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Gene actions for fruit yield and quality characters of tomato through generation mean analysis

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ABSTRACT

Nature of gene action for fruit yield and quality characters of tomato was determined analyzing the mean and variances of the six genetic populations (P_1, P_2, F_1, F_2 ,BC_1 and BC_2) of three cross combinations: Oregon Pride × BCT-115, Oregon Pride × CLN 2116 B and Oregon Pride × BC ps. The parthenocarpic line, Oregon Pride and three widely divergent non-parthenocarpic lines, dark green fruited genotypes, T 4099 dg og^c (BCT-115), heat tolerant line (CLN 2116 B) and positional sterile (*ps*) line BC ps. Non-additive gene action including non-allelic interactions was important for the genetic control of all the characters which indicated that yield components and fruit quality traits were predominantly under the control of non-fixable gene effects. Narrow sense heritability estimates in all the characters were low to moderate additive genes indicating that environment will have much influence on such traits. Presence of complementary type epistasis for fruit yield and lycopene content indicated the possibility of developing hybrids for high fruit yield and high lycopene content in fruits.

Key words: Gene action, generation mean, fruit characters, tomato.

INTRODUCTION

Generation mean analysis is an efficient tool to understand the nature of gene effects involved in the expression of the character. Diallel and line x tester analyses are generally employed to select the parents based on their combining ability but fail to detect the epistasis, which remains the most complex problem and on which it is extremely difficult to obtain reliable results. The presence and absence of epistasis can be detected by the analysis of generation means using the scaling test, which measures epistasis accurately whether complementary (additive x additive) or duplicate (additive x dominance) and (dominance x dominance) at digenic level. The objective of this study was to obtain information on the nature of gene action for fruit yield and quality characters to provide a basis for evaluation methods for the improvement of the important economic traits of tomato population.

MATERIALS AND METHODS

In this experiment spanning for two years (2005-06 to 2007-08), four lines including one facultative parthenocarpic line, "Oregon Pride" developed at USA and received from the Indian Institute of Vegetable Research, Varanasi and three widely divergent non-parthenocarpic lines, dark green fruited genotype from USDA, USA,T 4099 dg og^c (BCT-115), heat tolerant line selected from the material from AVRDC, Taiwan (CLN 2116 B) and positional sterile (*ps*) line "BC ps" were employed. The experiments involved the six basic generations (P_1 and P_2 parent lines, the F_1 and F_2, and the BC_1 and BC_2) of three combinations of the parental lines, these combinations being Oregon Pride x BCT-115, Oregon Pride x CLN 2116 B and Oregon Pride x BC ps. The genetic populations (50 each of P_1, P_2 and F_1; 80 F_2 and 60 each of BC_1 and BC_2 of these three crosses were grown in the three separate blocks without replication during autumn-winter season of 2007-08 and data were recorded from all the plants of the six genetic populations for fruit yield and associate characters (fruits/plant and fruit weight). Composite fruit samples were taken from all the plants of the populations to determine different fruit quality traits, *viz.*, TSS (^{0}Brix), total sugars (%), reducing sugar (%), β-carotene (mg/100 g fresh weight), lycopene (mg/100 g fresh weight) contents and acidity (%) following standard procedures as described by Sadasivam and Manickam (13).

The mean values, standard errors and variances of the different generations calculated over all the plants in each generation were used for scaling test. The genetic effects were estimated using the models suggested by Mather and Jinks (9), and the significance of the scales and gene effects were tested by using the't' test.

The A, B, C and D scaling tests were carried out for all the traits indicated the presence of non-allelic interactions in all the cases. The 'A' and 'B' scaling tests provided the evidence for the presence of additive x additive (i), additive x dominance (j) and dominance

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x dominance (l) types of gene interactions. The ‘C’ scaling test provided a test for ‘l’ type epistasis, whereas ‘D’ scaling test gave information about ‘i’ type of gene interaction.

