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Studies on Heterobeltiosis, Combining Ability and Gene Action in Tomato (*Solanum lycopersicum*)

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ABSTRACT

In this investigation, a 4 × 2 line × tester mating design was followed to record heterosis over better parent for 11 characters. Crosses showing high specific combining ability (SCA) and yield may be ascribed to their high general combining ability (GCA) for fruit number per plant or fruit weight or polar diameter of fruit. Two promising hybrids (CLN2777G x BCT-59 and CLN2777A x BCT-82P) were selected on the basis of their performance *per se*: heterosis was manifested in them and the SCA effects are relevant since they can be used commercially because of high yield, better quality traits, and low percent disease index (PDI) values for tomato leaf curl disease (ToLCV) disease. Predominance of additive gene action was evident in the control of characters like days to 50% flowering, and PDI. Both additive and non-additive gene action were important for polar diameter, pericarp thickness, and fruit acidity whereas fruit weight, fruit number per plant, locules per fruit, total soluble solids (TSS), and fruit yield per plant were governed by non-additive gene action.

Keywords: Combining ability, gene action, heterosis, ToLCV tolerance, tomato

INTRODUCTION

The phylogenetic classification of the *Solanaceae* family has recently been revised and the genus *Lycopersicon* re-integrated into the *Solanum* genus with its new nomenclature. *Solanum* section *Lycopersicon* includes the cultivated tomato (*Solanum lycopersicum*) and 12 additional wild relatives. *Solanum lycopersicum* is the only domesticated species (Peralta *et al.* 2006). From the first domestication to modern breeding, the tomato has been continually subjected to human selection for a wide array of applications in both science and commerce.

The major limiting factors towards production of optimum yield are considerable biotic stresses mainly *Tomato leaf curl virus* (ToLCV) in existing varieties and hybrids (Yadav and Awasthi 2009; Fazeli *et al*. 2009; Pandey *et al*. 2009; Chaudhary *et al*. 2010; Van Brunschot *et al*. 2010; Reddy *et al*. 2011). Moreover, most of the hybrids developed by private sectors are prone to attack of ToLCV. It is the most problematic and severe in case of early autumn crop which fetch 3-4 times more market price than the main winter harvest. The disease has risen to alarming proportions in the plains of India and has become a limiting factor in tomato cultivation particularly during summer crop (February to May) in southern Indian states (Saikia and Muniyappa 1989; Sadashiva *et al.* 2002) and autumn crop (August to December) in northern plains (Som 1973; Mayee *et al.* 1974; Banerjee and Kalloo 1987) and both early-autumn and autumn-winter (September to February) in Eastern India, particularly in West Bengal (Nath 2003; Anonymous 2006, 2007, 2008). Green and Kalloo (1994) reported that the disease can cause yield loss up to 100% under favourable conditions. According to a survey conducted by Kanjilal *et al.* (2000) in four major tomato growing districts (Coochbehar, Jalpaiguri, Nadia and Murshidabad) of West Bengal, India tomato leaf curl virus disease emerged as one of the main problems of hybrid crop culture.

ToLCV and *Tomato yellow leaf curl virus* replicates in the host cell (Gafni 2003) and resistance to the virus consisting in attenuation and delay in time of symptom development was correlated with reduction in virus accumulation in the host plant (Lapidot *et al.* 2001; Rubio *et al*. 2003; Perez de Castro *et al*. 2005). Delay in symptom expression and lack of disease severity in the plant were the chief resistance manifestation of the host which might be due to significant delay in accumulation of viral DNA inside the plant and inhibition of long distance virus movement (Rom *et al*. 1993; Michelson *et al*. 1994) because all tomato cultivars and wild *Lycopersicon* species excepting *L. chilense* LA1969 support propagation and accumulation of various amounts of virus, although some wild *Lycopersicon* accessions are symptomless (Zakai *et al*. 1990; Vidavsky *et al*. 1998). There have been considerable efforts towards breeding resistant cultivars using some wild *Lycopersicon* spp. accessions for introgression of resistance into the cultivated tomato. However, breeding tomatoes resistant to ToLCV or TYLCV has been slow because of the complicated inheritance of the resistance/tolerance traits and chances of considerable number of escapes regardless of the time of inoculation and level of inoculums. Some earlier studies showed that resistance to tomato leaf curl virus and tomato yellow leaf curl virus was controlled by a few major genes (Banerjee and Kalloo 1987; Nainar and Pappiah 2002; Boiteux *et al*. 2007) however, some other studies suggested the resistance to the disease to be quantitatively inherited and conditioned by polygenes (Pilowsky and Cohen 1990; Zakai *et al*. 1990; Vidavsky *et al*. 1998; Chandra Shekara *et al.* 2003; Hazra and Nath 2008).

