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Studies on Heterosis in Tomato (*Solanum lycopersicum*)

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Abstract

Throughout the last century, tomato (*Solanum lycopersicum*) breeding has been based on various standard methods, which has ultimately resulted in the development of improved tomato cultivars and hybrids having high quality and yield attributes. In the present study, a total of 25 entries consisting of 13 diversified genotypes of tomato along with their 12F_1 hybrids were evaluated during two consecutive *rabi* seasons. Data on quantitative characters were recorded and percent mid-parent heterosis and better-parent heterosis were determined. Pronounced heterosis over better- parent was observed for fruit yield plant^{-1}(148.82%), fruiting clusters plant^{-1}(111.64%), fruits plant^{-1} (103.33%), fruit weight(62.79%) and plant height(50.57%). The expression of fruit yield heterosis in the best crosses was realized through differential expression of heterosis in various yield contributing traits. Selection of crosses on the basis of performance *per se* seems to be reliable than selection based on the manifestation of heterosis alone.

1. Introduction

Tomato (*Lycopersicon esculentum* Mill) is one of the most popular and widely grown vegetable crops in the world. The productivity of tomato in India (19.6 mt ha^{-1}) is much less than the average productivity (28.2 mt ha^{-1}) of the world (Anonymous, 2009). To improve the productivity of tomato, primary consideration should be evaluation of the potentialities of the existing cultivars and development of scientific breeding programme based upon the available genetic variability. Heterosis in tomato can be commercially exploited because of its ease in crossing, fruits bearing large number of seeds, ease in growing under varied agro-climatic conditions. Present investigation was carried out to estimate the nature and magnitude of heterosis in yield and yield attributing traits and to identify the most heterotic cross combinations for different important economic characters to use them in different ongoing breeding programme.

2. Materials and Methods

In the first year, thirteen diversified genotypes of tomato (Table 1) were sown in seedbed during *rabi* season at the Horticulture Farm of Palli Siksha Bhavana (Institute of Agriculture), Visva-Bharati, Sriniketan (23°29' N latitude and 87°42' E longitude and at an altitude of 58.9 meters above mean sea level under sub-humid, sub-tropical, lateritic belt of West Bengal) and were transplanted to the main field at 25 DAS. Crossing among these parental lines was done at the flowering stage.

The tomato flower is normally perfect. There are four to eight flowers in each compound inflorescence. Emasculation by hand was done in afternoon and one day prior to anthesis. Before emasculation and pollination, a thorough examination of parental lines was done and off type plants were rouged out. Then regular daily emasculation and pollination were started. The suitable phase for flower emasculation was when the corolla leaves had just opened or the sepals had started to separate and the anthers and corolla had started to change from light to dark yellow. The stigma was fully receptive at this stage allowing for pollination even immediately after emasculation. Emasculation of flower buds, when the corolla leaves had a light yellow colour, was also allowed. During emasculation, the left hand was used to hold the flower at base, and then anthers were removed as a group with or without the surrounding corolla by inserting forceps between the sepals to grip the base of the anthers and/or petals which were then removed by a firm but steady pull and thus picking off the corolla leaves together with all stamens. After a little practice, the removal of

Table 1: Mean performance of parental and their hybrid population for some quantitative characters in tomato

