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Combining Ability and Gene Action for Yield and Processing Qualities in F_1 Tomato (*Lycopersicon esculentum* Mill.) Hybrids

C. Indu Rani[1*] • D. Veeraragavathatham[2]

[1] Department of Food and Agricultural Process Engineering, AEC & RI, TNAU, Coimbatore- 641 003, TamilNadu, India
[2] Horticultural College and Research Institute, TNAU, Coimbatore-641 003, TamilNadu, India

Corresponding author: * **indunathan@gmail.com**

ABSTRACT

Investigations were undertaken to study the combining ability and gene action for yield and processing qualities in F_1 hybrids of tomato (*Lycopersicon esculentum* Mill.) by studying 80 hybrids that were developed, involving 14 parents mated in a line × tester fashion (both direct and reciprocal crosses). Among the parents, PT 4716A was judged as the best general combiner for the characters viz., plant height and number of fruits/plant and SL 120 was judged as the best general combiner for fruit weight and yield. The hybrids CLN 2026C × SL120, CLN 2026E × SL 120, LE 812 × SL 120 and CLN 1464A × SL 120 were judged as being the best specific combiners for yield and processing qualities. SCA variance was higher than GCA variance for all the characters indicating a better role of the non-additive type of gene action, thus emphasizing the importance of heterosis breeding to improve all characters studied.

Keywords: heterosis breeding, hybrids, line x tester, tomato

INTRODUCTION

Tomato (*Lycopersicon esculentum* Mill.) is one of the most economically important vegetables in Asia. It tops the list of industrial crops because of its outstanding processing qualities. Tomatoes are mainly used as a food ingredient. The fruits are consumed raw, cooked or processed as juice, ketchup, sauce, paste, puree, etc. It is a good source of Vitamins A, B and C. In the recent past, exploitation of hybrid vigour and selection of parents on the basis of combining ability and gene action have been important breeding approaches in crop improvement. In tomato attention should be given to the breeding and inheritance of traits (Hannan *et al*. 2007).

Identification and selection of flexible parental lines are required to be used in any hybridisation programme to produce genetically modified and potentially rewarding germplasm by assembling fixable gene effects more or less in a homozygous line. Information pertaining to different types of gene action, relative magnitude of genetic variance, and combining ability estimates are important and vital parameters to mould the genetic makeup of tomato crop (Hannan *et al*. 2007).

The future of processing tomato in India is bright due to the rapidly increasing domestic consumption and export potential. This has made it necessary to evolve varieties with high productivity and processing qualities. A programme to combine good yield with favourable processing qualities thus assumes great importance. The line × tester analysis provides information about the general combining ability (GCA) of parents and specific combining ability (SCA) of hybrids and is also helpful in estimating the various types of gene effects. Exploitation of hybrid vigour is one of the important means by which crop yields can be increased. In such an attempt, it is important to select desirable parents and combining ability analysis would help this objective.

Genetic analysis provides a guideline for the assessment of relative breeding potential of the parents or identify best combiners in crops (Khattak *et al.* 2004; Weerasingh *et al.* 2004; Sulodhani Devi *et al*. 2005; Saleem *et al*. 2009) which could be utilized either to exploit heterosis in F_1 or the accumulation of fixable genes to evolve variety.

Identification and selection of flexible parental lines are required to be used in any hybridisation programme to produce genetically modified and potentially rewarding germplasm by assembling fixable gene effects more or less in a homozygous line. Information pertaining to different types of gene action, relative magnitude of genetic variance, and combining ability estimates are important and vital parameters to mould the genetic makeup of tomato crop. This important information could prove an essential strategy to tomato breeders in the screening of better parental combinations for further enhancement (Hannan *et al*. 2007). The analysis of combining ability helps the breeder in selecting suitable genotypes as parents for hybridization and for characterizing the nature and magnitude of gene action in the expression of particular trait.

