RESEARCH ARTICLE

Genetic analysis to identify good combiners for ToLCV resistance and yield components in tomato using interspecific hybridization

RAMESH K. SINGH[1,2,3], N. RAI[1]*, MAJOR SINGH[1], S. N. SINGH[2] and K. SRIVASTAVA[4]

[1]*Crop Improvement Division, Indian Institute of Vegetable Research, Banaras Hindu University, Varanasi 221 305, India*
[2]*Department of Botany, Udai Pratap Autonomous College, Varanasi 221 002, India*
[3]*AIP-USAID, Director Office and* [4]*Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi 221 005, India*

Abstract

The interspecific hybridization for tomato leaf curl virus (ToLCV) resistance was carried out among 10 genetically diverse tomato genotypes (diversified by 50 SSR markers). Among the 10 parents, four susceptible cultivars of *Solanum lycopersicum* were crossed with six resistant wilds, such as *S. pimpinellifolium*, *S. habrochaites*, *S. chemielewskii*, *S. ceraseforme, S. peruvianum* and *S. chilense* in a line × tester mating design. All the 24 hybrids and their parents were grown in the field and glasshouse conditions to determine the general-combining abilities (GCA) and specific-combining abilities (SCA). The variances due to SCA and GCA showed both additive and nonadditive gene effects. Based on GCA estimates, EC-520061 and WIR-5032 were good general combiners while based on SCA estimates, PBC × EC-520061 and PBC × EC-521080 were best specific combiners for coefficient of infection and fruit yield per plant in both the environments. These lines could be selected and utilized in ToLCV resistance and high yield breeding programme for improving the traits.

[Singh R. K., Rai N., Singh M., Singh S. N. and Srivastava K. 2014 Genetic analysis to identify good combiners for ToLCV resistance and yield components in tomato using interspecific hybridization. *J. Genet*. **93**, 623–629]

Introduction

Tomato (*S. lycopersicum*) is a herbaceous, usually sprawling plant of *Solanum* species that is typically cultivated for human consumption, like vegetables as well as fruits (Chomdej *et al.* 2008). Generally, wild species of tomato are polymorphic and most of the interspecific hybrids expressed their morphological attributes from wild taxa over the *lycopersicum* types (Chen *et al.* 2011). There is tremendous morphological variation among and within the species which provides a rationale to make the interspecific hybridization a success. If one accession of a species is not compatible, the other may be compatible and can be hybridized so there is a possibility of getting hybrid seeds in some combinations. F_1 hybrids of *S. lycopersicum* × *S. habrochaites f. glaboratum*, *S. lycopersicum* × *S. pimpinellifolium* and *S. lycopersicum* × *S. cheesmanii* were morphologically almost similar to their respective wild parents (Kalloo and Banerjee 1989; Chen *et al.* 2011). Molecular diversity through SSRs markers has been recently made achieving tools for identifying the interspecific relationship (Frary *et al.* 2005). Many genetic maps consisting molecular markers have been developed in recent years for many crop plants (Wu *et al.* 2009; Lioi and Galasso 2013).

Since ages, tomato leaf curl virus disease (ToLCV) has been a severe problem in tomato production causing up to 100% yield losses worldwide, especially in those areas where tomato is grown commercially (Singh *et al.* 2010; Banerjee and Kalloo 1987). To date no cultivars/hybrids are stable for resistance to ToLCV for a long duration, except for a number of wild species and their hybrids (Kalloo and Banerjee 1989; Chen *et al.* 2011). The quantitative characteristics and ToLCV resistance are controlled by a large number of genes and are strongly influenced by the environmental factors (Ahmad *et al.* 2009). Therefore, it is desirable to make a strict individual plant selection on quantitative characters which could be useful for combining ability (CA). Although, combining ability studies have been more reliable in providing useful information for the selection of diverse parents with regard to performance of the resistant hybrids, while elucidating the nature and magnitude of various types of gene effects involved in the expression of quantitative traits (with

*For correspondence. E-mail: nrai1964@gmail.com.

Keywords. tomato; ToLCV; molecular diversity; interspecific crosses; combining ability.

good-quality traits), production of resistant hybrids has been limited due to lack of superior combiners (Ahmad *et al.* 2009). Genetic analysis provides a guideline to assess the relative breeding potential of parents or identify best combiners in crop (Ahmad *et al.* 2009), which can be utilized either to exploit the combining ability in F_1's or accumulate fixable genes to evolve a variety. Entire genetic variability observed in the analysis for each trait was partitioned into components, i.e. GCA and SCA as defined by Sprague (1966) with additive and nonadditive gene actions, respectively. In this study, the diverse tomato parents are used for interspecific hybridization to identify good combiners for ToLCV resistance and yield components under two different environments.

