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Heterosis, Residual Heterosis and Inbreeding Depression Study in Tomato [*Solanum lycopersicum* (L.)]

Hiteksha I. Damor[1*], Kalyanrao Patil[2], Sushmita Pusarla[3], Shiwani[4] and Priyanka Pandya[4]
[1]Ph.D. Scholar, Department of Genetics and Plant Breeding,
Anand Agricultural University, Anand, (Gujarat), India.
[2]Assistant Professor, Department of Seed Science and Technology,
Anand Agricultural University, Anand, (Gujarat), India.
[3]Assistant Professor, Department of Seed Science and Technology,
MSSSOA, Centurian University, (Odisha) India,
[4]Ph.D. Scholar, Department of Plant Molecular Biology & Biotechnology,
Anand Agricultural University, Anand, (Gujarat), India.

(Corresponding author: Hiteksha I. Damor)*
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ABSTRACT: Tomato is a 'protective food' since it is rich in minerals, vitamins, antioxidants and organic acids, along with many nutraceutical benefits. It is well known for its nutraceutical and chemical content which strengthens immune systems and protect against certain diseases. For this reason, there has been recent emphasis on breeding cultivars with nutraceutical value combined with yield parameters. Although, tomato breeding programs are focused mainly on improving fruit yield as well as processing quality traits. One of the most important ways to improve yield and quality traits is heterosis, which is hybrid vigor that results in an improvement in fruit yield with early development and superior quality. Heterosis is a natural phenomenon whereby hybrid offspring of genetically diverse individuals exhibit improved physical and functional characteristics relative to their parents. The purpose of the present study is to obtain genetic information about the extent of hybrid vigour and inbreeding depression as well as residual heterosis in the five crosses of tomato. A population of five crosses was assessed with six-parameter test of generation mean analysis. The significant and positive heterosis (heterobeltiosis and standard heterosis) was depicted for days to first flowering in family II, III, and family IV with negative inbreeding depression, which indicates desirable earliness found in those families. The heterosis, as well as inbreeding depression (in negative direction) was observed in the desired direction in family IV for fruit yield per plant, for quality and biochemical traits *viz.*, pericarp thickness (family I and V) and lycopene content (family III and family V), indicating possibilities to get the desired segregants in a further breeding program.

Keywords: Generation mean analysis, Hybrid vigor, Heterobeltiosis, Residual heterosis, Inbreeding depression.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most important solanaceous vegetable crops all over the world. It was introduced in India by English traders of East India company in 1822 (Kalloo, 1988). The tomato originated in a wild form in Ecuador, Peru, and Bolivia of South America (also known as the center of diversity of wild tomato).

The total area of the world under tomato cultivation is 4.78 m ha, production of 177.04 MT with the productivity of 37.01 MT per ha. (FAOSTAT, 2018). India ranks second in the area (0.814 m ha) and production (19.197 MT) with a productivity of 24.93 MT per ha in the world (Anon., 2020). In Gujarat, tomato is grown in 0.047 m ha with an annual production of 1.38 MT and productivity of 29 MT per ha, respectively (Anon., 2020). The important tomato growing districts of Gujarat state are Anand, Kheda, Gandhinagar, Dang, Dahod, Narmada, Panchmahal, Banaskantha, Vadodara, Valsad, Sabarkantha, and Bhavnagar (Anon., 2018).

Tomato is consumed year-round and its importance is mainly derived in two forms: used as a fresh vegetable as well as an important source for the processing industry. At present time, superior quality and adequate quantity of vegetables for commercial agro-processing are not being grown sufficiently. Cultivation of tomatoes began to decline during the last few years, which requires conventional and scientific efforts to increase the production per unit area to compensate for the shortfall in the cultivated area. Many local farmers grow average yielding varieties, which are characteristically low yielding and of poor quality for the traits such as high-water content, poor color, and low Brix content against the increasing demand at the local and international levels for superior quality. To overcome these problems, the development of high-yielding and superior quality varieties of tomato is imperative in the cultivation to meet the total market demand.