GCA refers to the average performance of a line in a series of crosses where as SCA is a deviation from the performance predicted on the basis of general combining ability. In the recent past, exploitation of hybrid vigour and selection of parents on the basis of combining ability and gene action have been found important breeding approaches in crop improvement. The entire genetic variability observed in the analysis for each trait was partitioned into its components, i.e. general (GCA) and specific combining ability (SCA) as defined by Sprague (1966) and reciprocal effects as sketched by Griffing (1956). They stated that GCA effects were due to additive type of gene action and GCA effects were due to non-additive (dominant or epistatic) gene action. Several studies of combining ability for yield components are available in tomato. Some researchers found the predominance of GCA to be more important than that of SCA (Sharma *et al*. 1999; Bhatt *et al*. 2001), while others suggested that SCA was more important (Ortiz 2004; Biswas *et al*. 2005; Hannan *et al*. 2007).

In the light of above, an attempt was therefore made to study the GCA and SCA of the parents and hybrids and to elicit information on the nature of gene action for yield and its components.

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MATERIALS AND METHODS

Parents numbered 1 to 10 were used as female parents (lines) and 11 to 14 were used as male parents (testers). Ten lines and four testers were crossed in a line × tester fashion (Kempthrone 1957) to incorporate processing characters to nematode resistant lines in one set. In another set the parents numbered from 1 to 10 were used as male parents (testers) and 11 to 14 were used as female parents (lines). Four lines and 10 testers were crossed in a line × tester fashion to incorporate nematode resistance to processing lines. Eighty hybrids were obtained in the following pattern.

Lines	Testers	Lines	Testers
CLN 2026C (L_1)	Hisar N_1 (T_1)	Hisar N_1 (L_1)	CLN 2026C (T_1)
CLN 2026E (L_2)	Hisar N_2 (T_2)	Hisar N_2 (L_2)	CLN 2026E (T_2)
CLN 1466J (L_3)	Patriot (T_3)	Patriot (L_3)	CLN 1466J (T_3)
CLN 1466S (L_4)	SL 120 (T_4)	SL 120 (L_4)	CLN 1466S (T_4)
CLN 1464A (L_5)			CLN 1464A (T_5)
PT 4671A (L_6)			PT 4671A (T_6)
PT 4716A (L_7)			PT 4716A (T_7)
CO 3 (L_8)			CO 3 (T_8)
LE 812 (L_9)			LE 812 (T_9)
Arka Ahuti (L_{10})			Arka Ahuti (T_{10})

Observations recorded

The following observations were recorded in 10 plants per replication at random in each cross and parent.

1. Biometrical characters

Plant height: The height of the plant from the cotyledonary node to the tip of the plant was measure at the time of final harvest and expressed in cm.

Number of fruits per plant: The number of fruits in each harvest was counted and total fruits from all harvests were expressed as number of fruits/plant.

Fruit weight: The weight of one fruit was noted at each harvest and the mean of all the harvests was noted and expressed in g.

Yield per plant: All the red ripe fruits harvested were weighed in each harvest and all the recorded values were added for all the harvest, to get the yield/plant which was expressed in kg.

2. Biochemical characters

Total soluble solids (TSS): The TSS content in the fruit pulp was determined using a Zeiss hand refractometer and the readings were recorded as °Brix.

Acidity: The acidity in tomato was estimated by A.O.A.C. method (1975) and expressed in per cent.

Ascorbic acid: The ascorbic acid content in tomato was estimated by the A.O.A.C. method (1975) and expressed as mg/100 g of fresh sample.

Lycopene: Lycopene was estimated by a rapid spectrophotometric method as suggested by Adsule and Dan (1979). The absorbance value was recorded in a Beckman DU–64 spectrophotometer at 503 nm and expressed as mg/100 g.

Combining ability analysis

1. Analysis of variances

The observations recorded were subjected to line × tester analysis and the general combining ability effects of parents and specific combining ability effects of hybrids were worked out. The combining ability analysis was done based on the already developed method of Kempthrone (1957), which is related to experiment 11 of the estimation of average gene by Comstock and Robinson (1952).

The analysis of variance and the mean square expectations (Rao *et al.* 1968) are detailed in the table below: where r = number of replications, l = number of lines (female parents), t = number of testers (male parents), σ^2_e = error mean square.

Analysis of effects

The GCA and SCA effects of parents and crosses respectively were estimated as follows:

$$x_{ijk} = l + g_i + g_j + s_{ij} + e_{ijk}$$

where x_{ijk} = value of ijkth observation, i = population mean, g_i = GCA effect of ith line, g_j = GCA effect of jth line, s_{ij} = SCA effect of ijth hybrid, e_{ijk} = error effect associated with ijkth observation, i = number of lines, j = number of testers, k = number of replications.