Materials and methods

The experimental materials comprised of 10 diverse tomato genotypes of different species. Four cultivars (Punjab Chhuhara (PBC), Kashi Vishesh (H-86), Hissar Anmol (H-24) and Kashi Anupam (DVRT-2) of *S. lycopersicum* showed determined plant growth, high yield with superior fruit quality; while six wild species (EC-521080 (*S. pimpinellifolium*), EC-520061 (*S. habrochaites*), EC-520049 (*S. chmielewskii*), EC-528372 *(S. cerasiforme*), WIR-3957 (*Solanum peruvianum*) and WIR-5032 (*S. chilense*)) displayed vigourous plant growth, high fruit yield and resistance/tolerance to many biotic and abiotic stresses. These plants were selected from the germplasm stock and maintained at the Indian Institute of Vegetable Research (IIVR), Varanasi, India.

Genetic diversity analysis

Genomic DNA was isolated from young leaves of 10 parental lines using the modified DNA isolation cetyltrimethyl ammonium bromide (CTAB) method as suggested by Doyle and Doyle (1990). DNA samples were purified and quantified for the PCR amplification of SSR primers. A set of 50 SSR markers of tomato were selected from different chromosomal loci of Sol Genomic Network (http://www.sgn.cornell.edu) database for diversity analysis among 10 diverse parental lines. Cluster analysis was carried out on standardized data based on the Euclidian distance coefficient and unweighted pair group method with arithmetic means (UPGMA) using NTSYS-pc ver. 2.11a, an advanced version of 2.02 (Rohlf 1994).

Hybridization and evaluation

A crossing programme was conducted among four cultivars × six wild accessions in 'line × tester' mating design. Twenty-four interspecific hybrids were obtained through manual pollination during the months of October and November, 2006. The 34 genotypes (24 F_1's + 10 parents) of tomato were considered for the experiment and evaluated in two (field and glasshouse) environments during the months of October–February of 2007–2008. Twenty-one day-old seedlings were transplanted in a randomized complete block design (RCBD) with three replications in a well-prepared field. Each replication included 30 plants at a determined spacing of 45 cm (plant to plant) and 60 cm (row to row). The crop was raised with standard agrotechniques, without the application of any insecticide and fungicide. The recommended dosage and method of application of manures and fertilizers were used. Plants were examined for symptoms which appeared at 30, 60 and 90 days after transplanting (DATP). On the other hand, in glasshouse conditions (mass and cage inoculation) symptoms appeared at 15, 30, 45 and 60 DATP, as reported by Banerjee and Kalloo (1987) and Singh *et al.* (2010). In mass and cage inoculation condition, 24 F_1's and 10 parental tomato seedlings of each genotype were inoculated at two-week intervals using high pressure of whiteflies. These whiteflies used were collected from previous cultures already maintained in the glasshouse of IIVR, Varanasi. Plants were examined at weekly intervals for ToLCV symptom, expression and disease incidence was observed every 15th day interval which continued for up to 60 days after planting.

Measurement and statistical analysis

For data observation, five plants were randomly selected from each replication, avoiding the border row and were tagged before flowering to collect the data. The observations were recorded for only those traits which were affected by ToLCV disease e.g., coefficient of infection (CI%), plant height (PH) in cm, number of fruits per plant (NFPP), average fruit weight (AFW) in g and fruit yield per plant (FYPP) in kg.

The symptoms of disease was scored on 0–5 scale with some modifications (Banerjee and Kalloo 1987). The coefficient of infection was calculated by the following formulae: (PDI = (total number of diseased plants/total number of observed plants) × 100)

$$\mathrm{CI} = \mathrm{PDI} \times \mathrm{RV}.$$

RV is categorized by scoring on 0 = 0, 1 = 0.12, 2 = 0.25, 3 = 0.50, 4 = 0.75 and 5 = 1.00. Where PDI, per cent disease incidence; CI, coefficient of infection; RV, response value. The mean data was subjected to combined ability analysis of variance. Combining ability analysis was carried out according to Singh and Chaudhary (1979) fixed effect model using the following formula:

$$X_{ijk} = \mu + G_i + G_j + S_{ij} + E_{ijk},$$

where μ, general mean; G_i, GCA effect of ith line (female parent); G_j, GCA effect of jth tester (male parent); $S_{ij,}$ SCA effects of hybrids with the ith lines and jth tester; E_{ijk}, error associated with the ith observation at the plot; i 1, 2... (*l*) (number of lines), j =1, 2 . . . t (number of testers), k = 1, 2, 3 . . . r (number of replications).

