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ARTICLE

Genetics of qualitative and quantitative Traits in crosses involving cherry and purple tomato genotypes

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Abstract: *To exploit the genetic potential of cherry tomato, it is crucial to comprehend the inheritance pattern of qualitative and quantitative traits. Six genetic populations created from four crosses between pairs of cherry tomato and purple-fruited tomato genotypes were used to study the genetics of fruit colour and the nature of gene action for quantitative traits in cherry tomatoes. The study indicated purple fruit colour was dominant over red and yellow fruit colour in cherry tomatoes and was conditioned by mongenic dominant gene. Quantitative trait inheritance was governed by non-additive gene action and duplicate epistasis. It is advised to use the modified bulk selection strategy, in which selection is conducted only when homozygosity has been attained for the majority of the heterozygous loci. However, the ideal method for developing cherry tomato hybrids with purple-coloured fruit is to involve at least one purple-fruited parent in the cross.*

Keywords: *Cherry tomato, fruit colour, gene action, inheritance pattern, quantitative traits*

INTRODUCTION

Cherry tomatoes [*Solanum lycopersicum* var. *cerasiforme* (Dunnal) A. Grey] are actually a hybrid between wild currant-type tomatoes and domesticated garden tomatoes, not "ancestral" to cultivated tomatoes (Nesbitt and Tanksley 2002). Recently, cherry tomatoes are becoming popular in Brazil and other parts of the world, in a protected environment, due to their high concentration of phytochemicals and antioxidants, such as lycopene, β-carotene, flavonoids, vitamin C, and many other vital nutrients, as well as their delicious flavour and ability to set fruit even at high temperatures (Rosales et al. 2011; Fernandes et al. 2022). Field-produced cherry tomatoes have a higher flavour rating than those produced under greenhouse conditions (Singh et al. 2021).

There has been an increasing demand for anthocyanin-rich foods. This demand is related to research on the effect of anthocyanin in reducing the risk of chronic diseases in humans (Hassan and Abdel Aziz 2010). Purple-tomato breeding has become one of recent efforts for anthocyanin-rich food production, given the higher level of consumption of tomato compared to other anthocyanin-rich fruits,

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such as berries (Hazra et al. 2018). The presence of anthocyanin in cultivated tomato is a result of anthocyanin-coding genes, *Aft* (anthocyanin fruit), *Abg* (aubergine), and *atv* (atroviolaceum). A cross with *Solanum chilense* introduced the dominant gene *Aft* into domesticated tomato plants (Jones et al. 2003), an interspecific cross with *Solanum cheesmanii* yielded the *atv* gene, and a cross with *Solanum lycopersicoides* produced the *Abg* gene (Mes et al. 2008). Petunidin, followed by malvidin and delphinidinin, has been discovered by Jones et al. (2003) as the main anthocyanidin in *Aft*. This investigation of the genetic potential for raising the amounts of this significant class of phytonutrients in cherry tomato fruit was motivated by interest in the health advantages and antioxidant capability of anthocyanins. Utilising this gene in the current cherry tomato germplasm is possible due to simple inheritance of *Aft*.

Cherry tomatoes offer great potential in tomato breeding programs because of their valuable characteristics of genetic diversity for selection of parental material and their broad geographic range (Medina and Lobo 2001). Intense expression of anthocyanin is needed for strong antioxidant activity, and the introduction of the anthocyanin fruit trait into carotenoid-rich cherry tomatoes provides the opportunity to develop new cultivars rich in water- and lipid-soluble antioxidants. Jones et al. (2003) found that purple fruit colour is controlled by a single dominant gene, based on crossing purple tomato (LA1996) and red tomato (UC82B). Li et al. (2018) found a 1:3 (green: purple) distribution ratio with a major + polygene gene model interaction possibility using the results of crosses between purple tomato (Zi Ying) and green tomato (Lv Ying).

It is therefore necessary to develop purple cherry hybrid/line bred varieties with high yield and nutritional qualities, and better consumer acceptance. The present investigation was carried out to study the inheritance pattern of fruit colour in cherry tomato and to determine the gene action of different quantitative traits in crosses involving cherry and purple tomato genotypes.

MATERIAL AND METHODS

Plant materials

Based on fruit quality and other economically important traits, selection was initially made of two contrasting breeding lines of cherry tomato (18/ToCVAR-2, red-fruited, and BCCT-5, yellow-fruited) as testers, and two purple-fruited tomato genotypes (Bidhan Purple and Alisa Craig^{Aft}) as lines for development of hybrids.

Seeds from four contrasting crosses – Alisa Craig^{Aft} × 18/ToCVAR-2, Alisa Craig^{Aft} × BCCT-5, Bidhan Purple × 18/ToCVAR-2 and Bidhan Purple × BCCT-5 – in the F_1 generation were selfed during the year 2020-21 (December-January) to obtain F_2 progenies, as well as backcrossed with their respective parents to obtain the backcross progenies BC_1P_1 and BC_2P_2.