Since the 1980s, the emphasis of new cultivar development has been focused on the production of F_1 hybrids (Grandillo *et al.,* 1999). Generally, hybrids are preferred over pure line varieties in tomatoes due to their superiority in terms of yield as well as the quality of fruit. Hybrid breeding technology is greatly applied in cross-pollinated crops and is limited in autogamous crops due to the strict genetic makeup of the plant and floral biology. Commercial exploitation of heterosis in self-pollinated crops has been limited owing to technical difficulties involved in hybrid seed production. Tomato is a self-pollinated crop with hermaphrodite flower and can be easily emasculated for crossing technique, therefore it has a suitable mechanism to produce hybrid seed at a commercial scale. However, it adds a higher labor cost to the total production cost. Heterosis increases yield and quality in many crops and vegetables, and it has been intensively used in plant breeding. The identification of superior parental combinations that provide high heterosis for yield and quality is the most important factor in hybrid development. Heterobeltiosis is useful in the identification of promising cross combinations for the improvement of the crop through conventional breeding strategies. It may lead to an increase in yield, reproductive ability, adaptability to general vigour, different biotic and abiotic stresses, and also improve fruit quality.

Contrarily, inbreeding depression leads to decreased fitness and vigour due to the expression of lethal and sublethal alleles which are generally masked under heterozygosity. It leads to increased homozygosity and fixation of undesirable recessive genes in F_2 and successive generations, while in the case of heterosis, favorable dominant genes of one parent are masking the effect of harmful recessive genes of another parent. Molecular, genetic, and physiological mechanisms underlying this phenomenon are not well understood yet (Birchler *et al.,* 2010). Positive heterosis was observed for the traits *viz.,* plant height, number of branches per plant, early yield, total yield with positive inbreeding depression for elite tomato cultivars *viz.,* UC 97-3, Castle king, VFNT, and Early Stone (Nosser, 2012). Among eight parental lines of diverse origin of tomato, the most promising cross, Pant T-3 × H-24 showed highly significant positive heterosis over better parent for yield per plant along with considerable inbreeding depression (Kumar and Singh, 2016). The most desirable cross combination, KS-227 × Roma among 45 F_1 hybrid and its parents for fruit yield per plant and fruit size exhibited desirable better parent heterosis with minimal inbreeding depression (Amin *et al.,* 2017). However, diallel analysis of elite tomato lines along with its hybrids gave information about the TY-2 gene in the parental lines alone produced three useful hybrids expressing 19 to 28 % heterosis over top parent for total yield (Dhaliwal *et al.,* 2019).

The demand for tomatoes is increasing day by day but their production and quality is affected by many diseases, stresses, and many other factors. A considerable amount of important work has already been done in this crop, but a great amount of information is still needed for the understanding of the genetics of fruit yield, yield attributing traits, and quality parameters of this crop growing in the middle Gujarat agro-climatic condition. The purpose of this study was to estimate the heterosis of yield-related traits as well as inbreeding depression and residual heterosis in the F_2 generation. The experimental material is constructed in such a way that the estimation of the heterosis, inbreeding depression, and residual heterosis effect in a respective generation is possible.

MATERIALS AND METHODS

The experimental material comprises of five families, each representing six generations (P_1, P_2, F_1, F_2, B_1, and B_2) were raised in a compact family block design in field trials. Five families were derived from nine parents *viz.,* GAT-4, AVTOV 1002, ATL-11-05, GT-2, AVTOV 1008, AVTOV 1007, AVTOV 1005/2, IIHR-329, and IIHR-335 with hand emasculation and pollination.

Observations for the different traits under study were recorded on randomly selected and tagged plants from each experimental unit and each replication *i.e.,* five plants from each P_1, P_2, and F_1 and twenty plants from each F_2 generation.

The mean of F_1 hybrids and F_2 generation over replication were utilized for the estimation of heterosis, inbreeding depression, and residual heterosis.

1. Estimation of Heterosis. Heterosis expressed as a percent increase or decrease of F_1 hybrid over its better parent value (BP) and standard heterosis (SH) was computed using the following formulae.