Introgression of TYLCV or TolCV resistance alleles into cultivated tomato from the wild species started as early as 1974 (Pilowsky and Cohen 1990) and was completed successfully by several researchers (Kalloo and Banerjee 1990; Laterrot 1992; Zamir *et al.* 1994; Scott *et al.* 1995; Vidavsky and Czosnek 1998; Friedmann *et al.* 1998).

In India, H-24 was selected from a population that had undergone 4 backcrosses to *L. esculentum* (ToLCV susceptible recurrent parent Hisar Arun) followed by two generations of inbreeding (Kalloo and Banerjee 2000). Molecular

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mapping indicated that a wild tomato DNA fragment introgressed into chromosome '11' of tomato inbred line H-24, contains at least one gene conditioning ToLCV tolerance (Hanson *et al.* 2000). However, Banerjee and Kalloo (1987) studying the inheritance of TLCV resistance in *L. hirsutum* f. *glabratum* accession B 6013 concluded that two genes acting epistatically conditioned resistance. It was possible that during the backcrossing process, H-24 received only one major resistant gene from B 6013 (Hanson *et al.* 2000). However, H-24 is being used in developing ToLCV tolerant breeding lines for development of promising hybrids (Sadashiva *et al.* 2002; Hazra *et al*. 2009). A TYLCV tolerance gene originating from *L. chilense* LA 1969, *Ty-1*, has been mapped, using RFLP markers, to tomato chromosome 6 and has been introgressed into a cultivated tomato line (Zamir *et al.* 1994). Problems of such introgression breeding lay mainly on the difficulty in breaking close linkage between resistant gene and some undesirable characters of the wild species. It was suggested that combining various sources of tolerance in a single hybrid may provide improved tolerance (Vidavsky *et al.* 1998). However, after more than 30 years of research works, the best cultivars and breeding lines show only tolerance to the virus rather than immunity.

The proper choice of parents based on their combining ability is a prerequisite in any sound breeding programme. Such studies not only provide necessary information regarding the choice of parents but also simultaneously illustrate the nature and magnitude of gene action involved in the expression of desirable traits. Tomato offers much scope of improvement through heterosis breeding which can further be utilized for the development of desirable recombinants. Heterosis in tomato was first observed by Hedrick and Booth (1968) for higher yield and more number of fruits per plant. Heterosis manifestation in tomato is in the form of the greater vigour, faster growth and development, earliness in maturity, increased productivity, better quality attributes, and higher levels of resistance to biotic stresses (Yordanov 1983; Mahendrakar *et al.* 2005; Seeja *et al*. 2007; Hannan *et al*. 2007a; Gul *et al*. 2010; Patel *et al*. 2010). Line x tester is one of the useful tools for preliminary evaluation of genetic stock for use in hybridization programme with a view to identify good combiners. Keeping in view the importance of the above studies, the present research programme has been undertaken to determine the nature and magnitude of heterosis for yield component characters, quality characters and leaf curl tolerance and to determine the nature of gene action for yield component characters, quality characters and leaf curl tolerance with a view to identify good general combiners, as well as to frame the breeding approach for the genetic improvement of such characters.

MATERIALS AND METHODS

The investigation was carried out at C Block farm of Bidhan Chandra Krishi Viswavidyalaya, Kalyani, Nadia, West Bengal, India, under the research field of the All India Coordinated Research Project on Vegetable Crops situated at 23.5°N latitude and 89°E longitude at a mean sea level of 9.75 m.

