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GENE EFFECTS AND HERITABILITY FOR QUALITY TRAITS IN TOMATO (*Solanum lycopersicum* L.)

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ABSTRACT

The generation mean analysis in six populations, namely P1, P2, F1, F2, BC1 and BC2 revealed significant digenic interactions for all the characters in majority of the crosses studied. Character and cross combination revealed the adequacy of simple additive dominance model for titratable acidity (cross 5) indicating the absence of non-allelic interactions. Most of the crosses for all the quality traits showed low magnitude of dominance and environmental variances, revealing higher estimates of broad and narrow-sense heritabilities. Duplicate type of epistasis was observed in total soluble solids (cross 1,2,3,4), ascorbic acid (cross 1), titratable acidity (cross 1,2,3,4) and lycopene (cross 1,2,4) suggesting that the selection intensity should be mild in the earlier and intense in the later generations because it marks the progress through selection. These results indicated that for the improvement of tomato, additive variation is of great importance and makes it possible to successfully select better individuals in segregating populations, since the selective gains will depend only on gametic variation.

Keywords: Epistasis, Gene effects, Quality traits, tomato, yield.

Tomato is universally treated as 'Protective Food' since it is a rich of minerals, vitamins, antioxidants and organic acids (Kumar *et al*., 2013b). It is a good source of potassium, folate and vitamin E, soluble and insoluble dietary fibers. It has high levels of lycopene (71.6%) and ascorbic acid (12%) (Kaur and Kapoor, 2008). Among the most prominent phytochemicals in tomatoes are the carotenoids, of which lycopene is the most abundant in the ripened fruit, accounting for approximately 8090% of the total pigments (Hernandez *et al*., 2007, Helyes *et al*., 2009). Besides lycopene, tomatoes also contain -, -, -, -carotene, zeaxanthin and lutein and also neurosporene, phytoene, and phytofluene (Capanoglu *et al*., 2010; Ray *et al*., 2011).

In addition, tomatoes are an excellent source of potassium, pro-vitamin A and vitamin C (ascorbic acid), which are also antioxidants. Overall quality of tomato fruits is comprised of biochemical traits (total soluble solids and titratable acidity), which contribute to flavour, and appearance, which is defined by morphological features and colours. The nutrition importance of

the tomato indicates there is need to formulate breeding programme and to develop cultivar rich in lycopene, processing traits with high quality of fruit as well as yield (Kumar *et al.,* 2013a). These traits in part define quality and are important to consumers (Helyes *et al.,* 2008). The development of tomato varieties with improved quality traits, nutritive value and flavor is a major component of many tomato breeding programs (Rodriguez-Burruezo *et al.,* 2005).

The study was undertaken to estimate the main genetic effects including digenic non-allelic interactions controlling quality components in five tomato cross combinations.

Materials and Methods

Plant materials: Crosses *viz*., cross 1 (CO 3 x Floradade), cross 2 (Punjab Upma x Azad T5), cross 3 (Pant T3 x Azad T5), cross 4 (Kashi Amrit x Kashi Sharad), cross 5 (Pant T3 x Kashi Sharad) were made between six parents by manual emasculation and pollination. F_1 plants were selfed to obtain seed for the F_2 generation and backcrossed with their respective parents to generate BC_1 and BC_2 generations using a total of 20 pollinations per backcross. Thus, a total of six generations were obtained, corresponding to the two parents and the F_1, F_2, BC_1 and BC_2 generations.

Field trials: The six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) for each population were planted during the successive growing seasons of 2010-11, 2011-12 and 2012-13. In 2010-11 season, the crosses were made among the parents to produce F_1 hybrid seeds and designated as follows: In 2011/2012 season, F_1 plants were selfed to produce F_2 seeds and backcrossed to the parents to produce BC_1 and BC_2 seeds. The experiments were conducted at Vegetable Research Farm, Banaras Hindu University, Varanasi. This place is located in the middle Gangetic plain (latitude: $25^0$19'59" longitude: $83^0$00'00" EN elevation above sea level: 77 m) in the eastern part of the Uttar Pradesh. It is located in the Indo-Gangetic Plains of North India, a humid subtropical climate with large variations between summer and winter temperature. The average annual rainfall is 1,110 mm (44 Inch). Fog is common in the winters, while hot dry winds, blow in the summer. This location has alluvial soils of clay loam texture and pH of 7.6. Four populations were planted in a randomized block design with three replications at the spacing of 60 cm between rows and 45 cm between plants. All recommended cultural practices and plant protection measures were followed to raise a healthy crop.

