Vegetable Science (2021) 48 (1) : 22-29

Gene action for yield components and fruit quality characters of tomato genotypes possessing mutant genes through generation mean analysis

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Received: June 2021/ Accepted: July 2021

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 involving parental lines possessing mutant genes viz., Alisa Craig *AftAft*x Alisa Craig *hp-1 hp-1*, Alisa Craig *Aft Aft*x Alisa Craig $og^c og^c$ and Alisa Craig *AftAft*x BCT 115 *dg dg*. In most of the characters in three cross combinations, simple additive / dominance model was inadequate to explain the gene action which indicated the involvement of epistasis in the control of the character concerned. The characters were under the control of both fixable and non-fixable gene effects, but non-fixable gene effects were predominant. Duplicate type epistasis for most of the characters would hinder the pace of progress through selection. Postponement of selection in later generations and development of hybrids were the best breeding strategy because non-fixable gene effects were predominant for most of the characters.

Key words: Generation mean, Gene action, yield components, fruit quality, Tomato

Introduction

Tomato (*Solanum lycopersicum* L. 2n=2x=24) is one of the most popular vegetables in the world because of its wider adaptability, high yielding potential and suitability for variety of uses in fresh as well as processed food industries (Chaudury et al. 2019). The compositional fruit quality of tomato particularly, lycopene, flavonoids, ascorbic acid and chlorogenic acid in the human diet has received increasing interest because of their role in inhibition of some chronic disease (Devaux et al. 2005; Dixon 2005; Niggeweg et al. 2006; Rein et al. 2006; Niranjana et al. 2015). A better understanding of the mode of inheritance of fruit yield components and quality characters are crucial for adequate choice of breeding strategy for developing high-yielding cultivars and hybrids with enhanced fruit quality. Explanations for relative importance of additive and non-additive gene effects in planning more efficient breeding could be obtained from a comparative assessment of the linear components: additive (d), dominance (h), additive × additive (i), additive × dominance (j) and dominance × dominance (l) gene effects. Generation mean analysis (Mather and Jinks, 1982) is a useful technique that provides the estimation of main genetic effects (additive, dominance and their digenic interactions) involved in the expression of quantitative traits. In this model, presence and absence of epistasis could be detected by analysis of generation means using a scaling test, which measures epistasis accurately whether complementary (additive × additive) or duplicate (additive × dominance and dominance × dominance) at the digenic level. This model was successfully applied for determination of inheritance pattern of several characters of tomato (Foolad and Lin 2001; Bhatt et al. 2001; Abreu et al. 2008; Zdravkovic et al 2011; Akhtar and Hazra 2013; Dutta et al, 2013). This study was undertaken to determine the nature of gene action for 14 fruit yield components and fruit quality characters involving six basic generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of three cross combinations of the parental lines possessing mutant genes.

Materials and Methods

The study was carried out during autumn-winter seasons (October–March) between 2014 and 2017 at Central Research Farm, Gayeshpur, Bidhan Chandra Krishi Viswavidyalaya, Nadia, West Bengal situated at 22°572 N latitude and 88°202 E longitude with average altitude of 9.75 m above the mean sea level in open field condition under the average day temperature range of 22.5–31.9 °C and night temperature range of 8.4–22.4 °C, the

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average day/ night being 27.6/15.1 °C. Three near isogenic lines possessing anthocyanin fruit gene (*Aft*) and two lycopene enhancing gene (*hp-1* and og^c) *viz*., Alisa Craig *AftAft*, Alisa Craig *hp-1 hp-1* Alisa Craig og^cog^c received from the Institute of Genetics and Physiology, Bulgarian Academy of Science, Sofia, Bulgaria and other genotype possessing another lycopene enhancing gene (*dg*) *viz*., BCT 115 *dgdg* received from USDA were characterized (Biswas et al., 2016) before utilization to develop three hybrids, Alisa Craig *AftAft*x Alisa Craig *hp-1 hp-1*, Alisa Craig *Aft Aft*x Alisa Craig og^cog^c and Alisa Craig *AftAft*x BCT 115 *dg dg*. Conventional hybridization method was followed in which the matured flower buds that would open in the next day morning was emasculated in the afternoon hours and covered with thin cotton wad. In the next morning hours between 8-9, the emasculated flowers were pollinated by the pollens of the desired male parent in the crossing scheme.