Development of F_1 hybrids and their field growth

Seed of ToLCV-tolerant lines CLN 2777A, CLN 2777B, CLN 2777F and CLN 2777G imported from the Asian Vegetable Research and Development Centre, Taiwan and the testers BCT-82P and BCT-59 obtained from Bidhan Chandra Krishi Viswavidyalaya were used. Seed beds were prepared in a sandy loam soil and were 20 cm tall and 1.0 m wide. Weathered cowdung manure at 4 kg/m^2 was mixed into the beds. Beds were drenched with formaldehyde (4.0%) and covered with polythene sheet for 10 days to avoid damping off disease. Seeds, after treatment with Thiram (3 g/kg of seed), were sown during the 1st week of August, 2009 at a shallow depth 5 cm apart and covered with finely sieved well rotten leaf mold (leaves left to decompose for two year) which acts as soil improver and to prevent the soil drying out. After sowing, beds were covered with straw until germination which normally takes four days and hand watered regularly up to 3rd week of August, 2009. Nursery beds were covered with 200 µm ultraviolet (UV)-stabilized polyethylene film (product of Indian Petro-chemicals Ltd.) supported by bamboo poles with open sides to protect seedlings from rain and direct sunlight. Seedlings were hardened by withholding water 4 days before transplanting. One-month-old seedlings were transplanted to the main field during the 1st week of September, 2009. Four lines and two testers were planted separately in 6 rows spaced 60 cm (row to row) and 45 cm (plant to plant) in plots. Management practices for cultivation were followed as per Chattopadhyay *et al*. (2007).

During full boom, crossing was carried out. Flowers of each line were emasculated between 4 and 5.30 p.m. Male parent flower buds that would open the following day were picked in the afternoon, the anthers were separated that night to dry and the pollen were extracted the following morning for pollination, which was done from 8 to 10 a.m. Each parental line was crossed with each tester separately. Hybrid seed were extracted by the fermentation method (Rashid and Singh 2000). The red ripe fruits after finely chopped were kept for overnight for fermentation in a plastic bucket. This process frees the seeds from adhering pulp which settle down at the bottom and then washed thoroughly with clean water in the next day morning. Seeds which were floated in the water along with pulp were discarded and the decandated seeds were taken out, dried and stored in desiccators for sowing in the next season.

One-month-old transplants of 6 parental lines and 8 hybrids were transplanted in the 2nd week of September, 2010. The parents and hybrids were arranged in a randomized complete block design with 3 replications at 60 × 45 cm spacing with 36 plants for each replication in a 3.6 × 2.7 m plot. No protection against whitefly (*Bemisia tabaci* Genn.) was used. Observation on days to 50% flowering, equatorial diameter, polar diameter, fruit weight, number of fruit/plant, locules/fruit, total soluble solids (TSS), acidity, plant disease index (PDI) for ToLCV, and fruit yield/plant were measured on 20 randomly selected plants per plot.

Observations on disease parameters

The incidence of ToLCV was recorded from lines, testers and F_1s. Disease symptoms and disease severity were recorded from each plant of a genotype in each plot at 15-days intervals starting from 30 days after transplanting for up to 90 days. Several scoring techniques were advocated for field screening of tomato against ToLCV which were based on phenotypic expression of typical disease symptoms and manifestation of disease severity. Almost all the workers (Som 1973; Mayee *et al.* 1975; Varma *et al.* 1980) tried to assess the percentage of disease infection before scoring the infected plants. Assessment on the reaction of the genotypes to ToLCV was with the disease parameters, percent disease incidence, PDI, symptom severity and coefficient of infection (CI) (**Table 1**) according to Banejee and Kalloo (1987) and Kalloo and Banerjee (2000). The most efficient scoring technique and scale (0-4) was first adopted by Banerjee and Kalloo (1987). However, they assigned response value to each score of symptom severity grade as a 0 grade had response value of 0, 1 had 0.25, 2 had 0.50, 3 had 0.75 and 4 grade with a response value of 1.00. We also calculated coefficient of infection (CI) by multiplying the percent disease by the "response value" and Percent Disease Index (PDI) from the numerical ratings by the following formula:

PDI (%) = Σ Numerical ratings × 100/ Number of observation × Highest rating

The incidence of disease depends on the population build up of the vector (*Bemisia tabaci*) and the presence of virus source. White fly populations were monitored from September to February and were recorded on five leaves, two each from lower, middle and one from upper canopy of the plants at 6 a.m. from 5 randomly selected tagged plants of each plot at 7-day-intervals after transplanting. Infected plants of susceptible cultivars were planted and maintained around the field to ensure sufficient virus inoculum. Data on the same disease parameters were taken to assess ToLCV reaction in parents and F_1 hybrids.