The individual effects of GCA and SCA were obtained from the two way table of lines and testers, in which each figure was a total over replications as follows:

$$\mu = \frac{x}{r1t}$$

$$g_i = \frac{x_i}{rt} - \frac{x}{r1t}$$

$$g_j = \frac{x_j}{r1} - \frac{x}{r1t}$$

$$S_{ij} = \frac{x_{ij}}{r} - \frac{x_i}{rt} - \frac{x_j}{r1} - \frac{x}{r1t}$$

Variance due to general combining ability GCA (σ^2 GCA) and specific combining ability SCA (σ^2 SCA) were estimated as follows: GCA = Covariance of (H.S.); SCA = Covariance of (F.S.) - 2 Covariance of (H.S); X... = grand total of all hybrid combinations; X_i = total of ith line over 't' testers and 'r' replications; $X_{j.}$ = total of jth tester over 'l' lines and 'r' replications; $X_{ij.}$ = total of the hybrid ith line and jth tester over 'r' replications.

The standard errors pertaining to the GCA and SCA effects were calculated from the root of variance effects as indicated below:

$$\mathrm{SE}\,(g_i)\ \text{ovule parent} = \frac{\text{Error variance}}{rt}$$

Source	df	MSS	Expectations of mean squares
Genotypes	r (l+t+lt) –1		
Parents	(l+t) – 1		
Hybrids	(lt – 1)		
Lines	(l –1)	M_1	σ^2_e + r (COV (F.S.) – 2 COV (H.S.) + rt ([COV (H.S.)]
Testers	(t – l)	M_2	σ^2_e + r (COV (F.S.) – 2 COV (H.S.) + 2rl ([COV (H.S.)]
Line × tester	(l-1) (t – 1)	M_3	σ^2_e + r (COV (F.S.) – 2 COV (H.S.)
Error	(r –l) (l+t+lt-1)	M_4	σ^2_e

$$\text{Covariance of half sibs COV (H.S.)} = \frac{(M_1 - M_3) + (M_2 - M_3)}{r\,(1 + t)}$$

$$\text{Covariance of full sibs COV (F.S.)} = \frac{(M_1 - M_4) + (M_2 - M_4) + (M_3 - M_4) + 6r^2\text{COV(H.S.)} - r\,(1 + t)\,\text{COV (H.S.)}}{3r}$$

$$\text{SE}\,(g_j)\ \text{pollen parent} = \frac{\text{Error variance}}{\text{rl}}$$

$$\text{SE}\,(S_{ij})\ \text{ovule parent x pollen parent} = \frac{\text{Error variance}}{\text{r}}$$

RESULTS AND DISCUSSION

Analysis of variance for combining ability

The GCA and SCA variances for the eight characters were presented in **Tables 1** and **2**. The analysis of variance in a line × tester programme for the parents and hybrids in randomized block design showed significant differences among the genotypes for all the characters. Chandha *et al.* (2001), Dhaliwal *et al.* (2003) and Saleem *et al.* (2009) reported that lines exhibited significant variation for fruit weight and fruit length where as testers were significant for number of fruit per plant only.). In respect of interaction between the parents and hybrids, the effects were highly significant for all the characters, except for yield/plant and lycopene for direct crosses. For reciprocal crosses, the parents × hybrids interaction effects were highly significant for all the characters except for plant height.

The variance due to GCA was lower than that of SCA for all the characters (Hannan *et al.* 2007). In reciprocal crosses, highest GCA variance was observed for plant height. The ratio of GCA/SCA was less than one for all the characters. The ratio was highest for the character, number of fruits/plant (0.036) among the direct crosses and it was highest for plant height (0.033) among the reciprocal crosses.

GCA effects of parents and SCA effects of hybrids

The *P* gene from maize encodes a MYB-like TF and was The estimates of GCA for the parents and SCA for the hybrids are presented for eight characters in **Tables 3A-10B**.