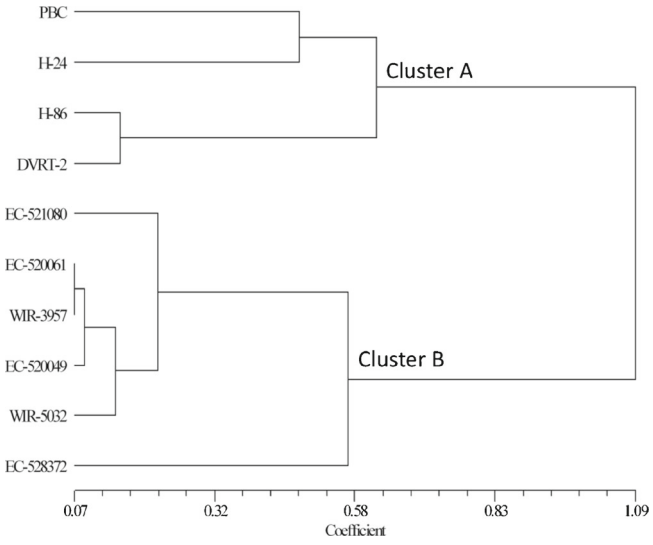

Figure 1. UPGMA dendrogram of 10 tomato genotypes generated using SSR markers.

Results and discussion

A cluster analysis was carried out among 10 tomato accessions using SSR markers from different chromosomal loci (figure 1). Out of 50 SSR markers, 16 (32%) failed to amplify the expected PCR fragments, 23 (46%) amplified monomorphic banding patterns, while the remaining 11 (22%) generated polymorphic banding patterns (table 1). The effects of morphological plasticity cluster were different in SSR analysis (Frary *et al.* 2005), which is the capacity of the organisms with different genotypes to vary in varying phenotypic and genotypic conditions and parallel evolution. A total of 116 alleles were detected by these polymorphic markers. The polymorphic information content (PIC) of the markers range from 0.33 to 0.81 with an average 0.47. The SSR304 marker gave the highest PIC of 0.81, the SSR350 had the lowest PIC of 0.33. The low correlation identified is due to a large portion of the variation detected by molecular markers being nonadaptive. Therefore, it is not subjected to either natural or artificial selection as compared with the phenotypic characters, which are also directly influenced by the environment (Vieira *et al.* 2007). The coefficient range was 0.07–1.09. The dendogram was generated in two clusters of major groups, i.e., cluster 'A' and cluster 'B'. Cluster 'A' consisted of cultivars (Punjab Chhuhara, H-24, H-86 and DVRT-2) having marketable yield quality, determinate plant height and susceptibility to ToLCV disease. Even cluster 'B' consisted of six wild species (EC-521080, EC-520061, EC-520049, EC-528372, WIR-3957 and WIR-5032) showing indeterminate plant growth and resistance to ToLCV disease. The Mantel test for association among the matrices derived from SSR and morphological data indicated a poor matrix correlation, showing that these methods discriminated very differently among the *S. lycopersicum* and wilds species (Chen *et al.* 2011).

Analysis of variances for combining ability (GCA and SCA) was found to be highly significant for all the characters in both field and glasshouse environments (table 2). Significant differences were observed in parents, parents vs crosses and 'line × tester' interactions among all the characters, indicating that both additive and nonadditive gene effects played significant roles for the expression of these characters

Table 1. Details of 11 polymorphic markers and their sequences used in diversity analysis of 10 tomato accessions.