Heterosis over better parent (Heterobeltosis) HB (%). The heterosis over better parent was calculated as per the Fonseca and Patterson, (1968).

$$\text{HB (\%)} = \frac{\overline{F_1} - \overline{BP}}{\overline{BP}} \times 100$$

Where, $\overline{F_1}$ = Mean value of F_1 hybrid *i.e* F_1

$\overline{BP}$ = Mean performance of better parent.

Standard heterosis SH (%). The heterosis over standard check was calculated as per the Meredith and Bridge, (1972).

$$\text{SH (\%)} = \frac{\overline{F_1} - \overline{SC}}{\overline{SC}} \times 100$$

Where, $\overline{SC}$ = Mean performance of standard check

2. Estimation of inbreeding depression (ID %). Inbreeding depression was computed by using the following formula,

$$\text{Inbreeding depression (\%)} = \frac{\overline{F_1} - \overline{F_2}}{\overline{F_1}} \times 100$$

3. Estimation of Residual Heterosis (%). The residual heterosis from F_2 generation was worked out as per the formula given below:

$$\text{Residual heterosis} = \frac{\overline{F_2} - \overline{HB}}{\overline{HB}} \times 100$$

RESULTS AND DISCUSSION

(i) Morphological field parameters. The magnitude of heterotic effect, *i.e.*, Heterobeltiosis (HB) and standard heterosis (SH), residual heterosis as well as inbreeding depression (ID) were estimated for all the traits under study which are presented in Table 1 and discussed within the following paragraphs.

The negative and significant estimates of heterosis (HB and SH) were found for days to first flowering in the family I, II, III, and in family IV with the nonsignificant impact of inbreeding depression, which is desirable for earliness. Significant residual heterosis was observed in the family I. Patel *et al.,* (2010); Singh *et al.,* (2012) obtained heterosis over superior parents in a negative direction for days to flowering. While, Kumar and Singh (2016), Amin *et al.,* (2017), Thainukul *et al.,* (2017); Dhaliwal *et al*. (2019) also reported negative heterobeltiosis for days to flowering in the tomato population. The estimates of better parent and standard heterosis were found in significant estimates with a higher amount in family III, followed by II, IV, and family I, respectively for plant height. There was a negative and non-significant estimate for inbreeding depression found for all five families. For primary branches per plant, significant estimates of heterobeltiosis and standard heterosis were exhibited by family I, III, and family IV; however, a significant effect of inbreeding depression was observed in the family I. Significant residual heterosis found in family II and V.

For the number of fruits, positive and significant estimates of heterobeltiosis were reported in family I. For standard heterosis, family I, II, III, IV, and family V depicted positive and significant estimates. The non-significant values of inbreeding depression in all the families indicated a presence of hybrid vigour (favorable gene combinations) in the F_2 generation. In addition to this, family V exhibited positive and significant estimates of residual heterosis. The magnitude of heterosis and inbreeding depression was following the findings of Kumar and Singh (2016), Kumar *et al.,* (2017); Amin *et al.,* (2017); Dhaliwal *et al*., (2019).

The estimate of heterosis for average fruit weight reported ranged from 27.38 (family IV) to 227.81 % (family II); -32.25 (family IV) to 35.67 % (family II) for better parent and standard check, respectively. All the families expressed non-significant values of inbreeding depression ranging from 6.09 % (family IV) to 62.25 % (family I), indicating improvement in average fruit weight in F_2 generation compared to F_1 generation may be due to the presence of a lower magnitude of unfavorable allelic combinations in this families. Similar findings were registered by Pandey *et al.,* (2006), Shalaby (2013); Dagade *et al.,* (2015); Amin *et al.,* (2017) for the fruit weight of tomato. Maximum inbreeding depression recorded in F_2 than F_3 generations. However, highest and significant heterosis observed in desirable direction for plant height with negligible residual heterosis in rice (Chavan *et al*., 2018).