The three F_1 hybrids were selfed to obtain F_2 progenies and backcrossed to their respective parents (P_1 and P_2) to obtain backcross progenies of $BC_1$and BC_2. The six genetic populations of the three crosses (50 plants each of P_1, P_2 and F_1; 200 F_2 and 100 each of BC_1 and BC_2) were field grown in autumn-winter season (October 2016 to March 2017) in 5 replications keeping 10 plants of P_1, P_2 and F_1; 40 plants of F_2 and 20 plants of BC_1 and BC_2 per replication. All the plants of each of six genetic populations were used for taking the observations on 14 different characters *viz*., days to first flower (after transplanting), fruits per plant, fruit weight (g), locule number per fruit, pericarp thickness (mm) and fruit yield per plant (kg) TSS, sugar, reducing sugar, tritrable acidity, ascorbic acid, lycopene, â carotene and anthocyanin contents of ripe fruits. Total fruit weight in the periodical harvest at advanced turning stage from all the plants of the6 genetic populations of the 3 cross combinations was averaged to depict fruit yield/ plant (kg). Five such fruits sampled periodically were kept in room temperature condition till ripe completely for estimation of different quality characters. After taking the fruit weight (g), the fruits were cut into two halves and pericarp thickness was measured with the help of digital slide callipers. The cut fruits were used to make composite sample to estimate different fruit quality characters on fresh weight basis *viz*., total soluble solids (ÚBrix) by hand refractometer, total, reducing and non-reducing sugar content (Dubois et al. 1951), ascorbic acid content (mg/100g fresh) by titration with 2.6-dichlorophenolindophenol sodium salt solution (AOAC 1990), lycopene and â carotene contents (mg/100 g fresh) spectrophotometrically (Davies 1976) and anthocyanin content (mg/100 g) spectrophotometrically (Sadasivam and Manickam 1996). Purple skin colour was not uniform throughout the fruit surface hence, areas of skin and pericarp tissue expressing high anthocyanin was sampled to estimate the anthocyanin content of fruits of *Aft* genotypes.

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 (1982), and the significance of the scales and gene effects were tested by using the 't' test against its standard error of estimate (Singh and Chaudhary 1985). The corresponding standard errors were calculated by taking the square root of the respective scaling test and subjected to 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. Data were analyzed with INDOSTAT (ver. 8.1, Indostat Services, Ameerpet, Hyderabad, India).

Results and Discussion

Mean performances of parental lines (P_1 and P_2), and their generations (F_1, F_2, BC_1, BC_2) of the 3 crosses and components of generation means for three crosses have been presented (Table 1, 2). Presence and absence of epistasis, whether complementary (additive x additive) or duplicate (additive x dominance and dominance x dominance) at digenic level could be detected by the analysis of generation means using the scaling test. The A, B, C and D scaling tests indicated the presence of non-allelic interactions in all the characters excepting locules /fruit, TSS, total sugar and reducing sugar contents in Alisa Craig *Aft Aft*x Alisa Craig og^cog^c; days to flower and tritrable acidity in Alisa Craig *AftAft*x Alisa Craig *hp-1 hp-1*; days to flower, reducing sugar and â carotene content in Alisa Craig *AftAft*x BCT 115 *dg dg*because no scale was significant for these characters. The 'A' and 'B' scaling tests provided the evidence for the presence of additive x additive (i), additive x dominance (j) and dominance 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. The type of epistasis was determined only when dominance (h) and dominance x dominance (l) effects were significant; when these effects had the same sign the effects were complementary while different signs indicated duplicate epistasis (Kearsey and Pooni 1996). Gene action determined from the analysis of generation means are documented.

Days to flower: No scale was significant in Alisa Craig *AftAft*x Alisa Craig *hp-1 hp-1* and Alisa Craig *AftAft*x

BCT 115 *dg dg* and only additive components of genetic variation was significant. However, the simple additive / dominance model was inadequate to explain the gene action in Alisa Craig *Aft Aft*x Alisa Craig $og^c og^c$ as a whole because of the significance of C scales. In this cross, both additive and dominance components of genetic variation were significant, but dominance variance was more important for this character. Only, additive x additive epistatic interaction effects were significant for this character hence, type of non-allelic interaction could not be determined.

Fruits/plant: A simple additive / dominance model was inadequate to explain the gene effects for this character because of the significance of the scales in all the three crosses. In Alisa Craig *Aft Aft*x Alisa Craig $og^c og^c$only dominance component of genetic variation was significant while in Alisa Craig *AftAft*x BCT 115 *dg dg*, only additive component was significant and in the other two crosses, both additive and dominance components of genetic variation were significant. Most of theepistatic components were significant in all the three crossesand epistasis was 'Duplicate' in type in two crosses however, it could not be determined in one cross.

Fruit weight: In all the cross combinations, both additive and dominance components of genetic variation were significant. Most of the epistatic components were significant in all the three crosses and dominance x dominance interaction effect was larger than additive x additive effectin all the crosses. Type of epistasis for this character was 'Duplicate' in all the crosses.

Locule number per fruit: A simple additive/ dominance model was inadequate to explain the gene effects in two crosses while, it was adequate in Alisa Craig *Aft Aft*x