1. Plant height

The GCA effect for plant height was highest in PT 4716A (29.170) among the parents of direct crosses and among the testers it is positive and significant in Hisar N_2 and Patriot (T_2 and T_3). The SCA effects for plant height was highest (26.953) in PT 4671A × Hisar N_2 (L_6 × T_2) in the direct crosses (**Tables 3A, 3B**).

2. Number of fruits/plant

The GCA was positive and significant in PT 4716A, CO 3 and LE 812 (L_7, L_8 and L_9). Positive and significant SCA was observed in 10 hybrids to a maximum of 8.710 in CLN 1466J × Hisar N_2 (L_3 × T_2). The GCA was significant and positive in Patriot and SL 120 (L_3 and L_4). Among the tester, the GCA effects were negative and significant in 6 testers viz., CLN 2026C, CLN 2026E, CLN 1466J, CLN 1466S, LE 812 and Arka Ahuti (T_1, T_2, T_3, T_4, T_9 and T_{10}), while PT 4716A (T_7) recorded positive and significant GCA (**Tables 4A, 4B**).

3. Fruit weight

The GCA was positive and significant in CLN 2026C, CLN 1466S, CLN 1464A, CO 3 and LE 812 (L_1, L_4, L_5, L_8 and L_9). Among the testers, the GCA was positive and significant (5.984) in SL 120 (T_4). The SCA was positive and significant in 10 cross combinations in the direct crosses. Among the pollen parents, the GCA effects were positive and significant in CLN 2026E, CLN 1466J, CLN 1466S, CLN 1464A, CO 3 and LE 812 (T_2, T_3, T_4, T_5, T_8 and T_9) (**Tables 5A, 5B**).

4. Yield/plant

The GCA for yield/plant was positive and significant in CLN 2026C (L_1), CLN 1464A (L_5), CO 3 (L_8) and LE 812 (L_9). Among the testers, the GCA effect was positive and significant in SL 120 (T_4) while negative and significant in Patriot (T_3). The GCA effects were positive and significant in Patriot and SL 120 (L_3 and L_4), while it was negative and significant in Hisar N_1 and Hisar N_2 (L_1 and L_2). Among the testes, the GCA effects were positive and significant in CLN 1464A, CO 3 and LE 812 (T_5, T_8 and T_9) (**Tables 6A, 6B**).

Table 1 Analysis of variance for combining ability (direct crosses).

Source	Plant height	Number of fruits per plant	Fruit weight	Yield per plant	TSS	Acidity	Ascorbic acid	Lycopene
Parents	460.935**	1177.678**	798.927**	0.127**	0.438**	0.022**	35.332**	2.385**
Hybrids	814.303**	293.489**	316.928**	0.444**	0.542**	0.025**	34.797**	3.247**
Parents × Hybrids	4611.514**	252.195**	339.725**	0.008	0.445**	0.003	137.909**	0.033
Lines	2311.471**	1139.919**	1043.525**	1.694**	1.336**	0.070**	102.129**	10.513**
Testers	177.143	35.595	327.103	0.153	0.761	0.012	12.704	1.231
Lines × Testers	386.042**	40.002**	73.598**	0.060**	0.253**	0.011**	14.807**	1.049**
Error	2.408	2.410	2.134	0.006	0.044	0.001	0.778	0.019
GCA	10.544	6.241	5.991	0.010	0.007	0.001	0.492	0.054
SCA	428.699	172.255	211.679	0.271	0.336	0.014	18.921	1.870
GCA/SCA	0.024	0.036	0.0283	0.035	0.021	0.002	0.026	0.029

* Significant at 5% level; ** Significant at 1% level

Table 2 Analysis of variance for combining ability (reciprocal crosses).