RESULTS AND DISCUSSION

The expected mean values (m) of the four possible homozygotes for the three characters were positive and significant in all the three crosses. Average number of fruits per plant was recorded from the periodical harvests of all the plants. Estimates of almost all the scales were significant revealing non-allelic interaction for the genetic control of fruits/plant (Tables 1 & 2). Both additive and dominance genetic variance were significant for all the three crosses but magnitude of the dominance was markedly higher than additive variance in all the crosses indicating the importance of non-fixable gene effects for the control of fruit number/plant. Almost all the epistatic interaction components were significant in all the three crosses further suggesting the importance of non-additive gene action for this trait. Additive x additive interaction was pre-dominant in Oregon Pride x BCT-115 cross, while both the components were equal for the rest two crosses, Oregon Pride x CLN 2116 B and Oregon Pride x BCps. Type of epistasis was complementary for Oregon Pride x CLN 2116 B and duplicate for the cross Oregon Pride x BCps.

Simple additive/dominance model was not adequate (Tables 1 & 3) to explain the gene effect for fruit weight because most of the scales were significant, revealing non-allelic interaction for the genetic control of this character. Both additive and dominance genetic variances were significant for all the three crosses but dominance variance was comparatively more important for the genetic control of this character. All the non-allelic gene interactions were significant in all the cross combinations, dominance x dominance (l) interaction component being predominant in magnitude in all the three crosses. Type of epistasis was duplicate in all the three crosses. Significant additive x additive (i) type gene interaction and duplicate epistasis seen in this trait suggested the possibilities of obtaining transgressive segregants in later generations.

The mean values for the six generations, scaling test and gene effects clearly indicated that simple additive/dominance model was inadequate to explain the genetic control of fruit yield per plant because all the scales were found significant (Tables 1 & 4). In

Table 1. Mean data for fruit yield components in genetic populations.

Cross	Generation	Fruit yield trait		
		Fruits/plant	Fruit weight (g)	Fruit yield/plant (kg)
Oregon Pride × BCT-115	P_1	19.64	68.53	1.28
	P_2	10.95	122.35	1.42
	F_1	19.53	106.44	1.97
	F_2	12.24	84.91	1.07
	BC_1	13.38	71.12	1.02
	BC_2	16.27	83.53	1.58
Oregon Pride × CLN 2116B	P_1	20.23	67.67	1.36
	P_2	37.94	57.48	2.19
	F_1	49.76	78.29	4.25
	F_2	20.25	71.93	2.37
	BC_1	18.08	82.61	1.78
	BC_2	33.64	72.56	1.96
Oregon Pride × BCps	P_1	19.86	68.34	1.47
	P_2	12.08	96.18	1.12
	F_1	26.43	73.76	2.26
	F_2	21.81	64.55	1.55
	BC_1	16.63	67.21	1.18
	BC_2	10.55	76.56	1.04

Table 2. Scaling test and gene effects for fruits per plant in three cross combinations.

Model and effects of estimates	Cross combination		
	Oregon Pride × BCT-115	Oregon Pride × CLN 2116 B	Oregon Pride × BCps
	Scaling test (Mather and Jinks, 1971)		
A	-12.98 ± 1.67**	-33.77 ± 2.55**	-11.79 ± 3.10**
B	2.60 ± 2.32	-20.37 ± 5.74**	-15.89 ± 2.21**
C	-1.73 ± 3.32	-31.26 ± 4.65**	48.61 ± 8.34**
D	-5.17 ± 2.14**	-13.41 ± 3.49**	25.74 ± 4.33**
	Six parameter model (Mather and Jinks, 1971)		
m	12.24 ± 1.41**	19.15 ± 1.79**	26.43 ± 3.59**
d	-2.88 ± 1.55*	-15.56 ± 3.42**	6.12 ± 1.96**
h	14.28 ± 3.18**	47.43 ± 5.45**	-42.83 ± 6.80**
i	10.34 ± 3.84**	26.82 ± 5.32**	-51.48 ± 8.49**
j	-7.52 ± 1.14**	-6.70 ± 2.54**	2.05 ± 1.54
l	0.59 ± 4.49	27.33 ± 8.82**	79.17 ± 8.13**
Non-allelic	-	Complementary	Duplicate

*, ** Significantly different at 5 and 1% probability levels, respectively

Table 3. Scaling test and gene effects for fruit weight (g) in three cross combinations.