	Parental Population								Hybrid Population								
Genotype	Days to 50% Flowering	Plant height (cm)	Primary branches $plant^{-1}$	Fruiting clusters $plant^{-1}$	Fruits $cluster^{-1}$	Fruits $plant^{-1}$	Fruit weight (g)	Yield (g) / plant	Genotype	Days to 50% Flowering	Plant height (cm)	Primary branches $plant^{-1}$	Fruiting clusters $plant^{-1}$	Fruits $cluster^{-1}$	Fruits $plant^{-1}$	Fruit weight (g)	Yield (g) / plant
1. S 15998(P_1)	40.00 (H)	86.67 (H)	7.67 (H)	6.00 (L)	4.50	29.00 (L)	26.00 (L)	753.00 (L)	14. P_1XP_2	36.33	76.50	7.00	14.00	5.00	68.33	35.67	2066.67
2. Roma (P_2)	37.33 (H)	59.00 (L)	6.33 (L)	7.00 (H)	5.00 (H)	37.00 (H)	45.00 (H)	1800.00 (H)	15. P_3XP_4	32.00	70.50	7.00	12.00	4.00	47.67	32.17	1533.33
3. Solan Gola(P_3)	38.00 (H)	88.00 (H)	6.10 (L)	4.33 (L)	5.00 (H)	22.00 (L)	45.00 (H)	1050.00 (L)	16. P_5XP_6	43.00	64.83	7.00	10.00	4.00	34.00	47.40	1612.00
4. Aruna(P_4)	41.33 (H)	55.00 (L)	7.00 (H)	5.67 (L)	4.00 (L)	26.00 (L)	69.00 (H)	1800.00 (H)	17. P_3XP_7	37.67	56.67	7.00	11.00	4.50	43.00	45.10	1800.00
5. Sel-12-(P_5)	42.00 (L)	57.67 (L)	6.30 (L)	6.00 (L)	4.00 (L)	23.00 (L)	25.70 (L)	591.00 (L)	18. P_8XP_6	37.00	116.67	8.00	10.67	5.0	37.67	32.53	1225.00
6. Utkal Deepti (P_6)	41.67 (L)	53.33 (L)	7.40 (H)	8.00 (H)	5.00 (H)	40.00 (H)	33.80 (L)	1350.00 (H)	19. P_9XP_7	37.33	95.00	7.50	15.00	5.0	61.00	31.67	1913.33
7. Pusa Ruby(P_7)	38.00 (H)	55.67 (L)	6.50 (L)	7.33 (H)	4.00 (L)	30.00 (L)	45.67 (H)	1370.00 (H)	20. $P_{10}XP_6$	43.33	122.33	9.00	12.00	6.0	56.00	28.00	1506.67
8. EC-12217(P_8)	42.00 (L)	87.00 (H)	6.60 (L)	6.67	4.87 (H)	30.67 (L)	33.43 (L)	1003.00 (L)	21. P_5XP_7	43.00	48.33	7.27	12.00	5.0	42.00	50.00	2100.00
9. Elegant(P_9)	45.00 (L)	63.33 (L)	5.33 (L)	6.00 (L)	4.67	27.00 (L)	28.30 (L)	766.00 (L)	22. P_8XP_2	38.67	131.00	10.33	11.00	5.07	41.33	43.00	1700.00
10. EC-110964(P_{10})	43.00 (L)	102.2 (H)	6.20 (L)	5.00	5.00 (H)	27.00 (L)	27.77 (L)	755.00 (L)	23. $P_{11}XP_{12}$	35.33	65.33	7.00	11.27	5.00	50.00	70.00	3170.00
11. Utkal Pallavi(P_{11})	41.00 (H)	44.53 (L)	5.53 (L)	8.00 (H)	5.00 (H)	43.00 (H)	29.63 (L)	1274.00 (H)	24. $P_{11}XP_4$	39.00	63.00	7.00	15.00	4.00	42.00	76.00	3136.67
12. Pathar Kuchi (P_{12})	41.67 (L)	57.00 (L)	5.53 (L)	6.67	4.00 (L)	26.00 (L)	43.00 (H)	1126.00 (L)	25. $P_{13}XP_4$	35.00	53.67	7.00	12.00	5.00	41.00	51.00	2060.00
13. Utkal Urbasi(P_{13})	41.00 (H)	69.00	7.00 (H)	8.00 (H)	4.00 (L)	38.63 (H)	27.27 (L)	1052.00 (L)									
Grand Mean	40.92	67.57	6.42	6.51	4.54	30.715	36.89	1130.00									
SEm±	0.596	4.86	0.198	0.321	0.130	1.877	3.44	106.20									

(H)= High performance per se (L)= Low performance per se the anthers became a simple matter although first two-to-three attempts almost resulted in breakage/wounding of the style. If, however, anther seemed reluctant to part company from flower receptacle as a group, single one was removed first by careful manipulation of the forceps. Following this, the remaining four were gripped firmly and pulled out without damaging the style. The remaining non- emasculated flowers in the inflorescence were removed with the help of scissors and the emasculated flowers were properly tagged.