Table 1 Scale used for classifying disease reaction of *Lycopersicon* sp. to *Tomato leaf curl virus* according to Banerjee and Kalloo (1987).

Symptom	Symptom severity grade	Response value	Coefficient of infection	Reaction
Symptomless	0	0	0-4	Highly resistant (HR)
Very mild curling, up to 25% of leaves	1	0.25	5-9	Resistant
Curling, puckering of 26–50% of leaves	2	0.50	10-19	Moderately resistant (MR)
Curling, puckering of 51–75% of leaves	3	0.75	20-39	Moderately susceptible (MS)
Severe curling, puckering of >75% of leaves	4	1.00	40-69	Susceptible (S)
			70 -100	Highly susceptible (HS)

Statistical analyses

Data were analyzed with the line × tester model of genetic analysis (Kempthorne 1957). Heterobeltiosis or better-parent heterosis (BPH) was estimated in terms of percent increase or decrease of the F_1 hybrid over its better parent (Hayes *et al*. 1965).

$$BPH (\%) = [F1-BP/BP] \times 100$$

Significance of better-parent heterosis was determined following the "t" test suggested by Wynne *et al*. (1970).

$$BP (t) = F_1\text{-}BP/ \sqrt{(2/r)EMS}$$

where F_1 = Mean of the F_1 hybrid for a specific trait, BP = Mean of better-parent in the cross, and EMS = Error mean square.

Combining ability analysis was carried out according to Singh and Chaudhary (1979) based on Griffing's (1956) fixed effect model using the following formula:

$$Y_{ij} = m + g_i + g_j + s_{ij} + ri_j + 1/bc\Sigma\Sigma_{ijkl}$$

where i, j = 1, 2……...n; k = 1, 2,……b. l = 1, 2,.....c; Y_{ij} is the mean of i × j genotype over k and l; m is the population mean; g_i is the GCA effect of the i^{th} parent; g_j is the GCA effect of the j^{th} parent; s_{ij} is the SCA effect; r_{ij} is the reciprocal effect; and $1/bc\Sigma\Sigma_{ijkl}$ is the mean error effect. Statistical analyses were done using SPSS Professional Statistics version 7.5 (SPSS Inc., Chicago, Ill.).

RESULTS AND DISCUSSION

Studies on heterobeltiosis

Data on heterosis for yield and contributing characters are presented in **Table 2**. For days to 1st flowering, three cross combinations (CLN2777F × BCT-59, CLN2777B × BCT-59 and CLN2777F × BCT-82P) exhibited negative heterosis over better-parent. Line CLN 2777 F, which was the earliest parent (45 days), was involved in the best hybrid combinations. Selection of hybrids showing negative heterosis over their better-parents for this character may be useful for developing early commercial hybrids. Negative heterosis for days to 50% flowering has also been observed by Girwani (2008). Regarding the equatorial diameter of fruit, the maximum hetero-beltiosis was found in CLN2777G × BCT-59 (20.35%) followed by CLN2777F × BCT-59 (4.17%) and CLN2777B × BCT-59 (3.58%). For polar diameter of fruit, the cross combinations *viz*., CLN2777G × BCT-82P (37.85%) and CLN2777G × BCT-59 (6.51%) exhibited positive and significant heterobeltiosis. Good hybrids showing significant heterobeltiosis for fruit weight were CLN2777G × BCT-59 (42.88%), CLN2777B × BCT-59

Table 2 Heterosis over better parent and their corresponding specific combining ability.