Model and effects of estimates	Cross combination		
	Oregon Pride × BCT-115	Oregon Pride × CLN 2116 B	Oregon Pride × BCps
	Scaling test (Mather and Jinks, 1971)		
A	-32.73±5.92**	14.40±5.43**	-7.83±6.53
B	-61.73±6.59**	39.36±4.81**	-56.76±7.89**
C	42.32±13.04**	73.29±12.15**	39.79±13.79**
D	15.17±8.17*	-34.38±6.16**	25.33±7.20**
	Six parameter model (Mather and Jinks, 1971)		
m	84.91±4.77**	71.90±4.32**	64.55±4.54**
d	-12.41±5.65*	-6.95±3.52*	10.64±4.78*
h	-19.34±12.59*	94.05±10.30**	-79.30±12.33**
i	-30.34±15.48*	68.76±11.83**	-50.66±13.79**
j	14.50±4.03**	-12.48±2.92**	24.47±3.93**
l	124.81±15.89**	-122.52±12.98**	115.24±16.01**
Non-allelic	Duplicate	Complementary	Duplicate

*, ** Significantly different at 5 and 1% probability levels, respectively

all the three crosses, both dominance and additive genetic variances were significant excepting significance of only dominance variance in Oregon Pride x CLN 2116 B, although dominance variance was relatively more important. All the non-allelic interaction components were significant in all the cross combinations but dominance x dominance component was predominant in all the cases. The epistatic effect was complementary in two crosses (Oregon Pride x BCT-115 and Oregon Pride x CLN 2116 B) and duplicate for Oregon Pride x BCps. Complementary epistasis indicated the possibility of effectively exploiting this character by heterosis breeding.

Table 4. Scaling test and gene effects for fruit yield per plant (kg) in three cross combinations.

Model and effects of estimates	Cross combination		
	Oregon Pride × BCT-115	Oregon Pride × CLN 2116 B	Oregon Pride × BCps
	Scaling test (Mather and Jinks, 1971)		
A	-1.36±0.14**	-2.44±0.23**	-0.69±0.34*
B	-0.55±0.24*	-2.99±0.28**	-1.83±0.18**
C	-0.71±0.34*	-2.18±0.40**	4.91±0.85**
D	-0.39±0.22*	-0.51±0.24**	2.94±0.45**
	Six parameter model (Mather and Jinks, 1971)		
m	0.97±0.13**	1.37±0.14**	2.20±0.32**
d	-0.51±0.16**	-0.21±0.19	0.62±0.22**
h	1.42±0.33**	3.56±0.39**	-5.49±0.72**
i	0.78±0.39*	1.02±0.42**	-5.88±0.89**
j	-0.41±0.12**	0.28±0.15*	0.57±0.17**
l	1.13±0.45**	4.41±0.56*	8.40±0.85**
Non-allelic	Complementary	Complementary	Duplicate

*, ** Significantly different at 5 and 1% probability levels, respectively

Mean of the six generations along with scaling test and gene effects for the fruit quality traits, *viz.,* TSS, total sugars, reducing sugar, β-carotene, lycopene and acidity of the juice in three cross combinations (Table 5) suggested appreciably high quality attributes for the parthenocarpic line Oregon Pride (TSS: 4.3°B; total sugars: 3.05%; reducing sugar: 1.89%; lycopene content: 4.24 mg/100 g fresh and acidity: 0.31%). The expected mean values (m) of the four possible homozygotes for all the six fruit quality traits were positive and significant in all the three cross combinations. In all cross combinations, a simple additive/ dominance model was inadequate in explaining the gene effects for all the fruit quality traits (Table 6). Significance of most of the scales suggested the contribution of non-allelic interaction for the genetic control of all the six fruit quality traits.