Table 1: Mean values for different characters in 6 generations of three crosses

Cross	Generation	Days to flower	Fruits/ plant	Fruit weight (g)	Locule / fruit	Pericarp thickness (mm)	Fruit yield/plant (kg)	TSS (°Brix)	Total sugar (%)
A C*Aft* x AC og^c	P_1	30.54 ±1.16	47.11±1.71	89.43±1.40	3.57±0.08	6.22±0.06	4.40±0.13	4.34±0.03	2.31±0.03
	P_2	33.89±0.47	75.60±1.10	53.85±1.54	2.06±0.10	5.35±0.03	3.63±0.11	5.03±0.07	2.96±0.07
	F_1	31.92±1.15	65.49±0.97	76.37±1.03	2.85±0.11	5.92±0.03	4.45±0.10	4.55±0.08	2.61±0.07
	F_2	28.71±1.05	70.58±1.34	71.74±2.09	2.84±0.05	5.51±0.03	4.97±0.16	4.82±0.12	2.73±0.14
	BC_1	29.82±0.63	81.17±3.03	81.39±1.52	3.24±0.16	5.98±0.12	4.85±0.26	4.52±0.06	2.49±0.08
	BC_2	33.61±1.11	85.29±1.23	49.57±2.52	2.46±0.04	5.59±0.05	3.95±0.26	4.86±0.05	2.99±0.14
A C*Aft* x AC *hp-1*	P_1	30.54 ±1.16	47.11±1.71	89.43±1.40	3.57±0.08	6.22±0.06	4.40±0.13	4.34±0.03	2.31±0.03
	P_2	33.75±0.85	77.96±0.86	43.59±0.74	2.27±0.05	4.61±0.03	3.27±0.06	4.94±0.07	2.64±0.07
	F_1	30.87±0.89	74.23±0.83	68.03±1.25	3.14±0.11	5.86±0.05	5.04±0.13	4.43±0.04	2.77±0.05
	F_2	32.07±0.92	80.83±1.06	71.83±1.41	3.05±0.09	5.72±0.06	4.79±0.12	4.47±0.05	2.97±0.23
	BC_1	28.95±1.15	73.91±0.73	61.89±0.78	3.42±0.07	5.87±0.08	4.52±0.07	4.32±0.08	3.38±0.16
	BC_2	33.68±1.14	87.81±1.62	38.97±2.08	2.32±0.03	5.14±0.06	2.89±0.18	4.41±0.07	2.82±0.14
A C*Aft* x BCT 115 *dg*	P_1	30.54 ±1.16	47.11±1.71	89.43±1.40	3.57±0.08	6.22±0.06	4.40±0.13	4.34±0.03	2.31±0.03
	P_2	30.86±0.42	37.76±1.24	104.19±1.17	3.72±0.05	6.77±0.04	4.01±0.07	4.68±0.07	2.68±0.05
	F_1	32.23±0.74	47.71±1.66	110.46±1.05	4.21±0.05	6.30±0.02	6.04±0.17	4.12±0.07	2.86±0.06
	F_2	27.99±1.39	59.76±1.91	100.16±0.85	4.17±0.12	5.74±0.04	5.81±0.19	4.14±0.07	2.89±0.13
	BC_1	32.29±0.97	65.30±0.82	97.83±1.02	3.65±0.09	5.72±0.08	5.57±0.15	3.84±0.08	2.76±0.09
	BC_2	26.13±0.82	44.22±0.87	76.27±0.77	3.47±0.07	6.82±0.08	5.18±0.32	3.86±0.11	2.52±0.12

	Generation	Reducing sugar (%)	Acidity (%)	Ascorbic acid (mg/100g)	Lycopene (mg/100g)	β carotene (mg/100g)	Anthocyanin (mg/100g)
A C*Aft* x AC og^c	P_1	1.54±0.04	0.51±0.03	23.62±1.18	4.08±0.10	0.52±0.04	14.67±0.47
	P_2	2.24±0.05	0.63±0.02	36.23±0.92	5.79±0.06	0.41±0.02	0.00
	F_1	2.11±0.07	0.61±0.01	28.96±0.87	3.97±0.09	0.54±0.02	11.87±0.19
	F_2	2.01±0.18	0.64±0.04	26.53±2.79	5.41±0.22	0.65±0.04	10.73±0.53
	BC_1	2.02±0.12	0.67±0.02	25.34±1.43	5.09±0.26	0.63±0.03	11.01±0.61
	BC_2	2.29±0.05	0.67±0.04	28.66±1.85	5.05±0.22	0.62±0.01	6.16±1.13
A C*Aft* x AC *hp-1*	P_1	1.54±0.04	0.51±0.03	23.62±1.18	4.08±0.10	0.52±0.04	14.67±0.47
	P_2	2.02±0.05	0.58±0.03	53.77±1.72	6.98±0.11	0.59±0.03	0.00
	F_1	1.75±0.07	0.61±0.02	39.63±1.15	4.04±0.04	0.62±0.02	13.07±0.43
	F_2	2.17±0.09	0.52±0.02	33.56±1.25	4.81±0.36	0.72±0.03	11.57±0.77
	BC_1	2.01±0.07	0.55±0.02	28.85±2.26	4.64±0.04	0.64±0.02	11.02±0.53
	BC_2	2.05±0.13	0.56±0.03	30.86±1.39	4.82±0.02	0.48±0.02	9.41±1.01
A C*Aft* x BCT 115 *dg*	P_1	1.54±0.04	0.51±0.03	23.62±1.18	4.08±0.10	0.52±0.04	14.67±0.47
	P_2	2.03±0.09	0.62±0.03	43.05±0.66	6.24±0.12	0.61±0.01	0.00
	F_1	2.21±0.05	0.68±0.01	29.47±1.04	4.67±0.07	0.57±0.02	12.68±0.62
	F_2	2.12±0.17	0.55±0.03	29.86±2.81	4.66±0.12	0.56±0.04	11.33±0.86
	BC_1	1.85±0.11	0.52±0.01	25.82±2.52	4.93±0.08	0.59±0.02	12.79±0.53
	BC_2	2.20±0.09	0.54±0.03	29.51±2.06	5.58±0.15	0.62±0.01	10.54±0.61

Alisa Craig $og^c og^c$. In two cross combinations, both additive and dominance component of genetic variation was significant; in one cross only dominance component was significant while in Alisa Craig *AftAft*x Alisa Craig *hp-1 hp-1*, only additive component was significant suggesting the importance of both additive and dominance component of variance in the inheritance of this character. All the epistatic components were significant in Alisa Craig *AftAft* x BCT 115 *dgdg,* however, in Alisa Craig *AftAft*x Alisa Craig *hp-1 hp-1*, only dominance x dominance epistatic component was significant. Type of epistasis was "Duplicate" in one cross but could not be determined in the other two crosses.