Each replication had one row each of two parents (P_1, P_2) and F_1, two rows of each backcross (BC_1, BC_2) and four rows of F_2. Each row consisted of 15 plants. The number of plants evaluated varied depending on the treatment and was larger for the segregation generations such as the F_2 (with 60 plants per repetition) and the BC_1 and BC_2 (with 30 plants per repetition each) than for treatments with non-segregating generations such as the P_1 and P_2 parents and the F_1 generation.

Statistical analysis: The generation mean analysis of the six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) and scaling tests (Cavalli, 1952; Mather, 1949) were performed based on the assumption that populations have non-homogenous variances (Mather and Jinks, 1971). The three-parameter model of Jinks and Jones (1958) was used to test the adequacy of the additive-dominance model in the absence of non-allelic gene interaction. The six parameter model of Hayman (1958) was used to estimate various gene effects including the non-allelic interaction. Variance components (additive, dominance and environment) were estimated as described by Mather and Jinks (1971). Broad and narrow-sense heritability was estimated using method proposed by Warner (1952). The degree of dominance ratio was measured using [H/D] 1/2, where H is the dominance variance and D is additive variance.

Result and Discussion

The result of analysis of variance revealed significant differences among generations for all the characters investigated indicating the presence of genetic variability and possibility of selection for quality traits in tomato.

Gene action

Total Soluble Solids: The mean total soluble solids was higher in F_1 of crosses 1 and 5. Genic interactions for total soluble solids showed a positive and significant dominance gene effect in cross 2, 3 and while interaction was significantly negative in crosses 1, 4 and 5. On the other hand, additive × additive (i) gene effects were significant in 2, 3, 5 crosses. All crosses accept 5 showed the

duplicate type of epistasis, our study are in accordance to the results of Dhaliwal and Chahal (2005)

Ascorbic acid: However, the F_1 generations of cross 4 showed highest magnitudes of ascorbic acid. The 6-parameter model indicated the significance of additive gene effect (d) only for ascorbic acid content in cross 2,5. Additive × additive (i) gene effect in crosses 1 and 2, additive × dominance and dominance × dominance (l) gene effect in crosses 4 and 5 were found significant.

Titratable acidity: Cross 4 showed maximum titratable acidity, which is of immense importance in controlling the degree of browning of fruit pulp. In six-parameter model, significant positive dominance gene effect was observed in crosses 1, 2 and 3. Additive × additive (i) gene effect for cross 1, 2 and 3 additive × dominance (j) gene effect for all crosses except cross 1 and 2, dominance × dominance (l) gene effect for cross 4 were observed significant positively. Therefore model confirmed the duplicate epistasis in crosses 1, 2, 3, and 4. Gaikwad and Cheema (2009) and Garg, *et al*., (2008) revealed the predominant role of non-additive gene actions in controlling titratable acidity.

Lycopene content: Mean comparison (Table 1) among the six generations of cross 4 showed higher levels of lycopene content in fruit peel. The results obtained from three parameter model revealed that the additive gene effect (d) was significant for lycopene content in all crosses while dominance gene effect (h) was significant positively in crosses 2 and 3. The role of dominance gene action in lycopene content was also noticed by Roopa *et al*., (2001). Gaikwad and Cheema (2009) reported non-additive gene action for lycopene content. In contrast, **Somraj *et al.* (2017)** revealed both additive and dominance types of gene effects for anthocyanin content. In case of 6-parameter model, positive and significant dominance gene effect was observed in cross 1 for lycopene content. Positively significant additive × additive (i) was found significant only in crosses 1, 2 and 5.