In all the cross combinations, both dominance and additive variance were significant and almost equally important for TSS content. All the epistatic components were also significant in all the cross combinations but dominance x dominance (l) interaction effect was the largest in all the cases. The epistatic effect was "Duplicate" in two crosses, Oregon Pride x BCT-115 and Oregon Pride x CLN 2116 B and "Complementary" in the cross of Oregon Pride x BCps.

In all the cross combinations, both dominance and additive genetic variances were significant for total sugars excepting Oregon Pride x BCps with only significant additive variance, dominance variance being relatively more important in rest of the two cross combinations. All the epistatic components were significant in all the crosses and both additive x additive (i) and dominance x dominance (l) interactions were almost equally important. The epistatic effect was "Duplicate" in all the three crosses.

In all the cross combinations, both dominance and additive genetic variances were significant, dominance variance being relatively more predominant for reducing sugar content. All the non-allelic interactions were significant in Oregon Pride x BCT-115, whereas only dominance x dominance type interaction was significant in other two crosses (Oregon Pride x CLN 2116 B and Oregon Pride x BC ps). The type of epistasis was duplicate in nature. In Oregon Pride x CLN 2116 B and Oregon Pride x BC ps, both dominance and additive variances were significant but dominance variance was comparatively more predominant for β-carotene content. In Oregon Pride x BCT-115, only dominance variance was significant. Significance of non-allelic interaction components varied with the cross combinations. Both additive x additive and dominance x dominance components were found almost equally important. Duplicate type epistasis was prevalent for β-carotene content. For lycopene content, in Oregon Pride x BCT-115 and Oregon Pride x BC ps both dominance and additive variances were found significant but in Oregon Pride x CLN 2116 B only additive variance was significant. All the epistatic components were significant in the cross Oregon Pride x BC ps, while 'j' and 'l' types of

Table 5. Mean data for fruit quality traits in genetic populations in tomato.

Cross	Generation	Fruit quality trait					
		TSS (°Brix)	Total sugars (%)	Reducing sugar (%)	β-carotene (mg/100 g)	Lycopene (mg/100 g)	Acidity (%)
Oregon Pride × BCT-115	P_1	4.32	3.05	1.89	2.37	4.24	0.31
	P_2	4.65	1.21	0.88	2.15	4.35	0.36
	F_1	5.60	2.31	1.65	2.06	5.06	0.38
	F_2	4.61	1.28	1.03	1.99	3.98	0.41
	BC_1	4.33	2.29	1.73	2.22	4.03	0.32
	BC_2	4.73	1.69	0.89	1.97	4.44	0.39
Oregon Pride × CLN 2116 B	P_1	4.32	3.05	1.89	2.37	4.24	0.31
	P_2	5.63	2.53	1.94	2.13	3.01	0.47
	F_1	4.95	2.27	1.40	2.27	5.14	0.36
	F_2	4.59	2.37	1.55	1.96	3.51	0.44
	BC_1	3.99	2.87	1.73	2.26	3.88	0.33
	BC_2	4.89	2.44	1.88	2.14	2.96	0.46
Oregon Pride × BCps	P_1	4.32	3.05	1.89	2.37	4.24	0.31
	P_2	5.63	2.76	2.09	2.40	3.49	0.39
	F_1	5.07	3.44	2.28	2.39	4.85	0.28
	F_2	4.12	3.23	1.99	2.11	3.89	0.38
	BC_1	3.87	2.99	1.71	2.23	4.09	0.32
	BC_2	4.69	2.61	1.89	2.41	3.51	0.37

Table 6. Scaling test and gene effects for fruit quality traits for Oregon Pride × BCT-115 (1), Oregon Pride × CLN 2116 B (2), and Oregon Pride × BCps (3) hybrids.