(ii) Fruit Morphological traits. Significant and higher estimates for heterosis (heterobeltiosis and standard heterosis) were observed with significant inbreeding depression in the family I, II, III, and family IV for fruit length; however, family II, III, and family V indicated significant values for residual heterosis and heterobeltiosis. For fruit girth, family II reported a higher magnitude for heterobeltiosis and standard heterosis. Family I and V indicated significant residual heterosis. However, a significant value of inbreeding depression was observed in family III with significant estimates of standard heterosis; this is in close agreement with findings of Patel *et al.,* (2010) and Singh *et al*. (2017).

Family III (20.38 %), family V (42.81 %), family II (46.11 %), and family I (50.15 %) reported significant and higher estimates of heterobeltiosis for locules per fruit. Positive estimates for residual heterosis were exhibited by family I and V. Besides this, all five families exhibit significant estimates for standard heterosis. A positive and significant estimate of inbreeding depression was found in the F_2 generation ranged from 7.99 (family III) to 37.36 % (family IV) in all the five families. The significant values of inbreeding depression confirmed the combination of inferior and superior alleles in the F_2 generation. Similar results in variable magnitude of heterosis for locules per fruit were also reported by Kurian *et al.* (2001); Amin *et al.,* (2017). Estimates of heterobeltiosis and standard heterosis for pericarp thickness were found positive and significant in the family I with negative inbreeding depression; while family II and III exhibited significant positive estimates of inbreeding depression, which may be due to association of favorable-unfavorable gene combination in F_1 and F_2 generations. Similar outcomes for pericarp thickness were also confirmed by Kurian *et al.,* (2001); Amin *et al.,* (2017); Kumar *et al.,* (2017); Dhaliwal *et al*., (2019). However, highest and significant heterosis observed in desirable direction for fruit diameter with negligible residual heterosis for length of fruit in rice (Chavan *et al*., 2018).

(iii) Fruit yield. Family I, II, and family V had a significant attribute for heterobeltiosis; however, all the five families exhibited positive and significant estimates of standard heterosis for fruit yield per plant. The positive significant and higher estimates of heterosis were found for fruit yield per plant, (104.51 %; 227.38 %) in family II and (16.54 %; 350.19 %) in family V over better parent as well as standard check. Family III and IV exhibited negative and/or non-significant heterobeltiosis; this indicates involvement of different types of non-favorable alleles in hybrid combinations. Higher heterosis (Family I, II, and V) for yield appears to be the consequence of heterosis of the yield attributing traits *viz*., Number of fruits per plant, average fruit weight, and size of the fruit. Significant and positive estimates of inbreeding depression were found in the family I and III. However, family I and IV exhibited positive and significant residual heterosis. There was a negative estimate for inbreeding depression found in family IV, suggesting an improvement in fruit yield per plant for subsequent generations in a positive direction *via* yield contributing traits. A similar result for heterosis was also recorded by Zdravkovic *et al.* (2011); Kumar and Singh (2016); Dhaliwal *et al.,* (2019) for fruit weight, fruit size, and fruit yield per plant.

Table 1: Heterobeltiosis (BP %), standard heterosis (SH %) and inbreeding depression (ID %) for various characters in five families in Tomato.