Duplicate Epistasis

The signs of dominance (h) and dominance x dominance (l) gene effects were opposite in the case of TSS, ascorbic acid, Titratable acidity and lycopene (cross 1); TSS, Titratable acidity and lycopene (cross 2); TSS and Titratable acidity (cross 3); TSS, titratable acidity and lycopene (cross 4); suggesting duplicate type of interaction in these traits. This kind of epistasis generally hinders the improvement through selection and hence, a higher magnitude of dominance and (l) type of interaction effects would not be expected. Since none of signs of (h) were similar to the (l) type of epistasis, it was concluded that no complementary type of interaction was present in the genetic control of the studied traits (Table 2).

Positive or negative sign of additive x additive (i) interaction shows association and dispersion of alleles in parents, respectively. Therefore, negatively significant values of (aa) in this study showed alleles dispersion in parents for TSS (cross 1, 4), ascorbic acid (cross 4, 5) and lycopene (cross 2, 4, 5).

Variance components and heritability estimates

Variance component estimates are presented in Table 3 and varied considerably across crosses. Large variations were observed for both components with $^{\sigma 2}A$ and $^{\sigma 2}D$. The additive and dominance variance differed greatly from cross to cross. Conversely, the magnitude of dominant variance is less than the additive variance for all reviewed traits so breeding methods based on backcross/SSD/ pedigree selection should be used for the above traits. The results of the estimates for the variance model, broad and narrow sense heritability values and the degree of dominance ratio are presented in Table 3.

The average dominance ratio was more than unity for lycopene (cross 2, 3, 5), for total soluble solids (cross 1, 3) which showed the importance of

the dominance gene effects that is in agreement with high narrow sense heritability for these traits.

Heritability (degree of genetic determination) is an expression of the extent to which the genotype of an individual determines its phenotype. Heritability in broad-sense reflects all possible genetic contributions to a population's phenotypic variance, and it includes gene effects due to allelic variation (additive variance), dominance variation or which act epistatically (Rao *et al.* 2008, Dhaliwal and Chahal 2005). Narrow sense heritability is expression of the reliability with which phenotypic value guides to the breeding value. Moreover, it is the breeder's best estimate of breeding value as represents the portion of phenotypic variation due to additive effects. Narrow-sense heritability estimates are based on additive genetic variance (fixable component) and are better predictors of the effectiveness of selection in genetically heterogeneous population than broadsense heritability (Robinson *et al.,* 1949).

Considerable differences were observed between broadsense and narrow-sense heritabilities in all crosses. Broadsense heritabilities were relatively high for all traits. The all traits had moderate to low heritability estimates. The heritability estimates in broad sense were high for TSS as well as heritability estimates in narrow sense were moderate for TSS content by Shalaby (2013). The narrow sense heritability almost high then broad sense heritability because characters governed by additive genes and selection for improvement of such character would be rewarding.

Estimates of narrow sense heritability indicated that additive effects were primarily responsible for the genetic variation in these hybrids. In the improvement of self-pollinated plants such as tomato, additive variation is of great importance and makes it possible to successfully select better individuals in segregating populations, since the selective gains will depend only on gametic variation (Warner, 1952). For this reason, pedigree, backcross, single-seed descent methods are recommended for advancing the segregating populations (Bernado, 2003).

Table 1: comparison of means (±SE) for various characters in five crosses of tomato