Field trials

Thirty-day-old, healthy seedlings of 6 generations (P_1, P_2, F_1, F_2, BC_1P_1, and BC_2P_2), raised in plastic protrays, were transplanted in the main field following a compact family block design with 3 replications in the 1st week of November 2021 within the research field of the All India Co-ordinated Research Project on Vegetable Crops, Bidhan Chandra Krishi Viswavidyalaya, West Bengal, India, situated at 23º N latitude and 89º E longitude at a alt of 9.75 m asl. The number of plants per replication was 25 each for the P_1, P_2, F_1, BC_1, and BC_2 generations, and 100 each for the F_2 generations. The plant spacing adopted was 60 cm (row to row) × 60 cm (plant to plant) in each plot. A fertilizer dose of 120 kg N, 60 kg P_2O_5, and 60 kg K_2O ha^{-1} was applied in split doses during the entire cropping season (Chattopadhyay et al. 2007). Bamboo sticks and jute rope were used to stake vines in order to maintain their indeterminate growth pattern. To guarantee a robust plant architecture, two primary branches were kept right below the first blossom (Mukherjee et al. 2019). All crop practices scheduled for growing cherry tomato were followed on time, according to Malik et al. (2017).

Observations recorded

The total number of plants with purple or non-purple tomato fruit colours was counted in each population after the fruit attained physiological maturity. Fifteen (15) plants in P_1, P_2, F_1, F_2, BC_1P_1, and BC_2P_2 and 50 plants in F_2 were randomly selected from each plot and replication to record number of days to 50% flowering, plant height (cm), number of flower clusters per plant, number of tomatoes per flower cluster, number of tomatoes per plant, tomato fruit weight (g), polar

diameter (mm), equatorial diameter (mm), pericarp thickness (mm), number of locules per tomato, and tomato yield per plant (kg). Samples of 30 randomly selected ripe tomatoes from each replication were used to determine tomato fruit firmness (kg cm^{-2}) with a penetrometer. Total soluble solids (TSS) as °Brix was estimated with an ERMA hand refractometer (Tokyo, Japan); and titratable acidity, lycopene, and the β-carotene content of tomato fruit were analysed as per Ranganna (1979). Ascorbic acid content of tomato fruit was estimated according to the method suggested by Sadasivam and Manickam (1996). Retinol activity equivalent (RAE) of tomato fruit was estimated with standard formulae. Total anthocyanin content of tomato fruit was estimated according to Ranganna (1979). Radical scavenging activity of tomato fruit was estimated according to the method of Marinova and Batchvarov (2011).

The severity of tomato leaf curl virus (ToLCV) disease was noted for all plants of each genotype in each plot at 15-day intervals starting from 30 days after transplanting (DAP) and continuing until 120 DAP. The disease rating scale (0-4) of Banerjee and Kalloo (1987) was followed. The percent disease index (PDI) was computed using numerical ratings as per McKinney and Davis (1925).

Statistical analysis

Chi-square (χ2) was used in quantitative analysis to separate the genotypes for the tomato fruit colour of cherry tomatoes in F_2 and backcross generations based on goodness of fit. Generation mean analysis was used to determine the genetic effects in the quantitative analysis. The scaling test (Mather 1949) and joint scaling test (Mather and Jinks 1982) were used to estimate the gene effects. The t test was used to assess the scales' significance as well as gene effects (Singh and Chaudhary 1985). The t test was used to test the relevant standard errors, which were computed by calculating the square root of the corresponding scaling test. INDOSTAT (ver. 8.1, Indostat services, Ameerpet, Hyderabad, India) was used to compute all analyses.

RESULTS AND DISCUSSION

Inheritance pattern of fruit colour in cherry tomato

The segregation pattern of purple and non-purple-coloured tomato fruit in the F_2 and backcross generations varied (Table 1). In the cross 'Alisa $Craig^{Aft}$ × 18/ToCVAR-2', all F_1 plants showed purple-coloured tomato fruit, indicating genetic dominance over non-purple tomato fruit colour. In the F_2 generation, 78 plants had purple-coloured tomato fruit and 22 plants had non-purple tomato fruit. These F_2 frequencies were found with goodness of fit ($\chi^2 = 0.48$, $p = 0.488$) for the expected 3:1 ratio, while BC_1 and BC_2 gave goodness of fit ($\chi^2 = \alpha$ and 0.04) for the expected ratios of 1:0 and 1:1, respectively, which suggested monogenic inheritance of the trait.