Pericarp thickness: The scales were significant in all the three crosses. In two crosses, only additive genetic variance was significant while in Alisa Craig *AftAft*x BCT 115 *dg dg*, both additive and dominance components of genetic variation were significant. Most of theepistatic components were significant in two crosses however in Alisa Craig *AftAft* x Alisa Craig $og^c og^c$, only additive x additive epistatic component was significant. Type of epistasis was "Duplicate" in two crosses, but it could not be determined in the other cross.

Fruit yield/ plant: The scales were significant in all the three crosses indicating presence of epistasis for the conditioning of this character. In two crosses, only additive genetic variance was significant while in Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1*, both additive and dominance components of genetic variation were significant, and all the epistatic components were significant in this cross while only additive x additive epistatic component was significant for the other two crosses. Type of epistasis was "Duplicate" in one cross but could not be determined in the other two crosses.

Total soluble solids content: The scales were significant in two crosses while, no scale was significant in Alisa Craig *Aft Aft*x Alisa Craig $og^c og^c$. In one cross combination, both additive and dominance component of genetic variation was significant; in one cross only

Table 2a: Scaling test and components of generation means for different characters

Cross	Model and effects	Days to flower	Fruits/plant	Fruit weight (g)	Locule / fruit	Pericarp thickness (mm)	Fruit yield/plant (Kg)	TSS (°Brix)
				Scaling test (Mather 1949; Hayman and Mather 1955)				
A C*Aft* x AC og^c	A	-2.86 ± 2.06	49.73 ± 6.38 **	-3.02 ± 3.51	0.072 ± 0.35	-0.16 ± 0.25	0.84 ± 0.55	0.15 ± 0.14
	B	1.42± 2.54	29.49 ± 2.87**	-31.08 ± 5.36**	0.013 ± 0.16	-0.07 ± 0.11	- 0.18 ± 0.55	0.17 ± 0.14
	C	-13.43± 4.94**	28.62 ± 6.06**	-9.05 ± 8.85	0.03 ± 0.32	-1.32 ± 0.15**	2.95 ± 0.68**	0.74 ± 0.52
	D	-5.99± 2.45*	-25.30 ± 4.24**	12.52 ± 5.11*	-0.03 ± 0.19	-0.54 ± 0.14**	1.14 ± 0.49*	0.21 ± 0.25
				Six parameter model (Jinks and Jones 1958; Mather and Jinks 1971)				
	m	28.71± 1.04**	70.58 ± 1.34**	71.74 ± 2.08**	2.83 ± 0.046**	5.51 ± 0.03**	4.97 ± 0.16**	4.79 ± 0.12**
	d	-3.81 ± 1.28**	-4.12 ± 3.27	31.81 ± 2.94**	0.78 ± 0.16**	0.39 ± 0.13**	0.89 ± 0.37*	- 0.34 ± 0.07**
	h	11.69 ± 5.08*	54.73 ± 8.59**	-20.32 ± 10.32*	0.97 ± 0.41*	0.12 ± 0.29	-0.18 ± 0.98	-0.53 ± 0.51
	i	11.99 ± 4.91*	50.59± 8.47**	-25.05 ± 10.22*	0.05 ± 0.38	1.08 ± 0.29**	-2.29 ± 0.98*	-0.42 ± 0.51
	j	-2.14± 1.42	10.12 ± 3.43**	14.03 ± 3.12**	0.03 ± 0.17	-0.04 ± 0.13	0.51 ± 0.38	-0.01 ± 0.08
	l	-10.54 ± 7.12	- 129.82 ± 14.43**	59.15 ± 14.73**	- 0.14 ± 0.74	-0.84 ± 0.55	1.63 ± 1.64	0.09 ± 0.59
	Non-allelic interaction	Could not be determined	Duplicate	Duplicate	Absence of non-allelic interaction	Could not be determined	Could not be determined	Absence of non-allelic interaction