Characters	Populations						
	P_1	P_2	F_1	F_2	B_1	B_2	CD (0.05)
Total soluble solids							
Cross 1	5.28±0.04	4.85±0.08	6.50±0.04	6.44±0.03	5.89±0.01	5.67±0.05	0.18
Cross 2	6.38±0.02	4.55±0.05	5.20±0.04	5.07±0.02	5.79±0.01	4.88±0.04	0.06
Cross 3	6.15±0.02	4.55±0.08	5.00±0.04	4.88±0.03	5.57±0.02	4.77±0.04	0.05
Cross 4	5.71±0.03	5.51±0.07	6.00±0.04	6.04±0.03	5.86±0.02	5.76±0.03	0.17
Cross 5	6.15±0.02	5.51±0.07	5.50±0.04	5.60±0.01	5.82±0.02	5.51±0.03	0.09
Ascorbic acid							
Cross 1	26.45±0.21	22.21±0.18	24.14±0.08	23.04±0.06	25.29±0.09	23.17±0.07	0.92
Cross 2	25.45±0.16	26.05±0.35	25.69±0.10	25.31±0.10	25.57±0.4	25.87±0.19	2.47
Cross 3	25.73±0.19	26.05±0.35	28.26±0.03	27.41±0.21	26.99±24	27.13±0.33	0.43
Cross 4	24.78±0.11	24.68±0.34	29.25±0.20	28.68±0.06	27.01±0.11	26.97±0.27	1.46
Cross 5	25.73±0.19	24.68±0.34	27.92±0.10	27.22±0.05	26.82±0.07	26.30±0.20	3.26
Titratable acidity							
Cross 1	0.58±0.00	0.51±0.00	0.41±0.00	0.39±0.00	0.49±0.00	0.46±0.00	0.001
Cross 2	0.61±0.00	0.58±0.01	0.52±0.01	0.50±0.00	0.56±0.00	0.55±0.00	0.001
Cross 3	0.61±0.00	0.58±0.00	0.59±0.00	0.57±0.00	0.60±0.00	0.59±0.00	0.000
Cross 4	0.56±0.01	0.58±0.01	0.64±0.01	0.63±0.00	0.59±0.00	0.61±0.00	0.031
Cross 5	0.61±0.00	0.58±0.01	0.58±0.01	0.57±0.00	0.60±0.01	0.59±0.01	0.000
Lycopene content							
Cross 1	5.48±0.04	5.52±0.03	3.08±0.07	3.17±0.03	4.28±0.05	3.80±0.05	0.03
Cross 2	5.67±0.03	5.34±0.11	6.60±0.04	6.55±0.04	6.13±0.02	5.97±0.05	0.38
Cross 3	6.60±0.05	4.52±0.03	5.84±0.04	5.71±0.03	6.22±0.05	5.17±0.02	0.08
Cross 4	5.39±0.04	5.56±0.13	7.51±0.05	7.40±0.04	6.45±0.02	6.54±0.07	0.33
Cross 5	5.84±0.10	5.84±0.11	6.76±0.12	6.61±0.09	6.30±0.02	6.05±0.11	0.73

Cross 1 (Co3 X Floradade), Cross 2 (Punjab Upma X Azad T5), Cross 3 (Pant T3 X Azad T5), Cross 4 (Kashi Amrit X Kashi Sharad), Cross 5 (Pant T 3 X Kashi Sharad)

Table 2 Estimates of gene effects (±SE of mean) for quality traits in five crosses using Mather and Jinks (1982) six-parameter model.

Characters	Gene effects							
	m	*d*	*h*	*i*	*j*	*l*	X^2	Epistasis
Total soluble solids								
Cross 1	4.67±0.03**	0.28±0.05**	-1.21±0.18**	-2.65±0.17*	-	2.65±0.17*	2.58	D
Cross 2	5.07±0.03**	0.92±0.45**	0.81±0.15**	1.07±0.14**	0.00±0.06	-1.09±0.24**	2.87	D
Cross 3	4.88±0.03**	0.80±0.05**	0.82±0.17**	1.17±0.16**	-	-1.18±0.26**	1.60	D
Cross 4	6.05±3.39**	0.10±0.04*	-0.55±0.19**	-0.93±0.18**	-	0.91±0.27**	3.04	D
Cross 5	5.61±0.02**	0.32±0.05**	-0.08±0.12**	0.25±0.12*	0.00±0.06	-0.25±0.22	7.21*	No epistasis
Ascorbic acid								
Cross 1	23.05±0.07**	2.12±0.12**	4.56±0.39**	4.75±0.30**	-0.003±0.19	-4.75±0.37**	0.00	D
Cross 2	25.31±0.10**	-0.29±0.20	1.58±0.38*	1.64±0.57**	0.003±0.28	-1.65±1.01	0.00	No epistasis
Cross 3	27.41±0.21**	-0.16±0.42	1.13±1.24	-1.36±1.19	-	1.37±2.00	3.02	No epistasis
Cross 4	28.68±0.06**	0.04±0.30	-2.25±0.71	-6.77±0.65**	0.002±0.35	6.77±0.65**	0.08	No epistasis
Cross 5	27.22±0.05**	0.52±0.22*	0.09±0.53	-2.62±0.48**	-0.002±0.29	2.62±1.00**	0.00	No epistasis
Titratable acidity								
Cross 1	0.40±0.01**	0.04±0.01**	0.19±0.01**	0.33±0.02**	0.002±0.00**	-0.32±0.02**	0.15	D
Cross 2	0.50±0.01**	0.01±0.00**	0.14±0.01**	0.22±0.01**	0.002±0.01**	-0.22±0.02**	0.20	D
Cross 3	0.58±0.01**	0.01±0.01**	0.12±0.02*	0.12±0.02**	-0.002±0.01	-0.12±0.03**	0.08	D
Cross 4	0.63±0.01**	-0.02±0.01**	-0.05±0.01**	-0.11±0.01	-0.01±0.01	0.12±0.23**	0.19	D
Cross 5	0.58±0.001**	0.01±0.01	0.07±0.05	0.08±0.04	-0.002±0.02	-0.09±0.07	7.68*	No epistasis
Lycopene								
Cross 1	3.18±0.03**	0.48±0.08**	1.55±0.22**	3.47±0.20**	0.00±0.08**	-3.47±0.38**	3.00	D
Cross 2	6.56±0.04**	0.17±0.06	-0.92±0.22**	-2.01±0.21**	-0.002±0.09**	2.02±0.34**	0.00	D
Cross 3	5.71±0.03**	1.04±0.05*	0.22±0.16	-0.06±0.16	0.01±0.06	0.07±0.26	0.19	No epistasis
Cross 4	7.41±0.04**	-0.09±0.07	-1.60±0.24**	-3.64±0.22**	-0.01±0.10	3.63±0.39**	3.02	D
Cross 5	6.61±0.10**	0.25±0.12*	-0.58±0.49	-1.75±0.47**	0.002±0.15	1.74±0.69*	0.00	No epistasis