The second cross was 'Alisa $Craig^{Aft}$ × BCCT-5', where in $F_{2,}$ 79 plants had purple- coloured tomato fruit and 21 had non-purple-coloured tomato fruit. These F_2 frequencies gave goodness of fit ($\chi^2 = 0.85$, $p = 0.355$) for the expected 3:1 ratio, while BC_1 and BC_2 gave goodness of fit ($\chi^2 = \alpha$, $p = \alpha$ and $\chi^2 = 0.04$, $p = 0.481$) for the expected ratios of 1:0 and 1:1, respectively.

In the third cross, 'Bidhan Purple × 18/ToCVAR-2', all F_1 plants expressed purple-coloured tomato fruit, which was inherited from the Bidhan Purple line. Out of 100 F_2 plants, 80 plants had purple-coloured tomato fruit and 20 plants had non-purple-coloured tomato fruit. These F_2 frequencies gave goodness of fit χ^2 (1, 100) = 1.33, p = 0.248, and the expected 3:1 ratio, indicating the involvement of a single dominant gene for purple-coloured tomato fruit. That was further supported by the expected segregation pattern in the BC_1 ($\chi^2 = \alpha$, $p = \alpha$) and BC_2 ($\chi^2 = 0.36$, p= 0.548) generations, with the expected ratios of 1:0 and 1:1, respectively.

The fourth cross, 'Bidhan Purple × BCCT-5', also expressed F_2 segregation, with the ratio 3:1, involving 76 plants with purple-coloured tomato fruit and 24 plants with non-purple tomatoes. These F_2 frequencies recorded goodness of fit ($\chi^2 = 0.053$, p = 0.817) with the expected ratio of 3:1. This was supported by the segregation pattern of BC_1 ($\chi^2 = \alpha$, p = α) and BC_2 ($\chi^2 = 0.36$, p= 0.548), with the expected ratios of 1:0 and 1:1, respectively.

Gene action for quantitative traits

The significance of the scaling tests indicated the presence of additive × additive (i), additive × dominance (j), and

Table 1. Chi-square test for different genetic ratios in crosses involving purple and non-purple fruit of cherry tomato and purple tomato hybrids

Cross combination	Generation	Number of purple-fruited plants	Number of non-purple-fruited plants	Total plant population	Genetic ratio	χ^2	Probability
Alisa Craig^{Aft} × 18/ ToCVAR-2	P_1	25	0	25	-	-	-
	P_2	0	25	25	-	-	-
	F_1	25	0	25	-	-	-
	F_2	78	22	100	3:1	0.48	0.488
	BC_1	25	0	25	1:0	∞	∞
	BC_2	13	12	25	1:1	0.04	0.481
Alisa Craig^{Aft} × BCCT-5	P_1	25	0	25	-	-	-
	P_2	0	25	25	-	-	-
	F_1	25	0	25	-	-	-
	F_2	79	21	100	3:1	0.85	0.355
	BC_1	25	0	25	1:0	∞	∞
	BC_2	13	12	25	1:1	0.04	0.481
Bidhan Purple × 18/ ToCVAR-2	P_1	25	0	25	-	-	-
	P_2	0	25	25	-	-	-
	F_1	25	0	25	-	-	-
	F_2	80	20	100	3:1	1.33	0.248
	BC_1	23	2	25	1:0	∞	∞
	BC_2	14	11	25	1:1	0.36	0.548
Bidhan Purple × BCCT-5	P_1	25	0	25	-	-	-
	P_2	0	25	25	-	-	-
	F_1	25	0	25	-	-	-
	F2	76	24	100	3:1	0.053	0.817
	BC_1	22	3	25	1:0	∞	∞
	BC_2	14	11	25	1:1	0.36	0.548

P_1 = Parent 1, P_2 = Parent 2, F_1 = first filial generation, F_2 = second filial generation, BC_1 = Back cross with P_1 (Female), BC_2 = Back cross with P_2 (Male).

dominance × dominance (l) effects for all the traits studied (Tables 2 and 3). The significance of the A, B, C, and D scales for all four crosses exhibited a simple additive/ dominance model, which was not sufficient to explain the gene effects of 21 traits. Dominance (h) and dominance × dominance (l) effects were only important when determining the type of epistasis; different signs suggested duplicate epistasis, while the same sign indicated complimentary effects (Kearsey and Pooni 1996).

The gene action derived from the four cross combinations under six genetic populations generally agreed that additive–dominance–epistasis interaction of polygenes dominated the inheritance of these features. For most traits under investigation in four cross combinations, all epistatic components were significant, indicating a highly complex inheritance pattern for these traits. The significance of the "d," "h," "i," "j," and "l" forms of gene interaction was revealed, and it seemed that both fixable and non-fixable gene effects controlled tomato fruit yield, yield components, and quality attributes. It also suggested that utilising both additive and non-additive gene effects present in these traits would be crucial for achieving a favourable change in the expression of the phenotypic mean.