Emasculated flowers were pollinated, generally, in the next morning. Pollen needed for pollination was collected from flowers in full bloom by slitting inside of the anthers of mature flowers (used as male) with the forceps in such a way that a small amount of pollen was collected at the tip of the forceps. This was then lightly applied to the stigmatic surface. Forceps were sterilized by dipping in alcohol after each pollination. Pollen was also collected in large amount by inverting the mature flower and tapping pollen into the thumbnail. Protection of pollinated flowers was achieved by covering them with butter paper packet with so many small perforations for easy air circulation. Required information (i.e. the particular cross, date etc.) was written on the tag.

Mature and well ripen fruits from successful crosses were harvested separately and seeds were collected following appropriate technique, dried and stored at 3-5% moisture level.

Crossed seeds (F_1 seeds) along with the seeds from parental lines were sown in seed bed during next *rabi* season and seedlings were transplanted in the main field 25 days after sowing. All the genotypes (13 parents and 12 F_1s) were grown in a complete randomized block design (CRBD) with 3 replications. The experimental plot of each genotype consisted of 3 rows of 3-meter length keeping plant-to-plant and row-to-row spacing of 50 cm apart. All recommended package of practices were followed during the crop season for raising a healthy crop.

Data on days to 50% flowering were recorded on plot basis. Data on other quantitative characters viz. plant height, primary branches plant^{-1} (at maturity), fruiting clusters plant^{-1}, fruits plant^{-1} (1st, 2nd and 3rd pickings), fruit weight (at maturity), and fruit yield plant^{-1} were recorded on 5 randomly selected competitive plants in each replication and their mean values along with the status of parents (high/low) for different characters are summarized in Table 1. The analysis of variance was performed, and heterosis (%) over mid-parent and better-parent values was calculated following Turner (1953).

3. Results and Discussion

Analyses of variance indicated significant differences among parents and hybrids for all the characters under study. Percent heterosis for each character over mid-parent (MP) and better-parent (BP) for yield and yield components are presented in Table 2.1 and 2.2.

A perusal of Table 2.1 and 2.2 revealed that heterosis over mid- parent and better-parent were substantially high in both positive and negative directions depending upon the nature of the cross as well as the characters studied.

For days to 50% flowering, most of the crosses showed significant and negative heterosis over the mid parent and better parent (except $P_5 \times P_6$, $P_{10} \times P_6$, $P_5 \times P_7$) and they had a tendency towards early flowering. Similar results were observed by Mahendrakar et al. (2005), Premalakshme et al. (2005) and Harer et al. (2006).

Significant heterosis for both tallness and dwarf habit was observed in different crosses. The positive significant heterosis towards tallness was registered in eight cross combinations (Table 2.1 and 2.2). Cross combination (P_8 x P_2) showed highest heterotic value over mid- parent (79.45%) and better- parent (50.57%), although the fruit yield was much low in this hybrid. However, F_1 hybrids (P_{11} x P_{12}, P_{11} x P_4, P_5 x P_7) showed highest amount of fruit yield *per se* (Table 1 and Table 2.1 and 2.2). In order to develop hybrid tomato possessing semi-dwarf to tall type, either both parents of hybrids should be dwarf possessing the same or different dwarfing gene(s) or one parent with dominant semi-dwarfing or tall gene(s). High vegetative vigour in the hybrids in terms of increased plant height as recorded in the present investigation agreed well to some earlier reports (Tiwari and Lal, 2004; Singh et al. 2005 and Harer et al. 2006). The negative significant heterosis towards dwarf habit was also noted over mid and better- parent in two and four cross combinations, respectively.

In character like primary branches plant^{-1}, positive and significant heterosis over mid parent and better parent was noted for eight crosses and in four crosses, respectively. Positive and significant heterosis for this character was also reported by Tiwari and Lal (2004), Harer et al. (2006). High amount of positive and significant heterosis over mid parent as well as over better parent for fruiting clusters plant^{-1} was observed in all the crosses. Highest amount of heterosis over mid parent (140%) and better parent (111.64%) were registered in cross combination $P_3 \times P_4$ (Table 1). These results are in line with Thakur et al. (2004) and Harer et al. (2006).