Characters	Three better crosses	Heterobeltiosis (%)	Specific combining effects	Best three general combiners
Days to 50% flowering	CLN2777F × BCT-59	-12.00**	-0.58**	CLN 2777 F (45.00)
	CLN2777B × BCT-59	-8.70**	-0.92**	CLN 2777 B (47.30)
	CLN2777F × BCT-82P	-4.35*	0.18	BCT-82P (49.00)
Equatorial diameter of fruit (cm)	CLN2777G × BCT-59	20.35**	0.15	CLN 2777 G (4.57)
	CLN2777F × BCT-59	4.17*	0.07	CLN 2777 A (5.20)
	CLN2777B × BCT-59	3.58*	0.05	BCT-59 (4.00)
Polar diameter of fruit (cm)	CLN2777G × BCT-82P	37.85**	0.33**	CLN2777G (4.50)
	CLN2777G × BCT-59	6.51**	0.06	CLN 2777 A (5.63)
	CLN2777 B × BCT-82 P	1.49	-0.14	BCT-82P (3.67)
Fruit weight (g)	CLN2777G × BCT-59	42.88**	5.91*	CLN 2777 G (69.50)
	CLN2777B × BCT-82 P	3.74*	2.16	CLN 2777 A (83.00)
	CLN2777A × BCT-82P	2.38*	-4.03*	BCT-82 P (91.50)
Fruit number per plant	CLN 2777 A × BCT-82 P	3.75*	3.62*	CLN 2777 A (34.70)
	CLN 2777 G × BCT-59	1.73	0.88	CLN 2777 G (26.70)
	CLN 2777 G × BCT-82 P	1.47	0.41	BCT-82 P (23.00)
Locules per fruit	CLN 2777 B × BCT-59	-1.95	-0.09*	CLN 2777 F (2.80)
	CLN 2777 G × BCT-82 P	-4.33*	-0.37**	CLN 2777 B (3.20)
	CLN 2777 F × BCT-59	-7.69*	-0.67**	BCT-59 (3.07)
Pericarp thickness of fruit (cm)	CLN2777F × BCT-82P	13.33**	0.06**	CLN 2777 F (0.90)
	CLN2777F × BCT-59	6.67**	0.03*	CLN 2777 B (0.61)
	CLN2777B ×BCT-59	1.61	0.01	BCT-59 (0.62)
Total soluble solids (°Brix)	CLN2777F × BCT-82P	27.71**	0.48**	CLN 2777 F (4.33)
	CLN2777G × BCT- 59	6.75*	0.23**	CLN 2777 G (3.80)
	CLN 2777 G × BCT-82 P	5.26*	0.18*	BCT-82 P (3.07)
Titratable acidity (%)	CLN2777F × BCT-82P	2.04	0.02	CLN 2777 F (0.49)
	CLN2777G × BCT-82P	2.02	0.01	CLN 2777 B (0.45)
	CLN 2777 A × BCT-82 P	2.00	0.01	BCT-82P (0.43)
Percent Disease Index (%)	CLN2777F × BCT-82P	-0.52	-1.20	CLN 2777 A (3.82)
	CLN2777G × BCT- 59	-0.56	-1.26	CLN 2777 F (7.74)
	CLN2777A × BCT-82P	-1.83	-3.10*	BCT-59 (22.77)
Fruit yield per plant (kg)	CLN2777G × BCT-59	48.10**	0.25**	CLN 2777 A (2.78)
	CLN2777A × BCT- 82P	14.74*	0.44**	CLN 2777 G (1.85)
	CLN2777G × BCT-82P	8.53	0.17*	BCT-82P (2.11)

*and ** significant at $P < 0.05$ and $P < 0.01$, respectively; Figures in parentheses indicate *per se* performance

Table 3 Maximum significant heterobeltiosis (%) observed for different quantitative characters of tomato.