Character	I				II				III			
	HB (%)	SH (%)	Residual HB (%)	ID (%)	HB (%)	SH (%)	Residual HB (%)	ID (%)	HB (%)	SH (%)	Residual HB (%)	ID (%)
	GAT-4 × AVTOV 1002				ATL-11-05 × AVTOV 1002				GT-2 × AVTOV 1008			
1. DFF	-5.94**	-20.26**	3.83*	-10.39	-21.95**	-30.71**	-12.43**	-10.09	-9.58**	-31.87**	-9.91	0.37
2. PH	28.96**	338.21**	11.95**	13.18	68.84**	307.61**	51.54**	10.25	70.95**	272.13**	24.51**	9.86
3. PBP	62.66**	44.57**	-15.57**	28.51*	28.07	22.42	20.96**	5.55	31.14**	31.95**	-9.14	20.13
4. FPP	22.26**	97.81**	-58.38**	65.96	-7.22**	45.94**	-8.70	-40.81	-2.84**	49.42**	-18.90**	4.14
5. FW	224.83**	23.57**	-41.25	62.25	227.81**	35.67**	-16.12	21.79	34.71**	-14.69**	-19.91**	20.60
6. FL	43.79**	22.30**	2.28	10.77**	13.40**	15.42**	145.64**	11.72**	12.71**	19.93**	6.95**	7.22**
7. FG	4.90	21.53**	28.17**	-7.96	29.07**	34.33**	-	11.86	-0.65	22.55**	4.57	6.47**
8. LPF	50.15**	87.48**	13.24	16.40**	46.11**	90.10**	-13.76**	12.23**	20.38**	17.36**	-7.07	7.99**
9. PT	24.70**	7.59**	25.52**	-3.08**	-6.98**	-8.96**	28.61**	8.18**	-1.17	22.08**	11.15**	7.80**
10. FYPP	18.36*	267.68**	19.11**	50.36**	104.51**	227.38**	-16.35**	28.22	-2.68	148.29**	-8.87**	13.32*
11. SPF	47.74**	31.06**	-19.84	17.03	19.71**	-0.23	0.24	12.03	-0.38*	-21.75**	-13.67**	-5.98
12. TSW	37.92**	75.80**	-38.88**	38.86**	-44.88**	-27.36**	-47.98**	-82.90**	-14.43**	12.07*	13.49**	-3.61**
13. TSS	-8.80**	64.41**	-10.76	11.93**	12.59**	31.53**	-12.06**	10.09**	24.38	44.22**	39.72**	15.20**
14. LYC	-12.70**	-21.99**	-9.042	30.91**	68.75	-61.70**	2.28**	48.15**	168.75**	-39.01**	8.53*	23.26**
15. TA	-28.95**	-90.88**	-15.67**	-25.93**	38.71**	-85.47**	0.81	34.88**	-5.00**	-93.58**	-11.34**	-63.16**

Character	IV				V			
	HB (%)	SH (%)	Residual HB (%)	ID (%)	HB (%)	SH (%)	Residual HB (%)	ID (%)
	AVTOV 1007 × AVTOV 1005/2				IIHR-329 × IIHR-335			
1. DFF	-16.03**	-20.90**	-12.53**	-4.16	-2.81	-33.17**	-2.34	-0.49
2. PH	31.92**	159.99**	24.21**	-0.86	8.11**	261.29**	1.74	5.88
3. PBP	29.87**	28.95**	-2.43	14.99	16.71	32.57	1.32	13.18
4. FPP	24.55	42.58**	-22.74**	26.71	16.82	185.81**	5.39**	9.78
5. FW	27.38**	-32.25**	-	6.09	49.95**	9.37	-7.09	24.24
6. FL	9.14**	16.13**	19.61**	1.94*	16.47	6.52	13.60**	-3.23*
7. FG	5.88	16.58**	7.14**	6.30	7.26	33.31**	20.36**	4.69
8. LPF	-2.83	67.60**	-3.09	37.36**	42.81**	67.60**	22.33**	14.32**
9. PT	-10.06	-3.79	-39.13**	-23.01	13.82	9.04	2.68	-4.93**
10. FYPP	3.38	144.11**	10.85**	-14.17*	16.54**	350.19**	19.69**	20.27
11. SPF	44.84**	1.78	-5.04	8.32	21.47**	39.66**	66.05**	17.98
12. TSW	-3.29	26.92**	4.14**	30.85**	-22.40**	2.89	-18.61**	-26.25**
13. TSS	29.38	51.14**	12.46**	13.74**	107.27**	39.89**	-5.75**	7.22**
14. LYC	32.56**	-19.15**	15.51**	21.05**	4.35	-31.91**	-0.36	20.83**
15. TA	-55.88	-89.86	-33.04**	-156.67**	2.13**	-67.57**	-2.24**	8.33**