We observed positive additive × additive (i) type gene action, duplicate epistasis for days to 50% flowering, tomato fruit weight, polar diameter, equatorial diameter, pericarp thickness, lycopene content, anthocyanin content, β-carotene content, retinol activity equivalent, radical scavenging activity, the PDI of leaf curl virus, and tomato fruit yield per plant in the 'Alisa Craig^{Aft} × 18/ToCVAR-2' cross (Table 4); days to 50% flowering, number of flower clusters per plant, tomato fruit weight, polar diameter, number of tomatoes per plant, pericarp thickness, tomato fruit firmness, total soluble solids content, ascorbic acid content, titratable acidity content, anthocyanin content of tomato fruit, the PDI of leaf curl virus, and tomato fruit yield per plant in the 'Alisa Craig^{Aft} × BCCT-5' cross (Table 4); plant height, number of flower clusters per plant, tomato fruit weight, polar diameter, equatorial diameter, pericarp thickness, tomato fruit firmness,

Table 2. Scaling test for different quantitative traits of two crosses: 'Alisa Craig^{Aft} × 18/ToCVAR-2' and 'Alisa Craig^{Aft} × BCCT-5'

	Scale							
	Alisa Craig^{Aft} × 18/ToCVAR-2				Alisa Craig^{Aft} × BCCT-5			
Trait	**A**	**B**	**C**	**D**	**A**	**B**	**C**	**D**
D50F	6.00**±1.41	9.00**±1.384	13.00**±2.693	-1.00**±1.41	7.00**±3.240	9.00**±2.756	8.00**±2.412	-4.00**±2.062
PH	-2.970**±2.01	-33.45**±1.98	-7.02**±3.590	14.7**±1.03	-44.7**±3.11	-7.510**±2.19	-1.88**±6.524	25.170**±3.278
NFCPP	0.375**±7.99	-6.92**±3.710	-5.831**±6.372	0.357**±4.31	12.477**±7.78	116.99**±121.7	-3.89**±7.596	-66.683**±60.98
NTFC	4.00**±2.44	-3.00**±1.414	1.00**±2.708	-	1.00**±1.414	-3.00**±1.414	8.00**±2.708	5.00**±1.414
TFW	-82.20**±0.14	0.80**±0.178	-89.86**±0.297	-4.23**±0.10	-77.25**±0.13	-7.67**±19.78	-101.34**±0.26	-8.210**±9.891
PD	-15.83**±0.55	1.06**±0.272	-45.67**±0.585	-15.45**±0.17	-12.88**±1.01	-4.930**±0.221	-40.21**±0.27	-11.2**±0.505
ED	-29.19**±0.37	-13.72**±0.29	-48.97**±0.598	-3.03**±0.07	-11.80**±0.16	-6.040**±0.103	-12.48**±1.31	2.68**±0.659
NTPP	64.673**±5.12	-89.14**±3.11	22.166**±11.04	23.31**±5.97	77.158**±2.20	787.148**±866.8	134.25**±5.80	-365.02**±433.4
NLPT	-1.00**±0.00	-	-1.00**±0.00	-	-1.00**±0.00	-	-1.00**±0.00	-
PT	-3.290**±0.23	-0.38**±0.232	-4.17**±0.506	-0.25**±0.11	-1.100**±0.14	1.870**±0.589	-10.67**±0.11	-5.72**±0.306
TFF	-1.170**±0.10	0.15**±0.089	-1.0**±0.184	0.01**±0.04	0.250**±0.08	0.600**±0.048	-1.79**±0.15	-1.32**±0.080
TSS	1.910**±0.07	-1.47**±0.085	4.02**±0.129	1.790**±0.06	3.110**±0.05	2.700**±0.046	2.75**±0.15	-1.53**±0.077
AAC	26.660**±0.94	-12.95**±0.38	23.01**±0.570	4.65**±0.46	20.75**±0.28	12.240**±0.49	-0.01**±1.36	-16.5*±0.666
TA	-0.210**±0.04	0.010**±0.035	-0.100**±0.069	0.05**±0.04	-0.12**±0.03	0.010**±0.025	-0.29**±0.03	-0.090**±0.022
LC	0.150**±0.26	-0.86**±0.242	-5.070**±0.446	-2.18**±0.24	-3.600**±0.08	0.270**±0.238	-1.37**±0.13	0.980**±0.126
AC	-3.420**±0.54	4.34**±0.194	-0.896**±1.060	-0.908**±0.6	-2.370**±1.17	1.770**±1.695	-3.72**±1.05	-1.56**±1.107
BCC	0.091**±0.009	0.14**±0.013	-0.649**±0.025	-0.44**±0.01	-0.194**±0.01	0.140**±0.014	0.046**±0.04	0.050**±0.022
RAE	45.50**±4.51	70.0**±6.403	-324.5**±12.40	-220**±5.67	-97.00**±7.75	70.00**±7.240	23.00**±21.55	25.00**±10.844
RSA	-52.94**±2.48	-21.22**±2.25	-97.38**±3.211	-11.61**±1.83	-63.923**±2.7	3.066**±0.996	-54.41**±3.38	3.223**±0.0867
PDI ToLCV	2.080**±0.18	-15.3**±0.329	-21.77**±0.701	-4.25**±0.33	-3.830**±0.25	4.680**±0.185	-2.494**±0.28	-1.672**±0.201
TFYPP	-3.177**±0.10	-1.68**±0.049	-4.912**±0.169	-0.03**±0.09	-2.207**±0.07	-1.050**±0.06	-4.097**±0.11	-0.420**±0.043