	Primers	Forward (F) and reverse (R) primer sequences	Annealing temperature (°C)	Number of bands	Number of polymorphic bands	Polymorphic %	Amplified alleles size (bp)
1	SSR 63	F:5′-CCA CAA ACA ATT CCA TCT CA-3′ R:5′-GCT TCC GCC ATA GTG ATA CG-3′	53.1	4	2	50	200–220
2	SSR 67	F:5′-GCA CGA GAC CAA GCA GAT TA-3′ R:5′-GGG CCT TTC CTC CAG TAG AC-3′	56.0	9	5	55.56	1000–900
3	SSR 73	F:5′-TGG GAA GAT CCT GAT GAT GG-3′ R:5′-TTC CCT TTC CTC TGG ACT CA-3′	54.6	8	8	100	900–600
4	SSR 104	F:5′-TTC CAT TTG AAT TCC AAC CC-3′ R:5′-CCC ACT GCA CAT CAA CTG AC-3′	53.7	5	3	60	900–1100
5	SSR 117	F:5′-AAT TCA CCT TTC TTC CGT CG-3′ R:5′-GCC CTC GAA TCT GGT AGC TT-3′	54.5	10	10	100	158–186
6	SSR 128	F:5′-GGT CCA GTT CAA TCA ACC GA-3′ R:5′-TGA AGT CGT CTC ATG GTT CG-3′	54.7	4	2	50	193–323
7	SSR 276	F:5′-CTC CGG CAA GAG TGA ACA TT-3′ R:5′-CGA CGG AGT ACT TCG CAT TT-3′	55.15	9	6	66.67	200–150
8	SSR 304	F:5′-TCC TCC GGT TGT TAC TCC AC-3′ R:5′-TTA GCA CTT CCA CCG ATT CC-3′	55.65	11	11	100	910–605
9	SSR 350	F:5′-GGA ATA ACC TCT AAC TGC GGG-3′ R:5′-CGA TGC CTT CAT TTG GAC TT-3′	54.2	9	4	44.44	240–265
10	SSR 557	F:5′- GCC ACA AGA AAC ATT GCT GA-3′ R:5′- TAC GCG CAC GTG CAT AAA TA-3′	54.45	12	7	58.33	540–230
11	SSR 603	F:5′-GAA GGG ACA ATT CAC AGA GTT TG-3′ R:5′-CCT TCA ACT TCA CCA CCA CC-3′	55.0	10	8	80	215–294

Table 2. Analysis of variance for CA and A, and D components of genetic variance for two environments (field and glasshouse).

Characters ↓	Sources → / Environments ↓	Analysis of variance for CA						Estimate of GCA and SCA variance and A and D components of genetic variance					
								σ^2GCA for parents					
		Replication	Crosses	Lines effect	Testers effect	Line × tester effect	Error	Female	Male	σ^2SCA	σ^2A	σ^2D	σ^2D/σ^2A
DF →		2	23	3	5	15	46						
CI (%)	Field	0.113	13.876	2.972	56.874	1.724	0.047	0.069	4.596***	1.880***	3.760	0.551	6.824
	Glasshouse	0.031	14.646	11.356	51.274	3.094	0.040	0.459*	4.015***	1.017***	3.763	1.017	3.701
PH (cm)	Field	83.068	5933.087	3562.757	19323.640	1974.302	185.188	88.248	1445.778***	586.010***	1262.520	586.010	2.154
	Glasshouse	210.470	5619.422	2951.695	20962.483	1038.614	176.561	106.282	1660.322***	291.890	1455.797	291.890	4.988
NFPP	Field	16.794	19926.198	4379.241	46880.198	14050.923	70.842	−537.316	2735.773**	4288.600	1543.839	4288.600	0.360
	Glasshouse	356.727	20440.840	13981.479	52708.353	10976.874	522.015	166.923	3477.624**	3406.027***	2982.406	3406.027	0.876
AFW (g)	Field	1.912	216.304	165.455	754.505	47.074	5.479	6.577	58.953***	−12.168	55.054	−12.168	−4.524
	Glasshouse	9.032	114.840	107.055	352.926	37.035	8.025	3.890	26.324***	8.482**	25.727	8.482	3.033
FYPP (kg)	Field	0.100	3.360	3.293	7.010	2.156	0.203	0.063	0.404*	0.632***	0.399	0.632	0.632
	Glasshouse	0.272	1.673	2.584	2.254	1.296	0.492	0.072	0.798	0.295**	0.150	0.295	0.508

*Significant at $P = 0.05$ level; **significant at $P = 0.01$ level; ***significant at $P = 0.001$ level; CI, coefficient of infection; PH, plant height; NFPP, number of fruits per plant; AFW, average fruit weight; FYPP, fruit yield per plant; DF, degree of freedom.

(Saleem *et al.* 2009). Lines exhibited significant variation for CI, AFW, FYPP whereas, testers were significant for CI, PH, NFPP, AFW and FYPP in both field and glasshouse conditions. Within the GCA effects female parents exhibited nonsignificant variation for each trait, while the male parents exhibited high significant values for each trait except FYPP. This may be due to female parents belonging to the cultivars of *S. lycopersicum* which do not tolerate disease pressure and are unable to express their vegetative and fruit characters in glasshouse condition (Singh *et al.* 2010). The SCA variances were also significant in both the environments for CI, PH, NFPP and AFW at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$%, respectively. Similar results were shown by Hannan *et al.* (2007) in their experiments.