Note: HB- Heterobeltiosis, **SH**- Standard heterosis, **RH**- Residual Heterosis, **ID**- Inbreeding depression, **DFF**-Days to first flowering**, PH**- Plant height**, PBP**- Primary branch per plant**, FPP**- Fruits per plant, **FW**- Fruit weight**, FL-** Fruit length**, LPF**-Locules per fruit**, PT**- Pericarp thickness**, FYPP**-Fruit yield per plant**, SPF**- Seeds per fruit**, TSW**-1000 seed weight, **TSS-** Total soluble solid**, LYC**-Lycopene content and **TA-** Titrable Acidity

(iv) Seed yield. Significant estimates of heterobeltiosis were observed for a number of seeds per fruit in the family I, II, IV, and family V. However, a significant as well as a positive estimate of standard heterosis was observed for family V (39.66 %) and family I (31.06 %). However, non-significant inbreeding depression in the F_2 generation of five families was ranged between -5.98 (family III) to 17.98 % (family V), indicating improvement in vigour in subsequent generations. Significant and positive residual heterosis found for family V. Among the five families, the family I had the highest and positive estimate of heterobeltiosis for 1000 seed weight. In addition to this, family I, III, and family IV reported significant estimates of standard heterosis for 1000 seed weight. However, positive and significant inbreeding depression was observed in the family I and IV with a moderate magnitude of heterosis. Similar findings were also observed by Bhalala (2018). However, heterotic effects were also reported in the hybrids which were developed from the parents having poor per se performance.

(v) Biochemical traits. Significant and higher estimates of heterobeltiosis (107.27 %) were reported in family V and family II; whereas, the significant estimates for standard heterosis was reported in all the five families (I, II, III, IV, and family V) for total soluble solids. Significant estimates for inbreeding depression for all the five families indicated an absence of hybrid vigour in F_2 generation for total soluble solids. Total soluble solids influence the flavor of tomato and it is precious for the processing industry. Similar findings were also reported for heterosis (HB and SH) for the trait under study by Dagade *et al.,* (2015); Amin *et al.,* (2017); Dhaliwal *et al*., (2019). For lycopene content, significant and positive estimates of heterobeltiosis, as well as residual heterosis, were observed in family III and IV. However, negative standard heterosis was observed for all the five families for the respective trait. Lycopene content is a most desirable trait for consumer preference in the processing industry, which affects fruit colour. Similar results are also obtained by Dagade *et al.*, (2015); Amin *et al.,* (2017) for lycopene content. The significant estimates of inbreeding depression in all five families indicate loss of viability and vigor in the F_2 generation. The significant and positive magnitude of heterosis was recorded in family II and family V over better parent heterosis; however, family I, II, III, and family V exhibited significant and negative estimates of heterosis over the standard check for titrable acidity. It is a critical constituent of flavor and other quality determinants in tomato fruit, as has the storabilityof processed products. All the crosses indicate non-significant residual heterosis. The significant and positive values of heterosis estimates are also reviewed by Vinod *et al.,* (2013); Amin *et al.,* (2017); Kumar *et al.,* (2017) for the trait under study. Family II and V exhibited significant estimates for inbreeding depression. A similar range of inbreeding depression and its effects were also reported by Pandey *et al.,* (2006); Patel *et al*., (2010) for titrable acidity.

CONCLUSION

Development of hybrid cultivars especially in autogamous crop plants is a remarkable success of plant breeding. The evaluation of available tomato germplasm revealed a significant heterotic effect for fruit yield, earliness, and quality traits. Highest and significant heterosis observed in desirable direction for the characters, *viz.*, days to first flowering, plant height, number of fruits per plant and seeds per fruit, however, residual heterosis observed for the characters, fruit girth, length of fruit as well as for fruit yield per plant. It discloses that heterobeltiosis/heterosis over mid-parent was significant for major traits in most of the crosses, indicating the importance of hybrids for the exploitation of genetic gain in the commercial crop. The estimates of significant inbreeding depression with significant heterosis represent the presence of over-dominant gene action. The estimates of low inbreeding depression exhibit a reduction in mean for the F_2 generation. However, low inbreeding depression allows the breeder to develop pure lines by going for prolonged selfing cycles. Further improvement can be made through emphasis on hybrid breeding by introducing more on male sterility and apomictic genes in self-pollinated crops.

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Conflict of Interest. None.

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