Model and effects of estimates	Fruit quality trait					
	TSS (°Brix)	Total sugars (%)	Reducing sugar (%)	β-carotene (mg/100 g)	Lycopene (mg/100 g)	Acidity (%)
	Scaling test (Mather and Jinks, 1971) for (1)					
A	-1.24 ± 0.50*	-0.78 ± 0.19**	-0.08 ± 0.02**	0.01 ± 0.01	-1.24 ± 0.62*	-0.05 ± 0.02*
B	-0.79 ± 0.43*	-0.14 ± 0.03**	-0.75 ± 0.30*	-0.27 ± 0.16	-0.53 ± 0.35	0.04 ± 0.02*
C	3.89 ± 0.53**	-1.45 ± 0.64*	-0.30 ± 0.09**	1.38 ± 0.67*	2.27 ± 0.89**	0.59 ± 0.24*
D	0.16 ± 0.03**	-1.42 ± 0.35**	-0.56 ± 0.32*	-0.21 ± 0.09*	-0.51 ± 0.24*	0.11 ± 0.04**
	Six parameter model (Mather and Jinks, 1971) for (1)					
m	4.61 ± 0.10**	1.28 ± 0.15**	1.03 ± 0.13**	1.99 ± 0.16**	3.98 ± 0.21**	0.41 ± 0.11**
d	-0.40 ± 0.19*	0.60 ± 0.16**	0.84 ± 0.18**	0.25 ± 0.17	-0.41 ± 0.14**	-0.07 ± 0.03*
h	0.81 ± 0.33*	3.02 ± 0.71**	1.39 ± 0.65*	0.22 ± 0.03**	1.79 ± 0.72**	-0.18 ± 0.07**
i	-0.32 ± 0.08**	2.84 ± 0.64**	1.12 ± 0.58*	0.42 ± 0.19*	1.02 ± 0.61	-0.22 ± 0.05**
j	-0.23 ± 0.11*	-0.32 ± 0.16*	0.34 ± 0.19*	0.14 ± 0.06*	-0.36 ± 0.13**	-0.05 ± 0.02*
l	2.35 ± 1.31*	-1.92 ± 0.91*	-0.29 ± 0.11**	-0.16 ± 0.07*	0.75 ± 0.33*	0.23 ± 0.09**
Non-allelic	Duplicate	Duplicate	Duplicate	Duplicate	Complementary	Duplicate