Cross 1 (Co3 X Floradade), Cross 2 (Punjab Upma X Azad T5), Cross 3 (Pant T3 X Azad T5), Cross 4 (Kashi Amrit X Kashi Sharad), Cross 5 (Pant T3 X Kashi Sharad)

Table 3 different components of genetics variance, degree of dominance and heritability estimates of various traits studied in five cross

Character	Additive variance (D)	Dominance Variance (H)	Environmental Variance (E)	Degree of Dominance($\sqrt{H}/\sqrt{D}$)	Heritability Broad sense (h^2b)	Heritability Narrow sense (h^2n)
Total soluble solids						
Cross I	0.00	1.36	0.11	45.31	-4.36	0.77
Cross II	0.99	-0.25	0.05	-0.50	-2.03	0.23
Cross III	0.85	-0.37	0.05	-0.66	0.17	0.68
Cross IV	0.07	0.38	0.09	2.39	0.03	1.31
Cross V	0.35	-0.33	0.08	-0.98	-5.06	-2.78
Ascorbic acid						
Cross I	1.99	0.24	0.87	0.34	-1.71	0.24
Cross II	-0.07	0.13	1.68	-1.36	-116	0.03
Cross III	-0.20	2.45	2.61	-3.51	0.07	0.07
Cross IV	-1.03	4.49	1.73	-2.09	-5.38	-8.51
Cross V	-0.04	2.17	1.65	-7.22	-6.79	-6.38
Titratable acidity						
Cross I	0.03	-0.13	0.01	-2.04	0.36	1.72
Cross II	0.00	-0.08	0.01	-5.48	-0.25	1.57
Cross III	0.01	0.00	0.01	-0.62	-0.06	0.45
Cross IV	-0.03	0.06	0.01	-1.29	-6.99	-3.08
Cross V	0.02	-0.02	0.03	-1.17	-0.13	-0.35
Lycopene						
Cross I	0.46	-2.53	0.09	-2.35	-1.09	-1.67
Cross II	0.01	1.00	0.17	10.29	-0.41	0.83
Cross III	1.05	0.28	0.06	0.52	-0.12	0.47
Cross IV	-0.48	1.77	0.24	-1.93	-0.95	0.38
Cross V	0.19	1.20	0.39	2.51	0.30	1.23

Cross 1 (Co3 X Floradade), Cross 2 (Punjab Upma X Azad T5), Cross 3 (Pant T3 X Azad T5), Cross 4 (Kashi Amrit X Kashi Sharad), Cross 5 (Pant T3 X Kashi Sharad)

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