** Significant at $P \leq 0.01$ level of probability; D50F = days to 50% flowering; PH = plant height (cm); NFCPP = number of flower clusters per plant; NTFC = number of tomatoes per flower cluster; TFW = tomato fruit weight (g); PD = polar diameter (mm); ED = equatorial diameter (mm); NTPP = number of tomatoes per plant; NLPT = number of locules per tomato; PT = pericarp thickness (mm); TFF = tomato fruit firmness (kg cm^{-2}); TSS = total soluble solids (°Brix); AAC = ascorbic acid content (mg 100 g^{-1}); TA = titratable acidity content (%); LC = lycopene content (mg 100 g^{-1}); AC = anthocyanin content (mg 100 g^{-1}); BCC = β-carotene content (mg 100 g^{-1}); RAE = retinol activity equivalent; RSA = radical scavenging activity (%); PDI ToLCV = percent disease index of tomato leaf curl virus (%); TFYPP = tomato fruit yield per plant (kg).

ascorbic acid content, titratable acidity content, anthocyanin content of tomato fruit, and the PDI of leaf curl virus in the 'Bidhan Purple × 18/ToCVAR-2' cross (Table 5); and days to 50% flowering, number of flower clusters per plant, tomato fruit weight, polar diameter, equatorial diameter, pericarp thickness, tomato fruit firmness, total soluble solids content, ascorbic acid content, lycopene content, β-carotene content, retinol activity equivalent, radical scavenging activity of tomato fruit, and the PDI of leaf curl virus in the 'Bidhan Purple × BCCT-5' cross (Table 5). The additive × additive type non-allelic interaction was significant and negative for the rest of the traits.

Tomatoes with a purple-coloured fruit are produced when the dominant allele of one gene expresses itself only when recessive homozygous alleles of the other gene are present. Based on crossing the purple tomato (LA1996) and red tomato (UC82B), Jones et al. (2003) discovered that a single dominant gene controls the purple-coloured tomato fruit. Li et al. (2018) used the result of a cross between purple tomato (Zi Ying) and green tomato (Lv Ying) and reported a 1:3 (green:purple) distribution ratio with a possibility of major + polygene gene model interaction. Consistent with the current findings, Hazra et al. (2018) discovered a segregation pattern of a 3:1 ratio for the single dominant *Aft* gene and a 1:3 ratio for the single recessive *dg* gene.

Gene action revealed that different crosses and traits had different types and magnitude of gene effects governing the inheritance of quantitative attributes in cherry tomatoes. Duplicate epistasis for most traits and positive additive × additive type gene effect suggested the potential for transgressive segregates in subsequent generations. Negatively correlated significant values of epistatic components suggested little room for improvement with simple selection. Better genetic combinations would arise via biparental hybridization between recombinants in early segregating generations, enabling the accumulation of favourable genes for enhanced physicochemical properties in individual lines.

Table 3. Scaling test for different quantitative characters of two crosses: 'Bidhan Purple × 18/ToCVAR-2' and 'Bidhan Purple × BCCT-5'