For fruits cluster^{-1}, the crosses ($P_5 \times P_7$ and $P_{13} \times P_4$) which recorded the highest heterosis (25%) for this character, also recorded the highest amount of heterobeltiosis (25%). Four crosses viz. $P_9 \times P_7$, $P_{10} \times P_6$, $P_5 \times P_7$ and $P_{13} \times P_4$ recorded significant heterosis, while three crosses viz. $P_{10} \times P_6$, $P_5 \times P_7$ and $P_{13} \times P_4$ recorded positive and significant heterobeltiosis for the

Table 2.1: Estimates of heterosis over mid parent (MP) and better parent (BP) for yield and yield contributing characters in tomato

Treatment	Days to 50% flowering		Plant height (cm)		Primary branches plant^{-1}		Fruiting clusters plant^{-1}		Fruits cluster^{-1}	
	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP
P_1XP_2	-6.039*	-9.175**	5.032*	-11.734**	0	-8.735	115.384**	100.00**	5.263	0
P_3XP_4	-19.324**	-21.95**	-1.398	-19.886**	6.870	0	140.00**	111.64**	-11.11	-20.00**
P_5XP_6	2.785	2.38	16.811**	12.415**	2.189	-5.405	42.857**	25.00**	-11.11	-20.00**
P_3XP_7	-0.868	-0.868	-21.111	-34.466**	11.111*	7.692	88.68**	50.058**	0	-10.00
P_8XP_6	-11.557**	-11.904**	66.279**	34.103**	14.285**	8.108	45.466**	33.36**	1.317	0
P_9XP_7	-10.048**	-17.044**	59.663**	50.007**	26.796**	15.384**	125.056**	104.64**	15.340*	7.066
$P_{10}XP_6$	2.350	0.767	57.307**	19.696**	32.353**	21.621**	84.615**	50.00**	20.00**	20.00**
P_5XP_7	7.50**	2.381	-14.71**	16.195**	13.594**	11.846	80.045**	63.71**	25.00**	25.00**
P_8XP_2	-2.508	-7.928*	79.452**	50.575**	59.783**	56.515**	60.936**	57.143**	2.735	1.40
$P_{11}XP_{12}$	-0.810	-15.215**	28.691**	14.614**	26.582**	26.582**	53.646**	40.875**	11.11	0
$P_{11}XP_4$	-5.259	-5.637	26.595**	14.545**	11.732**	0	119.458**	87.5**	11.11	-20.00**
$P_{13}XP_4$	-14.976**	-15.315**	-13.43**	-22.217**	0	0	75.567**	50.00**	25.00**	25.00**
PH	3(1)	3	8(8)	8(8)	10(8)	7(4)	12(12)	12(12)	9(4)	5(3)
NH	9(5)	9(7)	4(2)	4(4)	-	2(-)	-	-	2(-)	4(3)

*,**Significant at p=0.05 and 0.01, respectively; PH: Positive Heterosis; NH: Negative Heterosis; Value in parenthesis indicates cross combinations showing significant heterosis; P_1= S15998; P_2= Roma; P_3= Solan gola; P_4= Aruna; P_5= Sel-12; P_6= Utkal Deepti; P_7= Pusa Ruby; P_8= EC12217; P_9= Elegant; P_{10}= Ec110964; P_{11}= Utkal; Pallavi; P_{12}= Pathar Kuchi; P_{13}= Utkal Urbasi

Table 2.2: Estimates of heterosisover mid parent (MP) and better parent (BP) for yield and yield contributing characters

Treatment	Fruits plant^{-1}		Fruit weight (g)		Yield plant^{-1} (g)		Fruit yield per se
	MP	BP	MP	BP	MP	BP	
P_1XP_2	107.06**	84.675**	0.478	-20.73**	61.90**	14.82**	2066.67
P_3XP_4	98.625**	83.346**	-43.56	-53.377**	7.602	-14.81**	1533.33
P_5XP_6	7.936	-15.00**	59.327**	40.236**	66.099**	19.41**	1612.00
P_3XP_7	65.38**	43.33**	-0.518	-1.248	48.76**	31.39**	1800.00
P_8XP_6	6.608	-5.825	-17.05**	-27.711**	4.122	-9.259	1225.00
P_9XP_7	114.035**	103.33**	-14.37**	-30.654**	79.15**	39.66**	1913.00
$P_{10}XP_6$	67.164**	40.00**	-9.05	-17.159**	43.151**	11.61**	1506.67
P_5XP_7	58.49**	40.00**	40.12**	9.481*	114.23**	53.29**	2100.00
P_8XP_2	22.152**	11.703*	9.652*	-4.44	21.298**	-5.55	1700.00
$P_{11}XP_{12}$	44.927**	16.279**	92.76**	62.79**	164.16**	148.82**	3170.00
$P_{11}XP_4$	21.739**	-2.325	54.111**	10.145**	104.08**	74.26**	3136.67
$P_{13}XP_4$	26.876**	6.135	5.952*	-26.087**	44.46**	14.44**	2060.00
PH	12(10)	9(8)	7(6)	4(4)	12(10)	9(9)	
NH	-	3(2)	5(2)	8(6)	-	3(1)	

