃ x L₁) gave significantly higher fruit diameter than their respective better parent. The plant height varied from 80.84 (L₁) to 91.25 cm (L₂) in tester, 74.18 (P₂) to 89.45 cm (P₄) in Pi lines and 72.58 (P₁ x L₂) to 108.70 cm (P₄ x L₂) in progenies. 80.84 cm. The cross combinations (P₄ x L₂), (P₃ x L₃), (P₇ x L₂), (P₄ x L₃), (P₃ x L₂), (P₂ x L₂), (P₅ x L₂), (P₄ x L₁), (P₁₀ x L₁), (P₂ x L₁), (P₉ x L₁) and (P₈ x L₁) was superior to its respective better parent/tester. Eleven cross combinations surpassed in plant height than cultivar Arka Nidhi (AN), while five cross combinations performed significantly better than the cultivar Singh Nath (SN). The maximum increase in plant height was 34.46 and 19.12 per cent over AN and SN, respectively. Eight cross combinations exhibited more plant height over the L₃ tester, whereas seven cross combinations excelled in plant height over the best Pi line (P₄). The increase in plant height was to the extent of 21.52 and 22.21 per cent over Pi line (P₄) and L₃ tester, respectively. In respect to number of primary branches, the cross combinations (P₁₀ x L₁), (P₁₀ x L₃), (P₅ x L₁), (P₁ x L₂), (P₁ x L₁), (P₁ x L₃), (P₈ x L₁), (P₃ x L₃), (P₅ x L₂), (P₇ x L₂), (P₉ x L₂) and (P₈ x L₂) were significantly superior to their respective better parent/tester. For the fruit weight, The cross combinations (P₇ x L₂), (P₆ x L₂), (P₆ x L₁), (P₄ x L₂), (P₁₀ x L₂), (P₇ x L₁), (P₄ x L₃), (P₁₀ x L₃), (P₃ x L₃), (P₃ x L₁), (P₁ x L₂), (P₉ x L₁)

Table 2 : Analysis of variance for the design of experiment for fruit yield and related horticultural traits in triple test cross progenies of AN (L_1) and SN (L_2).

Treatments	df	Marketable fruit yield/plant (g)	Days to 50 per cent flowering	Days to first picking	Number of marketable fruits per plant	Fruit length (cm)	Fruit diameter (cm)	Plant height (cm)	Number of branches per plant	Fruit weight (g)	Pedicel length (cm)
Replicates	2	517.167	1.30	2.14	35.489	7.493	0.013	9.785	0.011	1.137	0.028
Treatments	42	1077.047**	97.870**	118.40**	18.265**	10.561**	0.106**	89.676**	0.360**	23.295**	0.502**
Error	84	39.390	2.82	3.79	0.967	0.826	0.006	5.554	0.006	1.967	0.008

Table 3 : Analysis of variance for epistasis i, j & l and D & H components for different characters in TTC progenies of AN (L_1) and SN (L_2).

Treatments	Marketable fruit yield/plant	Days to 50 per cent flowering	Days to first picking	Number of marketable fruits/plant	Fruit length	Fruit diameter	Plant height	Number of branches per plant	Fruit weight	Pedicel length
a) Epistasis ($L_{11} + L_{21} - 2L_{31}$)	3802.12**	31.53	525.03**	14.09**	25.97**	0.420	165.22**	1.33**	97.50**	0.227**
b) i type gene interactions	432.51	49.00**	381.63**	22.58**	5.52	0.237	138.58**	0.032	17.94	0.251**
c) j and l type gene interactions	4176.52**	27.92	540.96**	15.15**	28.69**	0.440	168.18**	2.36**	106.34**	0.150**
d) Sums ($L_{11} + L_{21}$)	1777.77**	318.05**	311.33**	9.87**	32.39**	0.84**	213.79**	0.94	36.13**	2.71**
e) Sums x Replicates	91.33	7.22	11.18	2.12	1.46	0.015	6.04	0.014	3.45	0.018
f) Differences ($L_{11} - L_{21}$)	2556.48**	103.57	197.79**	6.90**	28.39**	0.085	303.75**	1.88**	47.61**	0.36
g) Difference x Replicates	49.22	4.11	3.99	1.80	2.02	0.007	12.29	0.011	3.98	0.011
h) D	2248.59	414.44	400.19	6.80	18.51	0.30	143.66	1.15	43.57	2.26
i) H	3343.01	132.60	258.40	103.67	40.48	0.10	388.61	1.34	78.16	1.47
j) (H/D) ^{1/2}	1.21	0.56	0.80	3.90	1.47	0.58	1.64	1.07	1.20	0.80