Cross	Model and effects	Total sugar (%)	Reducing sugar (%)	Acidity (%)	Ascorbic acid (mg/100g)	Lycopene (mg/100g)	β carotene (mg/100g)	Anthocyanin (mg/100g)
				Scaling test (Mather 1949; Hayman and Mather 1955)				
A C*Aft* x AC og^c	A	0.06 ± 0.17	0.38 ± 0.25	0.22 ± 0.05**	-1.89 ± 3.21	2.12 ± 0.53**	0.20 ± 0.08**	-4.51 ± 1.33**
	B	0.42 ± 0.29	0.23 ± 0.12	0.11 ± 0.07	-7.88 ± 3.91*	0.34 ± 0.45	0.26 ± 0.03**	0.46 ± 2.27
	C	0.44 ± 0.57	0.06 ± 0.72	0.23 ± 0.16	-11.64 ± 11.41	3.83 ± 0.91**	0.60 ± 0.16**	4.39 ± 2.20*
	D	-0.02 ± 0.31	-0.27 ± 0.37	-0.05 ± 0.08	-0.93 ± 6.05	0.68 ± 0.55	0.07 ± 0.08	4.22 ± 1.67*
				Six parameter model (Jinks and Jones 1958; Mather and Jinks 1971)				
	m	2.73 ± 0.13**	2.01 ± 0.17**	0.64 ± 0.04**	26.53 ± 2.79**	5.41 ± 0.21**	0.65 ± 0.03**	10.70 ± 0.53**
	d	-0.51 ± 0.15**	-0.27 ± 0.12*	-0.002 ± 0.03	-3.31 ± 2.33	0.03 ± 0.34	0.29 ± 0.03**	4.84 ± 1.29**
	h	0.19 ± 0.64	0.76 ± 0.75	0.12 ± 0.17	12.16±0.89 **	-2.33 ± 0.11**	-0.06 ± 0.16	-3.91 ± 3.35
	i	0.05 ±0.63	0.54 ± 0.75	0.10 ± 0.17	1.86 ± 12.11	-1.37 ± 1.11	-0.13 ± 0.06*	-8.44 ± 3.34*
	J	-0.18 ± 0.16	0.07 ± 0.13	0.05 ± 0.04	2.99 ± 2.45	0.89 ± 0.34**	-0.03 ± 0.04	-2.48 ± 1.31
	l	0.53 ± 0.85	-01.15 ± 0.88	-0.44 ± 0.22*	7.91 ± 2.74*	-1.08 ± 1.63	- 0.32 ± 0.21	12.49 ± 5.61**
	Non-allelic interaction	Absence of non-allelic interaction	Absence of non-allelic interaction	Could not be determined	Could not be determined	Could not be determined	Could not be determined	Could not be determined

* and **= Significant at 5% and 1% level of significance respectively

dominance component was significant while in the other cross, only additive component was significant suggesting the importance of both additive and dominance component of variance in the inheritance of this character. Only additive x additive epistatic components were significant in one cross and both additive x additive and dominance x dominance epistatic components were significant in Alisa Craig *AftAft* x BCT 115 *dg dg* and epistasis was "Duplicate" in type.

Total sugar content: A simple additive / dominance model was inadequate to explain the gene effects in two crosses while, a simple additive / dominance model was adequate to explain the gene effects in Alisa Craig *Aft Aft* x Alisa Craig $og^c og^c$. In all the cross combinations, only additive component of variance was significant suggesting overwhelming importance of additive component of variance in the inheritance of this character. Only additive x dominance epistatic component was significant in two crosses, Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1* and Alisa Craig *AftAft*x BCT 115 *dg dg* and type of epistasis could not be determined for this character.

Reducing sugar content: A simple additive / dominance model was adequate to explain the gene effects in Alisa Craig *Aft Aft*x Alisa Craig $og^c og^c$ and Alisa Craig *AftAft* x BCT 115 *dg dg* while in the other cross, simple additive / dominance model was inadequate to explain the gene effects. In two cross combinations, only additive component of variance was significant while in the other, both additive and dominance component was significant suggesting overwhelming importance of additive component of variance in the inheritance of this character. Only dominance x dominance epistatic component was significant in Alisa Craig *AftAft*x Alisa Craig *hp-1 hp-1*suggesting comparatively less complex nature of inheritance for this character. Type of epistasis could not be determined for this character.

Tritrable acidity of fruit: In two cross, simple additive / dominance model was inadequate to explain the gene

Table 2b: Scaling test and components of generation means for different characters

Cross	Model and effects	Days to flower	Fruits/plant	Fruit weight (g)	Locule / fruit	Pericarp thickness (mm)	Fruit yield/plant (Kg)	TSS (ºBrix)
				Scaling test (Mather, 1949 and Hayman and Mather, 1955)				
A C*Aft* x AC *hp-1*	A	-3.51 ± 2.73	26.48 ± 2.39**	-33.66 ± 2.43**	0.08 ± 0.19	-0.34 ± 0.17*	-0.39 ± 0.23	-0.13 ± 0.17
	B	2.74 ± 2.59	23.42 ± 3.45**	-33.69 ± 4.41**	-0.76 ± 0.13**	-0.19 ± 0.13	-2.52 ± 0.38**	-0.55 ± 0.15**
	C	2.25 ± 4.33	49.79 ± 4.95**	18.23 ± 6.31*	0.05 ± 0.42	0.29 ± 0.26	1.42 ± 0.57*	-0.26 ± 0.23
	D	1.51 ± 2.45	-0.06 ± 2.77	42.79 ± 3.59**	0.36 ± 0.18	0.41 ± 0.15**	2.16 ± 0.31**	0.21 ± 0.14
				Six parameter model (Jinks and Jones, 1958; Mather and Jinks, 1971)				
	m	32.07 ± 0.92**	80.83 ± 1.06**	71.82 ± 1.39**	3.04 ± 0.08	5.71 ± 0.05**	4.79 ± 0.12**	4.47 ± 0.05**
	d	-4.73 ± 1.62**	-13.89 ± 1.77**	22.93 ± 2.22**	1.07 ± 0.07**	0.72 ± 0.09**	1.62 ± 0.19**	-0.09 ± 0.11
	h	-4.29 ± 5.03	11.81 ± 5.69*	-84.07 ± 7.28**	-0.51 ± 0.39	-0.38 ± 0.31	-3.13 ± 0.63**	-0.62 ± 0.29*
	i	-3.01 ± 4.90	0.12 ± 5.54	-85.59 ± 7.13**	-0.73 ± 0.37	-0.83 ± 0.31**	-4.33 ± 0.62**	-0.41 ± 0.29*
	j	-3.12 ± 1.77	1.53 ± 2.01	0.01 ± 2.36	0.43 ± 0.09	-0.07 ± 0.10	1.06 ± 0.20**	0.21 ± 0.11
	l	3.77 ± 7.81	-50.02 ± 8.66**	152.94 ± 10.91**	1.41 ± 0.32*	1.37 ± 0.47**	7.25 ± 0.95**	0.11 ± 0.48
	Non-allelic interaction	Absence of non-allelic interaction	Duplicate	Duplicate	Could not be determined	Duplicate	Duplicate	Could not be determined