Source	Plant height	Number of fruits per plant	Fruit weight	Yield per plant	TSS	Acidity	Ascorbic acid	Lycopene
Parents	460.935**	1177.678**	798.927**	0.127**	0.438**	0.022**	35.332**	2.385**
Hybrids	479.106**	197.646**	179.945**	0.150**	0.809**	0.013**	42.011**	1.152**
Parents × Hybrids	3.743	1040.221**	1646.282**	2.016**	0.769**	0.035**	317.240**	2.643**
Lines	33.701	173.898*	150.644*	0.718**	5.970**	0.102**	396.639**	1.354*
Testers	1731.944**	639.923**	591.318**	0.194	0.154	0.004	20.588	1.465
Lines × Testers	110.983**	52.860**	46.076**	0.072**	0.454**	0.006**	9.749**	1.027**
Error	4.036	2.591	2.239	0.012	0.029	0.001	1.511	0.046
GCA	9.064	3.565	3.296	0.002	0.009	0.000	0.794	0.003
SCA	268.456	126.513	114.839	0.149	1.041	0.018	66.700	0.603
GCA/SCA	0.033	0.028	0.028	0.012	0.008	0.011	0.012	0.005

* Significant at 5% level; **Significant at 1% level

Table 3A Estimates of general and specific combining ability for plant height (direct crosses).

Testers **Lines**	**T_1**	**T_2**	**T_3**	**T_4**	***gca* (Lines)**
L_1	-11.107**	0.686	9.735**	0.686	-9.264**
L_2	-19.420**	-21.576**	16.872**	24.124**	10.873**
L_3	1.615	-4.206**	-0.743	3.334**	-15.362**
L_4	5.784**	-4.166**	-4.068**	2.449*	20.563**
L_5	1.857	10.486**	-0.255	-12.088**	6.251**
L_6	24.740**	26.953**	-21.598**	-30.096**	6.743**
L_7	-4.771**	-4.848**	1.691	7.927**	29.170**
L_8	2.917*	-2.289*	1.219	-1.848	-15.009**
L_9	-5.320**	1.556	-0.543	4.304**	-16.862**
L_{10}	3.706**	-2.600*	-2.311*	1.206	-17.103**
gca (Testers)	-3.986**	2.720**	1.747**	-0.481	

SE (gi) = 0.549; SE (gj) = 0.347; SE (Sij) = 1.097; * Significant at 5% level; ** Significant at 1% level

Table 3B Estimates of general and specific combining ability for plant height (reciprocal crosses).

Testers **Lines**	**T_1**	**T_2**	**T_3**	**T_4**	**T_5**	**T_6**	**T_7**	**T_8**	**T_9**	**T_{10}**	***gca* (Lines)**
L_1	-4.629**	2.488	3.726**	-2.096	6.666**	0.566	-10.293**	0.985	-0.484	3.071**	-0.447
L_2	12.416**	2.544	-2.597	8.035**	-8.302**	1.063	-9.546**	-5.588**	0.921	1.053	-0.038
L_3	-5.614**	-3.936**	-5.152**	-4.565**	-2.912**	-0.212	1.217	7.386**	10.881**	2.907**	-1.298**
L_4	-2.173	-1.095	4.023**	-1.375	4.548**	-1.417	18.623**	-2.783	-11.318**	-7.032**	1.782**
gca (Testers)	-4.013**	-4.589**	-6.835**	-5.822	-2.465**	-1.449*	41.466**	-6.468**	-2.363**	-7.465**	

SE (gi) = 0.449; SE (gj) = 0.710; SE (Sij) = 1.420; * Significant at 5% level; ** Significant at 1% level

Table 4A Estimates of general and specific combining ability for number of fruits per plant (direct crosses).

Testers **Lines**	**T_1**	**T_2**	**T_3**	**T_4**	***gca* (Lines)**
L_1	0.341	2.442*	0.078	-3.562**	-0.269
L_2	-2.416**	3.205**	-0.548	-0.240	-0.977
L_3	0.543	8.710**	-6.583**	-2.670*	-11.982**
L_4	-1.994	0.807	0.770	0.417	-14.104**
L_5	-0.278	-1.867	1.570	0.573	-0.920
L_6	6.334**	-2.274*	2.713*	-6.774**	-3.663**
L_7	-5.290**	-2.609*	2.468*	5.431**	29.362**
L_8	-1.714	-0.718	3.850**	-1.417	4.336**
L_9	-1.774	0.187	0.015	1.572	3.696**
L_{10}	6.247**	-7.882**	-5.034**	6.668**	-5.480**
gca (Testers)	0.694	1.379**	-0.399	-1.673**	

SE (gi) = 0.549; SE (gj) = 0.347; SE (Sij) = 1.098; * Significant at 5% level; ** Significant at 1% level

Table 4B Estimates of general and specific combining ability for number of fruits per plant (reciprocal crosses).