Character	Maximum significant heterobeltiosis (%)	References
Total Soluble	33.33	Kumar *et al*. 2006
Solids (°Brix)	49.53	Singh *et al*. 2006
	6.09	Sharma *et al*. 2006
	106.70	Hannan *et al*. 2007b
Acidity (%)	58.12	Patil and Patil 1988
	17.37	Makesh *et al*. 2002
Fruit yield	29.89	Thakur *et al.* 2004
(kg/plant)	218.50	Akhilesh and Gulsham 2004
	99.47	Seeja *et al*. 2007
	172.00	Hannan *et al*. 2007b
	> 100.00	Girwani *et al*. 2008
	47.20	Saleem *et al*. 2009
	14.70	Gul *et al*. 2010
	98.62	Kumari *et al*. 2010

(3.74%) and CLN2777A × BCT-59 (2.38%). Significantly positive heterosis in fruit weight of tomato has also been observed by several groups (Singh *et al*. 2006; Hannan *et al*. 2007a; Salem *et al*. 2009; Gul *et al*. 2010). The maximum significant positive relative heterosis (18.60 %, 40.0%, 48.7%, and 172%) for average fruit weight was observed by Saleem *et al*. (2009), Singh *et al*. (2006), Gul *et al*. (2010) and Hannan *et al*. (2007a), respectively. Similarly, the maximum significant heterobeltiosis for fruit number/plant was exhibited by CLN 2777A × BCT-82 P (3.75%). This observation is supported by others (Kumar *et al*. 1997; Bartkaite 2001; Hannan *et al*. 2007a; Seeja *et al*. 2007). The best hybrid for number of locules/fruit was CLN2777F × BCT-59 (-7.69%) over the better-parent. Only few hybrids exhibited significantly negative heterobeltiosis that has also been observed by Mandal *et al*. (1989). Negative heterosis for fruit firmness is desirable since firm fruit keep and transport better (Atanassova *et al*. 2008). For pericarp thickness of fruit, significant positive heterobeltiosis was observed in CLN2777F × BCT-82P (13.33%) followed by CLN2777F × BCT-59 (6.67%). The observation finds support from previous studies (Singh *et al*. 2002; Sharma *et al.* 2006).

A high TSS value is the main quality component for the manufacture of different processed tomato products. Some investigators have reported that the sugar/acid ratio is important for differences in tomato flavour (Stevens 1972; Malundo *et al*. 1995). In the present investigation, good crosses showing heterobeltiosis for TSS content of fruit were CLN2777F × BCT-82P (27.71%) and CLN2777G × BCT-59 (6.75%). Similarly, the most positive heterosis for titratable acid content of fruit over the better-parent was found in CLN2777F × BCT-82P (2.04%) and CLN2777G × BCT-82P (2.02%). Significant positive heterobeltiosis for TSS content and acidity of the fruit has been observed by many researchers, reported the maximum extent of heterobeltiosis as depicted in **Table 3**.

Percent Disease Index (PDI) is one of the most important criteria in the present study to judge the tolerance level of tomato hybrids against ToLCV disease. Negative heterosis for such trait is to be considered desirable. Good crosses showing negative heterobeltiosis for this trait were CLN2777A × BCT-82P (-1.83%), CLN2777G × BCT-59 (-0.56%) and CLN2777F × BCT-82P (-0.52%). Previous results (Dharmatti *et al*. 1996, 2004; Shankarappa *et al*. 2008) also found some good heterotic cross combinations having tolerance against ToLCV in tomato.

For fruit yield/plant, the maximum significant heterobeltiosis was found in CLN2777G × BCT-59 (48.10%) followed by CLN2777A × BCT-82P (14.74%). These two hybrids also had heterosis over the better-parent for the number of fruit/plant and fruit weight. It appeared that heterosis for fruit yield/plant could be ascribed to heterosis for fruit number/plant and for fruit weight. Significant positive heterosis for early and total yield of tomato has been observed by several workers as depicted in **Table 3**.

Studies on combining ability

General combining ability studies indicated that three parents namely, CLN 2777 G, CLN 2777 A and BCT-82 P were good combiners for yield and contributing characters (**Table 3**). The present study also showed that the parents, who were the best combiners for high yield, exhibited the best combiner for fruit number per plant, fruit weight and polar diameter of fruit. This suggests that parent showing high specific combining ability and yield may be due to their high GCA for fruit number/plant or fruit weight or polar diameter of fruit.