The value of σ^2GCA female was less than that of σ^2GCA male for all the characters (table 2), thus indicating that the male parent was dominant on female for all characters. The σ^2GCA female was less than σ^2SCA though σ^2SCA was less than σ^2GCA male for all characters except NFPP, indicating predominance of both types of additive and nonadditive gene effects for the characters. The σ^2GCA male showed significance in both field and glasshouse environments for all characters, except FYPP, which was nonsignificant in glasshouse condition but significant in field condition at $P \leq 0.05$ level (table 2). However in case of σ^2SCA, all characters were significant in field condition, except NFPP and AFW, while in glasshouse only PH was nonsignificant and all the remaining characters were significant at <0.001. As per results, the ratio of σ^2GCA male/σ^2SCA was <1 (NFPP) and equal to 1 (FYPP), and the degree of dominance $(\sigma^2\text{D}/\sigma^2\text{A})^{1/2}$ was either equal to 1 or >1 (CI, PH and AFW), showing predominance for nonadditive gene effect, as recorded by Saleem *et al.* (2009). Contrary to this, the ratio of σ^2GCA male / σ^2SCA was >1 (CI, PH and AFW) and degree of dominance $(\sigma^2D/\sigma^2\text{A})^{1/2}$ was <1 (NFPP and FYPP), suggesting predominance of additive type gene action, as followed by Hannan *et al.* (2007).

GCA and SCA variances with each parent play a significant role in the choice of parents. The GCA component is primarily a function of the additive genetic variance. A parent with higher positive significant GCA effects is considered as a good general combiner. In the present study, all the female and male parents displayed highly positive significant values for CI, except H-86, H-24 and EC-520061 (table 3). These parents were found to exhibit negative significance in both field and glasshouse conditions, proving to be a good combiner for disease resistance as negatively significant CI value showed high disease resistance capacity of parents (Singh *et al.* 2011). For the plant height (PH), the parents H-86, H-24 and EC-520061 expressed high and positive significant values in both environments, while the remaining parents displayed either negative significance or nonsignificance, and this is also concordant with Hannan *et al.* (2007). Similarly, for the number of fruit per plant (NFPP), only two parents EC-521080 and EC-520061 showed highly positive and

Table 3. GCA effect in ToLCV (CI) and yield components of 10 parents (line vs tester) in two environments (field and glasshouse).

Sources→		Female parents				SE (GCA)	Male parents					SE (GCA)
Characters↓	Environments↓	PBC	H-86	H-24	DVRT-2	Line	EC-521080	EC-520061	EC-520049	EC-527372	WIR-3957	WIR-5032	Tester
CI (%)	Field	0.216**	−0.454***	−0.209**	0.446 ***	0.063	2.073 ***	−3.098***	−2.369***	0.656***	1.297***	1.442***	0.077
	Glasshouse	0.938***	−0.462***	−0.824***	0.349***	0.049	1.463***	−4.154***	0.679***	0.771***	0.888***	0.354***	0.061
PH (cm)	Field	−12.443***	12.013**	12.351***	−11.921**	3.466	−11.407*	80.776***	−16.915***	−24.549***	−6.257	−21.649***	4.245
	Glasshouse	−7.193*	14.507***	6.418*	−13.732***	3.009	−1.585	81.815***	−5.601	−22.160***	−17.893***	−34.576***	3.685
NFPP	Field	15.086	10.319	−6.658	−18.747*	8.114	94.064***	39.989***	−20.936*	−90.928***	−19.278	−2.911	9.938
	Glasshouse	40.894***	−7.967	−21.578**	−11.350	6.493	65.406***	92.464***	−23.119**	−82.053***	−41.819***	−10.878	7.952
AFW (g)	Field	−4.345*	0.947	0.691	2.706	2.155	**−7.239****	−6.143*	−4.922	13.397 ***	0.394	4.513	2.639
	Glasshouse	−2.754**	3.063***	0.490	−0.799	0.802	**−6.288****	−3.838***	−1.629	9.313***	0.754	1.688	0.983
FYPP (kg)	Field	−0.622***	0.139	0.128	0.355**	0.121	**−0.449****	−0.554***	−0.791***	0.523***	0.041	1.229***	0.148
	Glasshouse	−0.294	0.550***	−0.061	−0.194	0.151	**−0.631****	0.244	−0.297	0.361	−0.164	0.486*	0.185