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Model and effects of estimates	Fruit quality trait					
	TSS (°Brix)	Total sugars (%)	Reducing sugar (%)	β-carotene (mg/100 g)	Lycopene (mg/100 g)	Acidity (%)
Scaling test (Mather and Jinks, 1971) for (2)						
A	-1.27±0.40**	0.42 ± 0.12**	0.17±0.07*	-0.12 ± 0.06*	-1.62 ± 0.31**	-0.01 ± 0.09
B	-0.80±0.34*	0.08 ± 0.02**	0.42±0.21*	-0.18 ± 0.04**	-2.23 ± 0.30**	0.09 ± 0.02**
C	3.48±0.72**	1.63 ± 0.68*	0.97±0.41*	1.07 ± 0.68	1.65 ± 0.88*	0.62 ± 0.17**
D	0.30±0.13*	-0.57 ± 0.27*	-0.51±0.21*	-0.45 ± 0.17**	0.18 ± 0.08*	0.09 ± 0.03**
Six parameter model (Mather and Jinks, 1971) for (2)						
m	4.59 ± 0.17**	2.37 ± 0.15**	1.55 ± 0.19**	1.96 ± 0.16**	3.51 ± 0.21**	0.44 ± 0.11**
d	-0.90 ± 0.25**	0.43 ± 0.31	-0.15 ± 0.04**	0.15 ± 0.05**	0.92 ± 0.19**	-0.13 ± 0.08
h	-0.62 ± 0.33*	0.62 ± 0.29*	0.51 ± 0.24*	0.92 ± 0.46*	1.16 ± 0.69	-0.21 ± 0.08**
i	-0.60 ± 0.09**	1.14 ± 0.63*	1.02 ± 0.61	0.90 ± 0.68	-0.36 ± 0.13**	-0.18 ± 0.10*
j	-0.24 ± 0.07**	0.17 ± 0.03**	-0.13 ± 0.08	0.03 ± 0.01**	0.31 ± 0.21	-0.05 ± 0.02*
l	2.67 ± 1.24*	-1.64 ± 0.87*	-1.61 ± 0.79*	-0.60 ± 0.43	4.21 ± 1.18**	0.10 ± 0.07
Non-allelic	Duplicate	Duplicate	Duplicate	-	Complementary	-
Scaling test (Mather and Jinks, 1971) for (3)						
A	-1.63 ± 0.33**	-0.51 ± 0.29*	-0.75 ± 0.51	-0.30 ± 0.14*	-0.91 ± 0.44*	0.05 ± 0.02*
B	-1.32 ± 0.36**	-0.98 ± 0.40*	-0.59 ± 0.37	0.03 ± 0.01**	-1.32 ± 0.51*	0.07 ± 0.04*
C	1.48 ± 0.51**	3.67 ± 0.64**	1.70 ± 0.68*	1.28 ± 0.79	2.98 ± 0.91**	0.54 ± 0.40
D	-0.32 ± 0.15*	0.86 ± 0.42*	0.38 ± 0.17*	-0.42 ± 0.08**	0.18 ± 0.03**	0.07 ± 0.01**
Six parameter model (Mather and Jinks, 1971) for (3)						
m	4.12 ± 0.11**	3.23 ± 0.13**	1.99 ± 0.15**	2.11 ± 0.19**	3.89 ± 0.20**	0.38 ± 0.10**
d	-0.82 ± 0.23**	0.38 ± 0.20*	-0.18 ± 0.08*	-0.18 ± 0.07*	0.58 ± 0.30*	-0.05 ± 0.02*
h	0.75 ± 0.42*	-1.19 ± 0.85	-0.47 ± 0.19**	0.85 ± 0.29**	0.63 ± 0.23**	-0.21 ± 0.12*
i	0.64 ± 0.32*	-1.72 ± 0.78*	-0.76 ± 0.53	0.84 ± 0.44*	-0.36 ± 0.17*	-0.14 ± 0.06*
j	-0.16 ± 0.08*	0.24 ± 0.11*	-0.08 ± 0.05	-0.17 ± 0.11	0.21 ± 0.02**	-0.01 ± 0.03
l	2.31 ± 1.04*	3.21 ± 1.43*	2.10 ± 0.87*	-0.57 ± 0.16**	2.59 ± 1.51*	0.02 ± 0.01*
Non-allelic	Complementary	Duplicate	-	Duplicate	Complementary	Duplicate

*,** Significantly different at 5 and 1% probability levels, respectively

interaction were significant in Oregon Pride x BCT-115 and 'i' and 'l' types of interaction were significant for Oregon Pride x CLN 2116 B. Dominance x dominance interaction emerged as the most prominent in all the three crosses. Type of epistasis was complementary in all the crosses for lycopene content. In Oregon Pride x BCT-115 and Oregon Pride x BC ps both dominance and additive gene action were significant, dominance being more important for acidity of fruit juice. In Oregon Pride x CLN 2116 B, only dominance genetic variance was significant. Most of the interaction components were significant in all the three crosses but additive x additive interaction emerged as the predominant one. Duplicate type epistasis was operative for this character.

This study projected overwhelming importance dominance genetic variance for the control of all thecharacters which finds ample support from number earlier reports of such studies on tomato (Rai *et al.*, 11; Garg *et al.*, 5; Mandal *et al.*, 8).