Testers **Lines**	**T_1**	**T_2**	**T_3**	**T_4**	**T_5**	**T_6**	**T_7**	**T_8**	**T_9**	**T_{10}**	***gca* (Lines)**
L_1	-3.079*	-3.158**	-3.403**	2.391*	1.273	1.774	-5.582**	7.168**	1.028	1.587	-4.212**
L_2	-1.435	-2.308*	2.636*	-3.375**	3.148**	1.804	5.978**	-4.762**	-2.412*	0.726	0.144
L_3	2.092*	3.673**	-5.392**	-4.013**	-5.481**	4.675**	9.719**	-4.576**	0.484	-1.182	2.187**
L_4	2.422*	1.793	6.159**	4.997**	1.060	-8.254**	-10.115**	2.170	0.900	-1.131	1.882**
gca (Testers)	-4.523**	-1.550**	-4.480**	-4.918**	-0.731	0.073	24.814**	-0.891	-5.531**	-2.265**	

SE (gi) = 0.360; SE (gj) = 0.569; SE (Sij) = 1.138; * Significant at 5% level; ** Significant at 1% level

Table 5A Estimates of general and specific combining ability for fruit weight (direct crosses).

Testers **Lines**	**T_1**	**T_2**	**T_3**	**T_4**	***gca* (Lines)**
L_1	0.967	-8.280**	-2.293*	9.605**	10.313**
L_2	6.216**	-1.591	-5.009**	0.384	-2.791**
L_3	-1.181	-7.213**	6.333**	2.062	-2.323**
L_4	-0.130	2.427*	-0.886	-1.412	4.980**
L_5	-8.401**	1.366	-5.802**	12.807**	1.937*
L_6	-1.457	3.515**	-2.643*	0.585	-0.837
L_7	2.172*	1.940	2.886**	-6.999**	-26.382**
L_8	-0.565	2.057	-1.401	-0.091	4.530**
L_9	1.307	-0.740	2.646*	-3.214**	16.528**
L_{10}	1.070	6.487**	6.169**	-13.726**	-5.955**
gca (Testers)	-2.363**	-1.065**	-2.557**	5.984**	

SE (gi) = 0.517; SE (gj) = 0.328; SE (Sij) = 1.033; * Significant at 5% level; ** Significant at 1% level

Table 5B Estimates of general and specific combining ability for fruit weight (Reciprocal crosses).

Testers **Lines**	**T_1**	**T_2**	**T_3**	**T_4**	**T_5**	**T_6**	**T_7**	**T_8**	**T_9**	**T_{10}**	***gca* (Lines)**
L_1	-2.570*	-1.489	1.911	-0.021	-2.515*	2.841**	5.559**	-5.641**	-1.855	3.780**	-2.873**
L_2	-0.163	-1.357	1.923	3.011**	-6.193**	-4.337**	-1.614	2.766*	5.662**	0.302	-1.740**
L_3	1.701	1.178	4.933**	5.410**	2.307*	2.098	-5.330**	1.120	-6.353**	-7.063**	1.721**
L_4	1.031	1.668	-8.767**	-8.400**	6.401	-0.602	1.385	1.755	2.546	2.981**	2.891**
gca (Testers)	0.809	2.627**	1.402**	4.235**	1.573**	-8.323**	-20.040**	7.840**	10.144**	-0.267	

SE (gi) = 0.335; SE (gj) = 0.529; SE (Sij) = 1.058; * Significant at 5% level; ** Significant at 1% level

Table 6A Estimates of general and specific combining ability for yield per plant (Kg) (direct crosses).