*Significant at $P = 0.05$ level; **significant at $P = 0.01$ level; ***significant at $P = 0.001$ level; CI, coefficient of infection; PH, plant height; NFPP, number of fruits per plant; AFW, average fruit weight; FYPP, fruit yield per plant.

significant values in both the environments while the remaining parents exhibited less or nonsignificant values. These findings were supported by the study of Hannan *et al.* (2007). The average fruit weight (AFW) displayed a negative or nonsignificant GCA value for all parents, except H-86 (significant in glasshouse) and EC-528372 (significant in field and glasshouse). This is in accordance with the good combiner for fruit weight studied by Saleem *et al.* (2009) and Hannan *et al.* (2007). For the fruit yield per plant (FYPP), none of the parents were found significant in both the environments, except WIR-5032. They expressed their significant value for GCA either in field or in glasshouse condition. The parents, DVRT-2 and EC-528372, were significant in field condition, while H-86 was significant in glasshouse condition (table 3) and thus, these parents may be good combiners for yield capacity. These results are in accordance with the studies of Saleem *et al.* (2009) and Hannan *et al.* (2007). Specific combining ability (SCA) is based on nonadditive gene effect. Normally, SCA effects do not contribute much to the improvement of self-pollinated crops. As per the results, most of the crosses showed SCA values were either nonsignificant or negative significant for various characters. In the present study, low and negative significant CI values were found in the crosses, i.e., PBC × EC-520049, PBC × EC-520061, H-24 × EC-521080, DVRT-2 × EC-528372 and H-86 × WIR-5032 during both field and glasshouse trials (table 4). These crosses may be good combiners for progeny selection against ToLCV disease resistance, similar to the results of Singh *et al.* (2011). On the other hand, with regard to the plant height (PH), no cross combination could show a significant value in both field and glasshouse environments. These crosses showed significant values either in field or in glasshouse like, PBC × EC-520061 (significant in field) followed by DVRT-2 × EC-520061 (significant in field) and H-24 × EC-520061 (significant in glasshouse). Similar results of best cross combiners for PH was reported by Ahmad *et al.* (2009) and Hannan *et al.* (2007). For FNPP, chronologically high and positive significant values were found in the crosses of PBC × EC-521080, H-24 × WIR-3957, H-86 × EC-520049, PBC × EC-520061 and DVRT-2 × WIR-5032 in both field and glasshouse environments. The fruit yield was high in most crosses, this may be due to the use of wild male parents since they bear more and unexpected number of fruits as reported by Ahmad *et al.* (2009). Among the 24 F_1's, AFW did not show any positive significant values in any cross combinations in both the environments, except PBC × WIR-3957 (significant in glasshouse). This result may be a guide to any breeder who avoids developing the AFW characters by using interspecific crosses. Poor average fruit weight was reported by many workers (Ahmad *et al.* 2009; Saleem *et al.* 2009). Besides disease resistance, fruit yield was also an interesting character for developing a good hybrid by tomato breeders. In the present study, the SCA effect was negative and nonsignificant in most of the crosses for yield traits. No cross combinations exhibited significant results on yield for SCA effects in glasshouse. Only one cross combination (DVRT-2 ×

Table 4. SCA effect of 24 tomato hybrids in line × tester analysis for ToLCV (CI) and yield components in two environments (field and glasshouse).