	Scale							
	Bidhan Purple × 18/ToCVAR-2				Bidhan Purple × BCCT-5			
Trait	A	B	C	D	A	B	C	D
D50F	6.00**±2.50	11.00±2.14	21.00**±6.28	2.00**±3.41	6.00**±1.41	7.00**±1.41	7.00**±2.70	-3.00**±1.41
PH	2.800**±1.34	-52.460±2.75	-74.860**±2.5	-12.60**±1.48	-12.24**±1.82	-4.530**±1.90	-8.770**±3.98	4.00**±1.00
NFCPP	16.126**±5.41	-4.535±5.03	-1.924**±6.51	-6.757**±4.24	6.748**±5.92	-3.847**±4.39	-3.293**±6.63	-3.097**±4.08
NTFC	-	-	6.00**±2.708	3.00**±1.63	-2.00**±1.41	-5.00**±1.63	3.00**±2.82	5.00**±1.41
TFW	-85.26**±0.17	0.070**±0.14	-91.190**±0.32	-3.00**±0.12	-80.21**±0.35	-4.810**±0.18	-87.580**±0.64	-1.280**±0.28
PD	1.00**±0.91	-5.760**±0.4	-40.620**±0.83	-17.93**±0.41	-4.09**±2.87	-3.360**±0.45	-21.730**±0.71	-7.140**±1.43
ED	4.530**±0.53	-5.060**±0.36	-17.770**±0.71	-8.620**±0.19	-0.52**±0.49	2.760**±0.18	-33.920**±0.37	-18.080**±0.23
NTPP	72.452**±2.71	-32.06**±2.44	69.429**±3.38	14.519**±1.90	-14.87**±2.77	-93.08**±3.94	23.228**±7.15	65.590**±2.40
NLPT	-1.00**±0.00	-	-1.00**±0.00	-	-1.00**±0.00	-	-1.00**±0.00	-
PT	-0.910**±0.45	4.080**±0.17	-3.710**±0.20	-3.44**±0.24	-0.870**±0.56	0.470**±0.32	-10.560**±0.27	-5.080**±0.31
TFF	-1.320**±0.05	1.110**±0.03	-2.070**±0.04	-0.93**±0.03	-1.32**±0.06	1.310**±0.07	-1.750**±0.08	-0.870**±0.05
TSS	-3.970**±0.04	-0.840**±0.09	-3.430**±0.13	0.690**±0.07	-0.86**±0.03	-0.450**±0.12	-5.790**±0.06	-2.240**±0.06
AAC	10.820**±0.94	0.240**±0.51	-40.00**±0.51	-25.53**±0.49	8.38**±0.49	15.710**±1.16	-23.350**±1.20	-23.720**±0.02
TA	-0.206**±0.02	0.11**±0.027	-0.180**±0.05	-0.010**±0.02	-0.350**±0.02	0.00**±0.02	-0.130**±0.11	0.110**±0.05
LC	-1.180**±0.10	0.810**±0.27	0.930**±0.33	0.650**±0.17	0.61**±0.20	0.050**±0.30	-0.220**±0.26	-0.40**±0.22
AC	1.744**±1.97	4.114**±0.98	-7.614**±1.22	-6.736**±1.26	-1.067**±2.94	5.963**±1.35	5.336**±4.17	0.220**±2.63
BCC	-0.660**±0.03	-0.290**±0.04	-0.790**±0.06	0.080**±0.02	-0.730**±0.12	-0.030**±0.05	-.0.780**±0.14	-0.010**±0.08
RAE	-330.00**±19.14	-145**±21.01	-395.0**±33.04	40.00**±183.3	-365.0**±64.03	-15.00**±29.44	-390**±72.68	-5.00**±43.20
RSA	-70.364**±1.91	7.452**±3.21	-60.90**±7.76	1.006**±3.73	-55.453**±2.8	0.011**±3.59	-89.402**±3.15	-16.980**±2.72
PDI ToLCV	-1.730**±0.23	-13.88**±0.25	-17.150**±0.12	-0.770**±0.17	9.140**±0.06	15.240**±0.31	4.240**±0.12	-10.070**±0.15
TFYPP	-1.705**±0.08	-0.505**±0.05	-2.210**±0.09	0.00**±0.05	-3.465**±0.07	-2.670**±0.08	-3.175**±0.20	1.480**±0.076

**Significant at $P \leq 0.01$ level of probability; D50F = days to 50% flowering; PH = plant height (cm); NFCPP = number of flower clusters per plant; NTFC = number of tomatoes per flower cluster; TFW = tomato fruit weight (g); PD = polar diameter (mm); ED = equatorial diameter (mm); NTPP = number of tomatoes per plant; NLPT = number of locules per tomato; PT = pericarp thickness (mm); TFF = tomato fruit firmness (kg cm^{-2}); TSS = total soluble solids (°Brix); AAC = ascorbic acid content (mg 100 g^{-1}); TA = titratable acidity content (%); LC = lycopene content (mg 100 g^{-1}); AC = anthocyanin content (mg 100 g^{-1}); BCC = β-carotene content (mg 100 g^{-1}); RAE = retinol activity equivalent; RSA = radical scavenging activity (%); PDI ToLCV = percent disease index of tomato leaf curl virus (%); TFYPP = tomato fruit yield per plant (kg).

If selection is postponed until a later generation, when the dominance effect will have diminished, traits with a higher degree of dominance than additive can be improved through a conventional breeding approach, such as the pedigree or bulk or single seed descent method (Khattak et al. 2004, Punia et al. 2011). In contrast, the significant but negative values of h, i, j, and l for traits exhibited negative alleles that were also dispersed in the parents involved in the cross. When a cross for any trait has a negative sign for "h," it means that the parents with the alleles that cause the characteristics' low values contributed to the dominating effects. Therefore, when desirable segregants become available, selection for these features should likewise be postponed until a later generation (Latha et al. 2018).