(Mean Sum of Squares)

* Significant at 5 per cent level, ** Significant at 1 per cent level.

and ($P_2 \times L_1$) was superior to its respective better parent/ tester. The maximum increase in fruit weight was 39.79 and 15.30 per cent over AN and SN, respectively. Six and eight cross combinations were statistically at par for fruit weight with cultivar Arka Nidhi (AN) and Singh Nath (SN), respectively. Over the L_3 tester, 10 cross combinations produced significantly more fruit weight, while seven cross combinations excelled the superior Pi line (P_7) in fruit weight and the increase was observed to the tune of 23.99 and 12.52 per cent over L_3 tester and Pi line (P_7), respectively. For pedicel length ranged from 5.28 (L_1) to 7.02 (L_2) in testers, 4.95 (P_5) to 6.90 (P_9) in Pi lines and 4.70 ($P_5 \times L_1$) to 7.96 ($P_9 \times L_2$) in progenies. Twenty one cross combinations exhibited better pedicel length than the cultivar AN, whereas, seven cross combinations excelled in pedicel length than the cultivar SN. The maximum increase in pedicel length was to the extent of 50.75 and 13.39 per cent over AN and SN, respectively.

The existence of genetic variability among testers, parental lines and their progenies for marketable fruit yield per plant, days to 50 per cent flowering, days to 1st Picking, pedicel length, number of marketable fruits per plant, fruit length, fruit diameter, plant height, number of branches/plant, fruit weight and pedicel length. The progenies ($P_3 \times L_1$), ($P_3 \times L_2$), ($P_2 \times L_3$), ($P_5 \times L_2$), ($P_7 \times L_2$), ($P_7 \times L_3$) and ($P_9 \times L_3$) exhibited significantly higher mean values marketable fruit yield per plant, number of marketable fruits per plant, fruit length, fruit diameter, fruit weight, number of branches/plant. Epistasis was observed for these characters showing thereby epistasis played significant role in the inheritance of these traits. These results are in line with those of Bhakta *et al.* (2009), Kafyullah *et al.* (2011), Reddy and Patel (2014) and Chauhan and Chandel (2016). The manifestation of non-additive genetic effects and general trend of increase indicated that positive heterotic effects are visible.

The analysis of variance for detection of epistasis (table 3) revealed that Epistasis (*i*) and (*j+l*) type was significant in all the traits except days to 50 per cent flowering and fruit diameter (cm). Darrah and Hallauer (1972) suggested that non-additive interactions are more important for components of yield rather than plant characteristics. Since (*j+l*) type epistasis is more useful for hybrid development. This table also indicate that the variances due to sums ($L_{1i} + L_{2i}$) were used for estimating additive (D) component of genetic variation, whereas the variances due to difference ($L_{1i} - L_{2i}$) were used for estimation of dominance (H) component. The importance of additive and dominance components of variation were reported for fruit yield and its components traits in brinjal

by Thangavel *et al.* (2011), Chourasia and Shree (2012), Sidhu *et al.* (2012), Arunkumar *et al.* (2013) and Uddin *et al.* (2015). The degree of dominance (H/D)^{1/2} was in the range of over dominance marketable fruit yield per plant, number of marketable fruits per plant, fruit length (cm), plant height (cm), number of branches per plant and fruit weight (g). However the presence of partial dominance for, days to 50 per cent flowering, days to first picking, fruit diameter (cm) and pedicel length (cm). These results are also in line with Kafyullah (2011) in brinjal. This suggests that heterosis breeding and reciprocal recurrent selection would be an appropriate procedure for the improvement of these characters. Recurrent selection procedures may be useful in the sense that it will exploit both additive and non-additive components of genetic variation for bringing about improvement in yield and its related attributes. Such a strategy will help increase frequency of favourable alleles while maintaining genetic variation in breeding population (Doerksen *et al.*, 2003).

Conclusion

The triple test cross showed that the additive, dominance and epistasis gene actions were important in the inheritance of different characters. Under such a situation triple test cross mating as well as mating of selected plants in early segregating generations could be attempted for developing potential populations having optimum levels of homozygosity and heterozygosity. Although, transgressive segregants can be isolated by alternative intermating and subsequent handling of segregating generations in order to obtain high yielding stable lines in brinjal where all the three kinds of gene effects are present.

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