Cross	Model and effects	Total sugar (%)	Reducing sugar (%)	Acidity (%)	Ascorbic acid (mg/100g)	Lycopene (mg/100g)	β carotene (mg/100g)	Anthocyanin (mg/100g)
				Scaling test (Mather 1949; Hayman and Mather, 1955)				
A C*Aft* x AC *hp-1*	A	1.68 ± 0.32**	0.72 ± 0.16**	-0.005 ± 0.05	-5.53 ± 4.81	1.16 ± 0.13**	0.12 ± 0.06*	-5.71 ± 1.23**
	B	0.23 ± 0.29	0.33 ± 0.28	-0.05 ± 0.07	-31.68 ± 3.64**	-1.37 ± 0.12**	-0.25 ± 0.05**	5.75 ± 2.05**
	C	1.37 ± 0.91	1.62 ± 0.38**	-0.18 ± 0.09*	-22.41 ± 5.89**	0.05 ± 1.46	0.45 ± 0.13**	5.47 ± 3.22
	D	-0.27 ± 0.50	0.28 ± 0.23	-0.06 ± 0.05	7.40 ± 3.65*	0.13 ± 0.73	0.29 ± 0.06**	2.71 ± 1.91
				Six parameter model (Jinks and Jones 1958; Mather and Jinks 1971)				
	m	2.96 ± 0.22**	2.17 ± 0.08**	0.52 ± 0.02**	33.55 ± 1.25**	4.80 ± 0.36**	0.71 ± 0.03**	11.57 ± 0.76**
	d	0.56 ± 0.21**	-0.04 ± 0.15	-0.007 ± 0.03	-2.00 ± 2.65	-0.18 ± 0.04**	0.15 ± 0.03**	1.60 ± 0.43**
	h	0.84 ± 1.01	-0.59 ± 0.17*	0.17 ± 0.11	-13.87 ± 6.46*	-1.75 ± 0.46 *	-0.51 ± 0.13**	0.31 ± 3.85
	i	0.55 ± 1.03	-0.56 ± 0.46	0.12 ± 0.06*	-14.80 ± 7.31*	-0.26 ± 1.46	-0.58 ± 0.13**	-5.42 ± 3.82
	j	0.72 ± 0.21**	0.19 ± 0.15	0.02 ± 0.04	13.07 ± 2.85**	1.27 ± 0.08**	0.19 ± 0.04**	-5.73 ± 1.16**
	l	-2.47 ± 1.25	-0.48 ± 0.12**	-0.06 ± 0.18	52.02 ± 12.15**	0.47 ± 1.48	0.70 ± 0.18**	5.37 ± 5.58
	Non-allelic interaction	Could not be determined	Could not be determined	Could not be determined	Duplicate	Could not be determined	Duplicate	Could not be determined

* and **= Significant at 5% and 1% level of significance respectively

effects however, no scale was significant in Alisa Craig *AftAft* x Alisa Craig *hp-1hp-1*. In all the cross combinations, neither additive nor dominance component of variance was significant indicating simple nature of inheritance. Only dominance x dominance epistatic component was significant in two cross and additive x additive component in one cross.

Ascorbic acid content: A simple additive / dominance model was inadequate to explain the gene effects because of the significance of scales in all the three crosses. In all the cross combinations, dominance components of genetic variation were significant. In all the crosses dominance x dominance interaction effect was significant and larger in magnitude than additive x additive effect. Most of the epistatic components were significant in Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1*and epistasis was 'Duplicate' in type in two crosses but could not be determined in the other cross.

Lycopene content: A simple additive / dominance model was inadequate to explain the gene effects because of the significance of scales in all the three crosses. In two cross combinations, both dominance and additive components of genetic variation were significant while in one cross, only dominance component was significant indicating importance of both additive and dominance gene action for this character. In two crosses, additive x dominance interaction effect was significant while, all the epistatic components were significant in Alisa Craig *AftAft* x BCT 115 *dg dg.* Type of epistasis was 'Duplicate' in the cross Alisa Craig *AftAft* x BCT 115 *dg dg* however, it could not be determined in three other crosses.