Characters→	CI (%)		PH (cm)		NFPP		AFW (g)		FYPP (kg)	
Entries↓ Environments →	Field	Glasshouse	Field	Glasshouse	Field	Glasshouse	Field	Glasshouse	Field	Glasshouse
PBC × EC-521080	1.038***	1.088***	−6.632	−5.965	155.197***	109.622***	3.012	0.304	1.411***	0.569
PBC × EC-520061	−0.231	−0.963***	29.418**	3.268	−45.761*	60.864***	1.969	−2.146	−0.094	−0.406
PBC × EC-520049	−0.637***	−1.396***	17.976*	10.151	−35.403	−64.086***	2.635	−1.721	0.116	−0.764*
PBC × EC-528372	−0.332*	1.646***	−23.790**	−18.024*	−8.711	−29.153	−8.358	−1.729	−0.701*	−0.022
PBC × WIR-3957	0.577***	−0.471***	−2.715	3.743	−51.061*	−46.853**	4.239	6.163**	0.185	0.869*
PBC × WIR-5032	−0.415**	0.096	−14.257	6.826	−14.261	−30.394	−3.497	−0.871	−0.917**	−0.247
H-86 × EC-521080	0.218	0.087	−5.721	−4.632	−31.569	−27.383	−1.376	−1.913	−0.313	−0.408
H-86 × EC-520061	0.542***	0.471***	6.796	19.935**	45.739*	−11.842	−1.666	2.104	0.185	0.983*
H-86 × EC-520049	−0.204	0.971***	9.121	−3.315	64.397**	73.208***	−0.040	−3.071	0.812**	0.258
H-86 × EC-528372	0.431**	−0.421**	3.154	−5.024	−43.644*	−5.992	1.144	4.721*	−0.912**	0.067
H-86 × WIR-3957	−0.046	−0.738***	15.296	−2.157	−4.994	−7.225	−2.689	−4.421*	−0.253	−0.975*
H-86 × WIR-5032	−0.941***	−0.371**	−28.646**	−4.807	−29.928	−20.767	4.628	2.579	0.482	0.075
H-24 × EC-521080	−0.790***	−1.118***	−11.326	−1.810	−34.992	−6.172	−0.714	−0.707	−0.352	−0.097
H-24 × EC-520061	0.007	0.765***	13.224	20.857**	−40.650*	−81.597***	3.976	2.576	0.430	−0.106
H-24 × EC-520049	−0.415**	0.599***	−41.285***	−26.593***	−26.792	−0.281	−2.101	5.235*	−0.700*	0.769*
H-24 × EC-528372	0.740***	−0.093	14.482	14.732	8.767	6.886	3.219	−1.440	0.359	−0.322
H-24 × WIR-3957	−0.211	0.724***	3.057	4.032	100.650***	80.886***	−3.197	−3.115	0.748*	0.403
H-24 × WIR-5032	0.670***	−0.876***	21.849*	−11.218	−6.983	0.278	−1.183	−2.549	−0.484	−0.647
DVRT-2 × EC-521080	−0.465**	−0.057	23.679**	12.407	−88.636***	−76.067***	−0.922	2.315	−0.746*	−0.064
DVRT-2 × EC-520061	−0.318*	−0.274*	−49.438***	−44.060***	40.672*	32.575*	−4.279	−2.535	−0.521	−0.472
DVRT-2 × EC-520049	1.256***	−0.174	14.188	19.757*	−2.203	−8.842	−0.493	−0.443	−0.228	−0.264
DVRT-2 × EC-528372	−0.839***	−1.132***	6.154	8.315	43.589*	28.258	3.994	−1.551	1.255***	0.278
DVRT-2 × WIR-3957	−0.320*	0.485***	−15.638	−5.618	−44.594*	−26.808	1.648	1.374	−0.679*	−0.297
DVRT-2 × WIR-5032	0.685***	1.151***	21.054*	9.199	51.172*	50.883**	0.052	0.840	0.919**	0.819*
SE±	0.1535	0.121	8.491	7.370	19.876	15.904	5.278	1.965	0.295	0.371

*Significant at $P = 0.05$ level; **significant at $P = 0.01$ level, ***significant at $P = 0.001$ level; CI, coefficient of infection; PH, plant height; NFPP, number of fruits per plant; AFW, average fruit weight; FYPP, fruit yield per plant.

WIR-5032) was found significant in both the environments, while the remaining crosses showed significant SCA in field condition only, e.g. PBC × EC-521080, DVRT-2 × EC-528372 and H-86 × EC-520049. The best cross combiners for fruit yield were reported in many studies (Hannan *et al.* 2007; Ahmad *et al.* 2009; Saleem *et al.* 2009).

Based on results, it was concluded that the following parents were good general combiners for various characters namely, H-86 (CI, PH, AFW, FYPP), H-24 (CI, PH), DVRT-2 (FYPP), EC-521080 (FNPP), EC-520061 (PH, CI, FNPP), EC-528372 (AFW, FYPP) and WIR-5032 (FYPP). In case of SCA most of the characters were found to be better in various crosses namely CI (PBC × EC-520049, H-24 × EC-521080, DVRT-2 × EC-528372 and PBC × EC-520061), PH (PBC × EC-520061, DVRT-2 × EC-520061 and H-24 × EC-520061), AFW (PBC × WIR-3957), NFPP (PBC × EC-521080, H-24 × WIR-3957 and H-86 × EC-520049) and FYPP (PBC × EC-521080, DVRT-2 × WIR-5032, DVRT-2 × EC-528372 and H-86 × EC-520049). These parents and hybrids could be utilized as good combiners and isolated to obtain desirable segregates for improving respective characters. This study was suggested for a breeding programme for which, the advantages of both types of variances, namely additive and nonadditive are chosen. Due to the presence of additive genetic variance, disease resistant capacity can be improved which may prove highly useful in yield improvement.