A joint analysis was done taking together GCA and SCA effects and *per se* performance of the genotypes for different characters so as to identify suitable parents to be utilized in breeding programme. Parents involved in the best specific combinations showed high GCA effects and high *per se* performance for several characters studied. The best SCA effect for fruit yield/plant was shown by the cross CLN2777A × BCT-82P and these two parents recorded significantly positive GCA effects and *per se* performance for this character (**Table 3**). It may be suggested that parents with H × H GCA effect could produce desirable transgressive segregants in advance generation because additive genetic system present in the good combiner and complementary epistatic effect in F_1 may act in the same direction to maximize the desirable plant attributes.

Studies on gene action

The results presented in **Table 4** indicated that preponderance of additive gene action was evident in the control of characters like days to 50% flowering and PDI as their predictability ratio were more than 0.80. So, pure line selection in the advanced generations from the highly heterotic cross is suggested to improve these characters. The results are in conformity with the findings of earlier workers (Vidavsky *et al.* 1998; Hazra and Nath 2008; Ahmad *et al*. 2008). Both additive and non-additive gene action was important for the conditioning of polar diameter, pericarp thickness and acidity of the fruit as their variances due to GCA and SCA were in equal magnitude. There is possibility of deriving high performing pure line for these characters because longer proportion of non-additive effects in self-pollinated crops seems to be due to additive × additive epistatic effect. So, deferred selection would be profitable for improving these traits. Rest of the characters like fruit weight, fruit number per plant, locules per fruit, TSS and fruit yield per plant were governed by non-additive gene action which suggested heterosis breeding as the best possible option for improving the above traits of tomato. Our observations find ample support from the earlier works which are presented in **Table 5**.

Table 4 Estimates of component of variance.

Component of genetic variance	D50F[z]	ED	PD	FW	FNPP	LPF	PT	TSS	ACD	PDI	FYPP
α^2 GCA	1.08	0.025	0.07	3.68	-1.78	-0.08	0.01	0.035	0.005	28.45	-0.03
α^2 A (2 α^2 GCA)	2.16	0.05	0.14	7.36	-3.57	-0.16	0.02	0.07	0.00	56.91	-0.06
α^2 SCA (α^2 D)	0.26	-0.15	0.07	31.74	10.51	0.35	0.00	0.19	0.00	9.14	0.17
Predictability ratio (α^2 A/ α^2 A + α^2 D)	0.89	-0.33	0.66	0.18	-0.51	-0.84	0.00	0.27	0.00	0.86	-0.54

[z] D50F = days to 50% flowering; Ed = equatorial diameter; PD = polar diameter; FW = fruit weight; FNPP = fruit number per plant; LPF = locules per fruit; PT = pericarp thickness; TSS = total soluble solids; ACD = acidity; PDI = percent Disease Index; FYPP = fruit yield per plant.

Table 5 Nature of gene action governing some quantitative traits of tomato.

Character	Nature of gene action	References
Fruit weight	Non-additive	Dhaliwal *et al*. 2002
Fruit number per plant	Non-additive	Dhaliwal *et al*. 2000; Garg *et al.* 2007
Locules per fruit	Non-additive	Dhaliwal *et al*. 2004; Garg *et al.* 2007
TSS (°Brix)	Non-additive	Kumar *et al.* 1997; Dhaliwal *et al*. 2000; Dhatt *et al*. 2001; Mondal *et al*. 2009; Indu Rani and Veeraragavathatham 2011
Fruit yield per plant (kg)	Non-additive	Dhaliwal *et al*. 2000; Mahendrakar *et al*. 2005; Garg *et al*. 2007; Saidi *et al*. 2008; Singh *et al*. 2010; Indu Rani and Veeraragavathatham 2011

CONCLUSIONS

Three parents namely, CLN 2777 G, CLN 2777 A and BCT-82 P were identified as good combiners for yield and contributing characters. The present study also showed that the parents, who were the best combiner for high yield, exhibited the best combiner for fruit number per plant, fruit weight and polar diameter of fruit. Two cross combination CLN2777G × BCT-59 and CLN2777A × BCT-82P could be exploited commercially because of high yield and better quality traits coupled with low PDI values for ToLCV disease. Most of the characters under study were governed by non-additive gene action for which heterosis breeding could be recommended for improving these traits.

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