character under study. Three crosses ($P_3 \times P_4$, $P_5 \times P_6$ and $P_{11} \times P_4$), however, showed negative and significant heterosis over better parent for this character. Significantly positive heterosis over mid parent and better parent for this character were earlier reported by Joshi and Thakur (2003), Bhatt et al. (2004) and Harer et al.(2006), while in some of the crosses, significant negative heterosis for this character were reported by Baishya et al. (2001) and Thakur et al. (2004).

The positive significant heterosis for number of fruits plant^{-1} was registered over mid and better-parent by ten and eight cross combinations. The range of heterosis over mid and better-parents was observed from 6.61 to 114.03% and -15 to

103.33% respectively. One cross ($P_5 \times P_6$), however, recorded significant negative heterosis over better parent. The parental combination, $P_9 \times P_7$ (Elegant × Pusa Ruby) recorded highest heterosis over mid- parent as well as over better parent. Joshi and Thakur (2003), Thakur et al. (2004), reported significant heterosis for higher number of fruits plant^{-1} in tomato suggesting good scope for yield improvement through this component. However, Premalakshme et al. (2005) revealed negative heterosis for this trait.

Heterosis over mid parent for fruit weight varied from-43.56 to 92.76% (Table 2). Six crosses showed desirable heterosis over mid- parent. Likewise heterosis over better- parents varied from -53.37% to 62.79%. Only four crosses showed significant positive heterosis, while negative significant heterosis for this character prevailed in six crosses. The findings of the present investigation were similar to those of other workers like Tiwari and Lal (2004), Harer et al. (2006) and Seeja et al. (2007).

Out of twelve cross combinations studied, eleven of them exhibited significant and positive heterosis for fruit yield plant^{-1} over the mid parent, while significant positive heterosis over better parent was exhibited by nine hybrids. None of the crosses showed significant negative heterosis over the mid parent but one of the crosses ($P_3 \times P_4$) showed significant negative heterosis over the better parent. The results obtained in this study are in conformity with Bhatt et al (2004), Mahendrakar et al. (2005) and Garg et al. (2007), who also reported significant heterosis for improved fruit yield in tomato.

The results obtained in the present investigation revalidates that the magnitude of heterosis differed widely for traits and crosses as well. The fruit yield *per se* of the five hybrids (P_{11} x P_{12}, P_{11} x P_4, P_5 x P_7, P_1 x P_2 and P_{13} x P_4) showing significant heterosis was high (Table 2.1and 2.2). High level of heterosis in these hybrids was also associated with positive and significant heterosis for fruit weight, fruiting clusters plant^{-1} and (or) fruits cluster^{-1}. In addition to these three characters, the majority of the crosses showed positive heterosis for one or more of the yield component characters like plant height, primary branches plant^{-1}, and fruits plant^{-1}. Heterosis for fruit yield would be more stable, if it is accompanied with heterosis in a number of component characters, that heterosis alone in fruit yield.

In the present investigation, most of the crosses showing heterosis over better parent revealed the effect of performance *per se* of parents involved in a particular cross. A good relation between performance *per se* of the parents and GCA has been reported in many crops. The performance *per se* of parents was determined by comparing the mean of a parent over the general mean of the character giving 'high' (H) status if it exceeded the general mean and 'low'(L) status if it was below that value. Low performance *per se* of parents does not always produce low heterotic response and vice-versa (Table 1). The crosses P_9 x P_7, P_{11} x P_{12} (for plant height); P_8 x P_2, P_{11} x P_{12}, P_9 x P_7, P_5 x P_7 (for primary branches plant^{-1}); P_3 x P_4, P_5 x P_7 (for number of clusters plant^{-1}); P_5 x P_7, P_{13} x P_4, P_9 x P_7 (for number of fruits cluster^{-1}); P_9 x P_7, P_3 x P_4, P_3 x P_7 (for fruits plant^{-1}) and P_5 x P_6 (for fruit weight) showing significant positive heterosis over better parent were in the category of low x low (L x L) parental combinations. Heterosis in such crosses may be due to accumulation of 'good' alleles from both the parents in hybrid combination or may be from overdominance type of gene action in some loci, or a combination thereof.