References

Ahmad S., Quamruzzaman A. K. M. and Nazimuddin M. 2009 Combining ability estimates of tomato (*Solanum lycopersicum*) in late summer. *SAARC J. Agri.* **7**, 43–56.

Banerjee M. K. and Kalloo G. 1987 Sources and inheritance of resistant to leaf curl virus in *Lycopersicon*. *Theor. Appl. Genet.* **73**, 707–710.

Chen H., Fu R. and Li X. 2011 Tomato yellow leaf virus (TYLCV): the structure, ecotypes and the resistance germplasm resources in tomato. *Afr. J. Biotech.* **10**, 13361–13367.

Chomdej O., Whankaew S., Chatchawankanpanich O., Kositratana W. and Chunwongse J. 2008 Resistance to tomato yellow leaf curl Thailand virus, TYLCTHV-[2] from *Solanum habrochaites* accession (L06112) in F_1 and BC_1F_1 generations. *Songklanakarin J. Sci. Technol.* **30**, 441–446.

Doyle J. J. and Doyle J. L. 1990 A rapid DNA isolation procedure from small quantity of fresh leaf material. *Phytochem. Bull.* **119**, 11–15.

Frary A., Xu Y., Liu J., Mitchell S., Tedeschi E. and Tanksley S. D. 2005 Development of a set of PCR-based anchor markers encompassing the tomato genome and evaluation of their usefulness for genetics and breeding experiments. *Theor. Appl. Genet.* **111**, 291–312.

Hannan M. M., Biswas M. K., Ahemed M. B., Hossain M. and Islam R. 2007 Combining ability analysis of yield and yield components in tomato (*Lycopersicum esculentum* Mill.). *Turk. J. Bot.* **31**, 559–563.

Kalloo G. and Banerjee M. K. 1989 Transfer of tomato leaf curl virus resistance from *Lycopersicon hirsutum f. glabraum* to *L. esculetum*. *Plant Breed.* **105**, 156–159.

Lioi L. and Galasso I. 2013 Development of genomic simple sequence repeat markers from an enriched genomic library of grass pea (*Lathyrus sativus* L.). *Plant Breed.* **132**, 649–653.

Rohlf F. J. 1994 NTSYS-PC: numerical taxonomy and multivariate analysis system version 2.2. State University of New York, Stony Brook, NY, USA.

Saleem M. Y., Asghar M., Haq A., Rafique T., Kamran A. and Khan A. A. 2009 Genetic analysis to identify suitable parents for hybrid seed production in tomato (*Lycopersicon esculentum* Mill.). *Pak. J. Bot.* **41**, 1107–1116.

Singh R. K. and Chaudhary B. D. (ed.) 1979 *Biometrical methods in quantitative genetics analysis*. Kalyani Publishers, New Delhi, India.

Singh R. K., Rai N. and Singh S. N. 2010 Response of tomato genotypes to tomato leaf curl virus. *Ind. J. Agri. Sci.* **80**, 755–758.

Singh R. K., Rai N., Singh M., Singh A. K., Kumar P., Singh R. and Singh S. N. 2011 Molecular diversity in tomato genotypes and their exploitation of heterosis against tomato leaf curl virus (ToLCV) and yield traits. Abstract in National Symposium on Vegetable Biodiversity, pp. 47–48. Department of Horticulture, Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur, India.

Sprague, G. F. (ed.) 1966 *Plant breeding*. Iowa State University Press, Ames, USA.

Vieira E., Carvalho F., Bertan I., Kopp M., Zimmer P., Benin G. *et al.* 2007 Association between genetic distances in wheat (*Triticum aestivum* L.) as estimated by AFLP and morphological markers. *Gen. Mol. Biol.* **30**, 392–399.

Wu F., Eannetta N. T., Xu Y., Durrett R., Mazourek M., Jahn M. M. and Tanksley S. D. 2009 A COSII genetic map of the pepper genome provides a detailed picture of synteny with tomato and new insights into recent chromosome evolution in the genus *Capsicum*. *Theor. Appl. Genet.* **118**, 1279–1293.

Received 5 September 2013, in revised form 17 December 2013; accepted 26 February 2014
Published online: 10 November 2014