The gene action types of dominance (h) and dominance × dominance (l) were found to have significant values with opposite signs. This suggests that there is a duplicate kind of epistasis, or gene effect, for all the attributes studied in four crosses. Because of the cancellation of the dominance and epistatic effects, the duplicate type of epistasis will decrease the net gain from heterozygosity (Dhall and Hundal 2006). Hasanuzzaman and Golam (2011) claim that heterosis is inhibited by duplicate gene action. It was also proposed that duplicate epistasis might lead to reduced variance in the F_2 and following generations, slowing down the rate of advancement through a traditional selection process. Duplicate epistasis, considerably larger dominance (h) gene effects, and comparatively small dominance × dominance (l) interactions were observed for most traits. Due to large additive × additive (i) gene effects and duplicate type epistasis, selection must be postponed until advanced generations in order to take advantage of the reduction in non-fixable genetic variation and to utilise transgressive segregants.

It is advised to delay tomato yield selection until selfing reduces dominance and epistatic components due to the presence of the dominance gene effect and additive × additive components. The primary gene effects governing tomato yield and quality traits were non-additive gene action and duplicate epistasis. Selecting in later segregating generations (F_4 or F_5) and allowing intermating among the selected segregates, followed by one or two generations of selfing, is

Table 4. Gene effects for different traits of two crosses: 'Alisa Craig^{Aft} × 18/ToCVAR-2' and 'Alisa Craig^{Aft} × BCCT-5'

Trait	'Alisa Craig^{Aft} × 18/ToCVAR-2'							'Alisa Craig^{Aft} × BCCT-5'						
	m	d	h	i	j	l	Epistasis	m	d	h	i	j	l	Epistasis
D50F	+**	-**	+**	+**	-**	-**	Duplicate	+**	-**	+**	+**	-**	-**	Duplicate
PH	+**	-**	-**	-**	+**	+**	Duplicate	+**	+**	-**	-**	-**	+**	Duplicate
NFCPP	+**	+**	-**	-**	+**	+**	Duplicate	-**	+**	+**	+**	-**	-**	Duplicate
NTFC	+**	-**	+**	-	+**	-**	Duplicate	+**	-**	-**	-**	+**	+**	Duplicate
TFW	+**	+**	-**	+**	-**	+**	Duplicate	+**	+**	-**	+**	-**	+**	Duplicate
PD	+**	+**	+**	+**	-**	-**	Duplicate	+**	+**	+**	+**	-**	-**	Duplicate
ED	+**	+**	-**	+**	-**	+**	Duplicate	+**	+**	-**	-**	-**	+**	Duplicate
NTPP	+**	-**	-**	-**	+**	+**	Duplicate	-**	-**	+**	+**	-**	-**	Duplicate
NLPT	+**	+**	-**	-	-**	+**	Duplicate	+**	+**	-**	-	-**	+**	Duplicate
PT	+**	+**	-**	+**	-**	+**	Duplicate	-**	+**	+**	+**	-**	-**	Duplicate
TFF	+**	+*	-**	-**	-**	+**	Duplicate	-**	+**	+**	+**	-**	-**	Duplicate
TSS	+**	-**	-**	-**	+**	+**	Duplicate	+**	-**	+**	+**	+**	-**	Duplicate
AAC	+**	-**	+**	-**	+**	-**	Duplicate	-**	+**	+**	+**	+**	-**	Duplicate
TA	+**	+**	-**	-**	-**	+**	Duplicate	+**	+**	+**	+**	-**	-**	Duplicate
LC	+**	-**	+**	+**	+**	-**	Duplicate	+**	+**	-**	-**	-**	+**	Duplicate
AC	+**	+**	+**	+**	-**	-**	Duplicate	+**	+**	+**	+**	-**	-**	Duplicate
BCC	-**	-**	+**	+**	-**	-**	Duplicate	+**	-**	-**	-**	-**	+**	Duplicate
RAE	-**	-**	+**	+**	-**	-**	Duplicate	+**	-**	-**	-**	-**	+**	Duplicate
RSA	+**	+**	-**	+**	-**	+**	Duplicate	+**	+**	-**	-**	-**	+**	Duplicate
PDI ToLCV	+**	-**	-**	+**	+**	+**	Duplicate	+**	+**	+**	+**	-**	-**	Duplicate
TFYPP	+**	+**	-**	+**	-**	+**	Duplicate	+**	+**	-**	+**	-**	+**	Duplicate

** Significant at $P \leq 0.01$ level of probability; D50F = days to 50% flowering; PH = plant height (cm); NFCPP = number of flower clusters per plant; NTFC = number of tomatoes per flower cluster; TFW = tomato fruit weight (g); PD = polar diameter (mm); ED = equatorial diameter (mm); NTPP = number of tomatoes per plant; NLPT = number of locules per tomato; PT = pericarp thickness (mm); TFF = tomato fruit firmness (kg cm^{-2}); TSS = total soluble solids (°Brix); AAC = ascorbic acid content (mg 100 g^{-1}); TA = titratable acidity content (%); LC = lycopene content (mg 100 g^{-1}); AC = anthocyanin content (mg 100 g^{-1}); BCC = β-carotene content (mg 100 g^{-1}); RAE = retinol activity equivalent; RSA = radical scavenging activity (%); PDI ToLCV = percent disease index of tomato leaf curl virus (%); TFYPP = tomato fruit yield per plant (kg).