â carotene content: Simple additive / dominance model was inadequate to explain the gene actionin two crosses. However, it was adequate in Alisa Craig *AftAft*x Alisa Craig *dg dg*. In one cross combination, both dominance and additive components of genetic variation were significant while in one cross each only dominance and additive component was significant indicating importance of both additive and dominance gene action

Table 2c: Scaling test and components of generation means for different characters

Cross	Model and effects	Days to flower	Fruits/plant	Fruit weight (g)	Locule / fruit	Pericarp thickness (mm)	Fruit yield/plant (kg)	TSS (°Brix)
				Scaling test (Mather 1949; Hayman and Mather 1955)				
A C*Aft* x BCT 115 *dg*	A	1.80 ± 2.37	35.78 ± 2.89**	-4.28 ± 2.68	-0.47 ± 0.19*	-1.12 ± 0.16**	0.71 ± 0.36	-0.78 ± 0.18**
	B	-10.83 ± 1.84**	2.96 ± 2.70	-62.12 ± 2.20**	-0.95 ± 0.15**	0.56 ± 0.16**	0.31 ± 0.66	-1.09 ± 0.24**
	C	-13.90 ± 5.89*	58.75 ± 8.53**	-13.92 ± 4.39**	1.01 ± 0.48*	-2.62 ± 0.16**	2.75 ± 0.86**	-0.71 ± 0.33*
	D	-2.43 ± 3.06	10.00 ± 3.97*	26.24 ± 2.13**	1.22 ± 0.25**	-1.03 ± 0.13**	0.86 ± 0.52	0.57 ± 0.20**
				Six parameter model (Jinks and Jones 1958; Mather and Jinks 1971)				
	m	27.99 ± 1.39**	59.75 ± 1.89**	100.15 ± 0.85**	4.17 ± 0.11**	5.74 ± 0.03**	5.81 ± 0.19**	4.13 ± 0.07**
	d	6.15 ± 1.26**	21.08 ± 1.19**	21.53 ± 1.27**	0.17 ± 0.11	-1.12 ± 0.11**	0.39 ± 0.15*	-1.74 ± 0.13**
	h	6.39 ± 6.19	-14.72 ± 8.19	-38.83 ± 4.46**	-1.86 ± 0.51**	1.86 ± 0.27**	0.10 ± 1.06	-1.54 ± 0.41**
	i	4.86 ± 6.12	-19.99 ±7.95**	-52.48 ± 4.25**	-2.44 ± 0.51**	2.06 ± 0.27**	-1.73 ±0.55**	-1.15 ± 0.40**
	j	6.31 ± 1.41**	16.40 ± 1.59**	28.91 ± 1.56**	0.24 ± 0.11*	-0.84 ± 0.11**	0.20 ± 0.36	0.15 ±0.14
	l	4.15 ± 7.78	-18.75 ± 9.79*	118.89 ± 6.73**	3.87 ± 0.65**	-0.14 ± 0.48	0.71 ± 1.65	3.02 ± 0.65**
	Non-allelic interaction	Could not be determined	Could not be determined	Duplicate	Duplicate	Could not be determined	Could not be determined	Duplicate

Cross	Model and effects	Total sugar (%)	Reducing sugar (%)	Acidity (%)	Ascorbic acid (mg/100g)	Lycopene (mg/100g)	β carotene (mg/100g)	Anthocyanin (mg/100g)
				Scaling test (Mather 1949; Hayman and Mather 1955)				
A C*Aft* x BCT 115 *dg*	A	0.34 ± 0.18	-0.06 ± 0.23	-0.19 ± 0.04**	-1.45 ± 5.28	1.13 ± 0.20**	0.09 ± 0.06	-1.76 ± 1.32
	B	-0.52 ± 0.26*	0.16 ± 0.19	-0.21 ± 0.06**	-13.50 ± 4.29**	0.26 ± 0.33	0.02 ± 0.03	8.39 ± 1.36**
	C	0.88 ± 0.55	0.48 ± 0.71	-0.30 ± 0.12**	-6.15 ± 11.51	-1.01 ± 0.51*	-0.04 ± 0.16	5.26 ± 3.67
	D	0.53 ± 0.31	0.19 ± 0.37	0.05 ± 0.06	4.40 ± 6.49	-1.19 ± 0.29**	-0.08 ± 0.08	-0.68 ± 1.89
				Six parameter model (Jinks and Jones 1958; Mather and Jinks 1971)				
	m	2.89 ± 0.13**	2.11 ± 0.17**	0.54 ± 0.03**	29.86 ± 2.81**	4.66 ± 0.11**	0.55 ± 0.03**	11.32 ± 0.85**
	d	0.25 ± 0.05**	-0.35 ± 0.13**	-0.04 ± 0.03	-3.69 ± 1.25**	-0.64 ± 0.17**	0.01 ± 0.2	2.25 ± 0.81**
	h	-0.70 ± 0.62	4.50 ± 0.74	0.01 ± 0.12	-12.66 ± 3.04**	1.91 ± 0.58**	0.17 ± 0.06**	6.71 ± 2.84**
	i	-1.06 ± 0.61	-0.38 ± 0.74	-0.11 ± 0.12	-8.79 ± 12.98	2.39 ± 0.57**	0.16 ± 0.16	1.35 ± 3.78
	j	0.43 ± 0.15**	-0.11 ± 0.14	0.007 ± 0.03	6.02 ± 3.32	0.43 ± 0.18**	0.03 ± 0.03	-5.07 ± 0.84**
	l	1.24 ± 0.82	0.28 ± 0.90	0.52 ± 0.17**	23.75 ± 7.38**	-3.78 ± 0.86**	- 0.27 ± 0.18	-7.98 ± 3.90**
	Non-allelic interaction	Could not be determined	Absence of non-allelic interaction	Could not be determined	Duplicate	Duplicate	Absence of non-allelic interaction	Duplicate