The crosses P_8 x P_2, P_8 x P_6, P_{10} x P_6 (for plant height); P_{10} x P_6 (for primary branches plant^{-1}); P_9 x P_7, P_1 x P_2, P_{11} x P_4 (for no. of fruit clusters plant^{-1}); P_8 x P_2 (for fruits cluster^{-1}); P_1x P_2, P_{10} x P_6 (for fruits plant^{-1}) ; P_{11} x P_{12}, P_{11} x P_4 (for fruit weight) and P_{11} x P_{12}, P_5 x P_7, P_9 x P_7, P_3 x P_7 (for yield plant^{-1}) with 'low' and 'high' status of the parents showed significant positive heterosis over better-parent (with low x high or high x low combination). Superiority in such H x L crosses might involve dominant x recessive type of gene action, and therefore might tend to be unfixable (Singh and Gupta, 1969). For days to 50% flowering, P_3 x P_4 and P_{13} x P_4 exhibited maximum desirable heterobeltiosis and average heterosis, as well as significant negative effects. The involvement of parents with 'high' performance *per se* (H x H) suggested the role of additive types of gene interaction for early flowering. The presence of additive gene action suggested that part of heterosis can be fixed in subsequent generation. Similarly, it was also noted that crosses with high x high status as in P_{11} x P_4 (for yield plant^{-1}); P_8 x P_2 (for fruit weight); P_{10} x P_6 (for fruits cluster^{-1}) can produce desirable transgressive segregants if additive genetic system is present in these parents. Arunachalam (1977) reported that pure additive gene action at individual loci coupled with favorable additive x additive interaction could produce heterotic combination. For fruit yield plant^{-1}, the parents having high and low yield *per se* resulted in the hybrids with maximum yield and high heterosis over mid parent and better parent. In cross combinations like P_{11} x P_{12} (Utkal Pallavi x Pathar Kuchi), the parents having high and low yield *per se* showed highest yield (3170 g plant^{-1}) and also highest amount of heterosis over mid parent (164.16%) and better parent (148.82%). In the present study, some of the lines like P_{11} (Utkal Pallavi), P_{12} (Pathar Kuchi), P_3 (Solan Gola), P_4 (Aruna), P_8 (EC12217), P_5 (Sel 12), P_7 (Pusa Ruby) etc. had the potentiality for generating high heterotic cross combinations for most of the traits under study.

4. Conclusion

For yield and yield component traits, most of the crosses exhibited positive and significant heterosis over mid parent and better parent for almost all the characters indicating accumulation of increasing alleles from both the parents involved in a cross. Pronounced heterosis over mid parent and better parent were observed in fruit yield plant^{-1} (164.16%, 148.82%), followed by fruiting clusters plant^{-1} (140.0%, 111.64%), fruits plant^{-1} (114.03%, 103.33%), fruit weight (92.76%, 62.79%), plant height (79.45%, 50.57%) etc.

Considering performance *per se*, highest significant heterobeltiosis (148.82%) along with contribution of significant heterobeltiosis for other yield components, the most outstanding hybrid identified was P_{11} x P_{12} (Utkal Pallavi x Pathar Kuchi, giving an average yield of 3170.00 g plant^{-1}) followed by P_{11} x P_4 (Utkal Pallavi x Aruna, giving an average yield of 3163.00 g plant^{-1}), P_5 x P_7 (Sel 12 x Pusa Ruby, giving an average yield of 2100 gm plant^{-1}). These hybrids could be exploited commercially. Some of the parental lines like Utkal Pallavi, Pathar Kuchi, Solan Gola, Aruna, Sel 12, Pusa Ruby and EC 12217 had the potentiality for generating high heterotic cross combination for most of the yield contributing traits under study. So, keeping in view the objectives of heterosis breeding, the selection of crosses on the basis of *per se* performance seems to be reliable, rather selection based on the manifestation of heterosis alone.

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