Table 5. Gene effects for different traits of two crosses: 'Bidhan Purple × 18/ToCVAR-2' and 'Bidhan Purple × BCCT-5'

Trait	'Bidhan Purple × 18/ToCVAR-2'							'Bidhan Purple × BCCT-5'						
	m	d	h	i	j	l	Epistasis	m	d	h	i	j	l	Epistasis
D50F	+**	+**	+**	-**	-**	-**	Duplicate	+**	-**	+**	+**	-**	-**	Duplicate
PH	+**	-**	-**	+**	+**	+**	Duplicate	+**	-**	-**	-**	-**	+**	Duplicate
NFCPP	+**	-**	+**	+**	+**	-**	Duplicate	+**	-**	+**	+**	+**	-**	Duplicate
NTFC	+**	-**	-**	-**	-	+**	Duplicate	+**	-**	-**	-**	+**	+**	Duplicate
TFW	+**	+**	-**	+**	-**	+**	Duplicate	+**	+**	-**	+**	-**	+**	Duplicate
PD	+**	+**	+**	+**	+**	-**	Duplicate	+**	+**	+**	+**	-**	-*	Duplicate
ED	+**	+**	+**	+**	+**	-**	Duplicate	+**	+**	+**	+**	-**	-**	Duplicate
NTPP	+**	-**	+**	-**	+**	-**	Duplicate	+**	-**	-**	-**	+**	+**	Duplicate
NLPT	+**	+**	-**	-	-**	+**	Duplicate	+**	+**	-**	-	-**	+**	Duplicate
PT	-**	+**	+**	+**	-**	-**	Duplicate	-**	+**	+**	+**	-**	-**	Duplicate
TFF	-**	+**	+**	+**	-**	-**	Duplicate	-**	+**	+**	+**	-**	-**	Duplicate
TSS	+**	-**	-**	-**	-**	+**	Duplicate	+**	+**	+**	+**	-**	-**	Duplicate
AAC	-**	-**	+**	+**	+**	-**	Duplicate	-**	+**	+**	+**	-**	-**	Duplicate
TA	+**	+**	-**	**	-**	+**	Duplicate	+**	+**	-**	-**	-**	+**	Duplicate
LC	+**	+**	-**	-**	-**	+**	Duplicate	+**	+**	+**	+**	+**	-**	Duplicate
AC	-**	+**	+**	+**	-**	-**	Duplicate	+**	+**	+**	-**	-**	-**	Duplicate
BCC	+**	+**	-**	-**	-**	+**	Duplicate	+**	+**	-**	+**	-**	+**	Duplicate
RAE	+**	+**	-**	-**	-**	+**	Duplicate	+**	+**	-**	+**	-**	+**	Duplicate
RSA	+**	+**	-**	-**	-**	+**	Duplicate	+**	+**	-**	+**	-**	+**	Duplicate
PDI ToLCV	+**	-**	-**	+**	+**	+**	Duplicate	-**	+**	+**	+**	-**	-**	Duplicate
TFYPP	+**	+**	-**	-	-**	+**	Duplicate	+**	+**	-**	-**	-**	+**	Duplicate

*, ** Significant at $P \leq 0.05$ and $P \leq 0.05$ level of probability, respectively; m = mean, d = additive effect, h = dominance effect, i = additive × additive type gene interaction, j = additive × dominance type gene interaction and l = dominance × dominance type gene interaction; D50F = days to 50% flowering; PH = plant height (cm); NFCPP = number of flower clusters per plant; NTFC = number of tomatoes per flower cluster; TFW = tomato fruit weight (g); PD = polar diameter (mm); ED = equatorial diameter (mm); NTPP = number of tomatoes per plant; NLPT = number of locules per tomato; PT = pericarp thickness (mm); TFF = tomato fruit firmness (kg cm^{-2}); TSS = total soluble solids (°Brix); AAC = ascorbic acid content (mg 100 g^{-1}); TA = titratable acidity content (%); LC = lycopene content (mg 100 g^{-1}); AC = anthocyanin content (mg 100 g^{-1}); BCC = β-carotene content (mg 100 g^{-1}); RAE = retinol activity equivalent; RSA = radical scavenging activity (%); PDI ToLCV = percent disease index of tomato leaf curl virus (%); TFYPP = tomato fruit yield per plant (kg).

advised in order to break the undesirable linkage and allow the accumulation of beneficial alleles for improving these traits of cherry tomatoes.

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