* and **= Significant at 5% and 1% level of significance respectively

for this character. Only additive x additive epistatic component was significant in Alisa Craig *Aft Aft* x Alisa Craig *og^{c}og^c* while all the epistatic components were significant in the cross Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1*.Type of epistasis was 'Duplicate' in the cross Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1* however, it could not be determined in two other crosses.

Anthocyanin content: A simple additive / dominance model was inadequate to explain the gene effects because of the significance of scales in all the three crosses. In two cross combinations, only additive components of genetic variation were significant while in the other cross both additive and dominance component was significant indicating overwhelming importance of additive gene action for the control of this character. In Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1*, additive x dominance interaction effect was significant; in Alisa Craig *Aft Aft* x Alisa Craig *og^{c}og^c*,both additive x additive and additive x dominance epistatic components were significant and in Alisa Craig *AftAft* x BCT 115 *dg dg*additive x dominance and dominance x dominance epistatic components were significant suggesting differential manifestation of the *Aft* gene in combination of other genes. Type of epistasis was 'Duplicate' in the cross Alisa Craig *AftAft*x BCT 115 *dg dg* however, it could not be determined in three other crosses.

In most of the characters in three cross combinations, simple additive / dominance model was inadequate to explain the gene action because of the significance of A,B,C,D scales which indicated not only the involvement of epistasis in the control of the character but also complexity in nature of inheritance for the character concerned. 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 but non-fixable gene effects were predominant which has found ample support from number earlier reports of such studies (Rai et al. 2005; Garg et al. 2007; Mandal et al. 2009). It 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 and dominance x dominance 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 hinder the pace of progress through selection as recorder earlier (Dhankar et al. 2003; Dixit et al 2006; Dutta et al 2013). However, positive additive x additive type gene action and duplicate epistasis seen in some characters like, fruit weight in Alisa Craig *Aft Aft*x Alisa Craig *og^{c}og^c*, Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1* and Alisa Craig *AftAft* x BCT 115 *dg dg*; pericarp thickness, fruit yield, ascorbic acid and â carotene contents in Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1* and locules / fruit, TSS and lycopene contents in Alisa Craig *AftAft*x BCT 115 *dgdg* indicated the possibility of obtaining transgressive segregates in later generations which was also suggested earlier (Sharmila et al. 2007; Dutta et al. 2013). Additive x additive type non-allelic interaction was found significant but with negative sign for many important characters *viz*., fruits/ plant, fruit weight, fruit yield/ plant, locules/ fruit and TSS content in Alisa Craig *AftAft* x BCT 115 *dg dg* and fruit weight, fruit yield/ plant, pericarp thickness, TSS, â carotene and ascorbic acid contents in Alisa Craig *AftAft* x Alisa Craig *hp-1 hp-1* which indicated little scope of improvement through simple selection. The following breeding strategy is suggested with a view to the gene effects determined for different characters:

- 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.
- Development of hybrids for improved fruit yield and quality characters because non-fixable gene effects were predominant for most of the characters.

Acknowledgments

The study was supported financially by the Department of Science and Technology, Govt. of India.

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टमाटर की फसल में फल उपज तथा गुणवत्ता घटकों के निर्धारण हेतु जीन की प्रकृति विश्लेषण औसत मध्य तथा विविधता का अनुवांशिक समूहों (पी1, पी2, एफ1, एफ2, बीसी, बीसी2) में उत्परिवर्तित जीनो–एलिसा क्रैग, एएफटी एएफटी एक्स एलिसा क्रैग एचपी–1, एच पी–1, एलिसा क्रैग एएफटी एएफटी एक्स, एलिसा क्रैग ओजीसी, ओजीसी तथा एलिसा क्रैग एएफटी ए एफ टी एक्स बीसीटी–115 डीजीडीजी को समाहित कर संकरण संयोज्य तैयार किये गये। सभी 3 संकरण संयोज्यों में लगभग सभी गुणों के लिये सामान्य संयोज्य/ प्रभावी माडल जीन प्रक्रिया को स्पष्ट करने हेतु पर्याप्त है जिससे पता चलता है कि गुण विशेष के नियंत्रण में एपीस्टासिस की सहभागिता होती है। गुण, दोनों योज्य व अयोज्य जीनों के प्रभाव के नियंत्रण में होते हैं लेकिन अयोज्य जीन का प्रभाव मुख्य रूप से प्रबल होता है। प्रतिलिपि प्रकार का एसीस्टासिस लगभग सभी गुणों के लिये चयन प्रक्रिया में छिपे रहने की प्रवृत्ति रखता है। आगामी पीढ़ियों में चयन को रोक देना तथा संकरों का विकास करना सर्वोत्तम प्रजनन रणनीति होगी क्योंकि अयोज्य जीन का प्रभाव मुख्य रूप से प्रबल सभी गुणों के लिये होत है।

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