The effectiveness of selecting for a particular characteristic depends on the relative importance of heredity and environment in the development of that trait. Heritability is a measure of the degree to which a phenotype is genetically influenced and therefore, can be modified by phenotypic selection. Heritability in narrow sense is the ratio of its additive genetic variance to total variance. When narrow sense heritability is low, the greater part of the observed variation in that trait is environmental and the trait is mostly under the control of non-fixable gene effects. Both broad sense and narrow sense heritability estimates emanated from three cross combinations (Table 7) suggested comparatively much higher broad sense heritability estimates than that of the narrow sense for all the characters. Low to moderate narrow sense heritability estimates in most of the characters agreed well to several earlier reports (Markovic *et al.*, 7; Da Silveira and Maluf, 1; Sekar, 14; Hanson *et al.*, 6; Rodriguez *et al.*, 12; Mohamed and Badr, 10) which indicated that that all these traits were influenced by additive genes and environment will have much influence on such traits.

Gene action from the six generations of three cross combinations somewhat agreed well. It appeared the yield components and fruit quality traits were under the control of both fixable and non-fixable gene effects because of the revelation of significance of 'd', 'h', 'i' and 'l' types gene interaction for most of the traits which indicated that to have a positive shift in the expression of the phenotypic mean it would be essential to harness both the additive and non-additive gene effects prevalent in the characters. In most of the cases, the dominance (h) and dominance x dominance (l) effects were significant and were in opposite direction suggesting duplicate type epistasis which indicated predominantly dispersed alleles at the interacting loci which will decrease variation in the F_2 and subsequent generations and will hider the pace of progress through selection as recorder earlier (Dhankar *et al.*, 2; Dixit *et al.*, 3). However, positive additive x additive (i) type gene action and duplicate epistasis seen in some traits like locules/fruit and β-carotene content in Oregon Pride x BCT-115 indicate the possibility of obtaining transgressive segregants in later generations (Sharmila *et al.*15). Additive x additive type non-allelic interaction was found significant for most of the characters but with negative sign which indicated little scope of improvement through simple selection. Presence of complementary type epistasis for fruit yield and lycopene content is encouraging for the development of hybrids of high fruit yield and high lycopene content in fruits. The following breeding strategy is suggested with a view to the gene effects determined for different characters, namely, (a) Single seed descent method of breeding with progeny row testing and selection since backcrosses are not suitable for fixing such traits as suggested by Frimpong and SafoKantanka (4); (b) Use of reciprocal recurrent selection or bi-parental mating when both additive and non-additive gene effects are involved in expression of the traits; (c) Postponement of selection in later generations or inter mating among the selected sergeants followed by one or two generation(s) of selfing to break the undesirable linkage and allow the accumulation of favourable alleles for improvement of the trait, and (d) Development of hybrids for improved fruit yield and lycopene content because of the revelation of complementary epistasis for these characters because important part of heterosis results from non-linear interaction of genes at different loci, from interaction between alleles at the same locus or from both causes in combination.

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Table 7. Heritability (both broad sense and narrow sense) for different characters in three cross combinations.

Trait	Heritability (%)					
	O. Pride × BCT-115		O. Pride × CLN 2116 B		O. Pride × BCps	
	Broad sense	Narrow sense	Broad sense	Narrow sense	Broad sense	Narrow sense
Fruits/ plant	83.02	45.85	85.61	33.39	96.98	32.86
Fruit weight (g)	97.22	48.67	94.64	47.78	96.86	58.54
Yield/ plant (kg)	84.23	77.49	90.47	69.29	98.69	31.15
TSS (°B)	73.68	21.05	78.18	23.64	69.09	25.64
Total sugars (%)	69.77	55.81	51.16	48.33	51.52	46.27
Reducing sugars (%)	65.63	45.31	82.54	34.92	57.14	58.57
β-carotene (mg/100 g)	93.88	57.14	90.91	38.64	54.84	55.32
Lycopene (mg/100 g)	91.14	42.15	89.16	40.96	83.68	47.24
Acidity (%)	95.24	67.62	95.45	68.64	94.44	57.22

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