Testers Lines	T_1	T_2	T_3	T_4	*gca* (Lines)
L_1	0.068	-0.183**	-0.030	0.146*	0.415**
L_2	0.108	0.036	-0.190**	0.045	-0.060*
L_3	0.024	0.102	-0.059	-0.068	-0.491**
L_4	-0.075	0.097	0.040	-0.063	-0.371**
L_5	-0.326**	-0.028	-0.145**	0.501**	0.105**
L_6	0.182**	0.035	0.033	-0.250**	-0.114**
L_7	-0.041	0.006	0.154**	-0.119*	-0.470**
L_8	-0.116*	0.046	0.084	-0.014	0.435**
L_9	-0.070	-0.017	0.080	0.007	0.894**
L_{10}	0.247**	-0.095	0.033	-0.185**	-0.344**
gca (Testers)	-0.035	0.032	-0.100**	0.103**	

SE(gi) = 0.029; SE (gj) = 0.018; SE (Sij) = 0.057; * Significant at 5% level; ** Significant at 1% level

Table 6B Estimates of general and specific combining ability for yield per plant (Kg) (reciprocal crosses).

Testers Lines	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	gca (Lines)
L_1	-0.201*	-0.080	-0.091	0.057	-0.072	0.125	0.202*	0.025	-0.072	0.108	-0.191**
L_2	0.005	-0.438**	0.245**	0.039	-0.035	-0.038	0.034	-0.043	0.114	0.115	-0.123**
L_3	0.148	0.329**	-0.037	0.031	-0.108	0.239**	-0.138	-0.115	-0.123	-0.227**	0.099**
L_4	0.047	0.189*	-0.117	-0.128	0.216**	-0.326**	-0.098	0.134	0.081	0.002	0.215**
gca (Testers)	-0.045	-0.006	-0.060	0.007	0.102**	-0.196**	-0.233**	0.281**	0.162**	-0.020	

SE (gi) = 0.025; SE (gj) =0.039; SE (Sij) = 0.079; * Significant at 5% level; ** Significant at 1% level

Table 7A Estimates of general and specific combining ability for TSS (°Brix) (direct crosses).

Testers Lines	T_1	T_2	T_3	T_4	*gca* (Lines)
L_1	-0.218	0.341*	-0.246	0.123	-0.219**
L_2	-0.033	-0.184	0.079	0.138	-0.179**
L_3	0.330*	-0.210	-0.097	-0.023	0.307**
L_4	0.560**	0.000	-0.452**	-0.108	-0.388**
L_5	0.069	0.269	-0.248	-0.090	-0.307**
L_6	0.269	-0.021	-0.058	-0.190	-0.282**
L_7	0.229	0.223	0.037	-0.490**	-0.883**
L_8	-0.547**	-0.223	0.700**	0.069	-0.291**
L_9	-0.758**	0.151	0.294	0.313**	0.121
L_{10}	0.098	-0.347*	-0.009	0.259	0.355**
gca (Testers)	-0.188**	-0.073	-0.011	0.271**	

SE (gi) = 0.075; SE (gj) = 0.047; SE (Sij) = 0.150; * Significant at 5% level; ** Significant at 1% level

Table 7B Estimates of general and specific combining ability for TSS (°Brix) (reciprocal crosses).

Testers Lines	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	*gca* (Lines)
L_1	0.108	-0.480**	-0.463**	-0.538**	0.602**	0.551**	-0.345**	-0.039	-0.217	0.822**	-0.728**
L_2	0.213	-0.050	-0.028	-0.308**	-0.023	0.441**	0.419**	-0.399**	-0.077	-0.188	-0.083*
L_3	-0.011	0.405**	0.167	0.107	-0.442**	0.006	0.260*	0.051	-0.301**	-0.242	0.526**
L_4	-0.310**	0.126	0.323**	0.738**	-0.136	-0.100**	-0.334**	0.387**	0.595**	-0.391**	0.285**
gca (Testers)	0.083	-0.103	0.125*	-0.195**	-0.055	0.156*	-0.013	-0.079	-0.141**	0.220**	

SE (gi) = 0.038; SE (gj) = 0.061; SE (Sij) = 0.121; * Significant at 5% level; ** Significant at 1% level

5. TSS

Among the ovule parents, Arka Ahuti (L_{10}) recorded the highest positive significant effect of 0.355 and the highest negative significant effect of -0.883 was noticed in PT 4716A (L_7). The positive and significant SCA was recorded in 5 hybrid combinations, while it was negative and significant in 5 cross combinations in the direct crosses. Among the lines, Patriot (L_3) (0.526) and SL 120 (L_4) (0.285) recorded positive and significant GCA. Among the crosses, 9 hybrids showed positive and significant SCA, while it was negative and significant in 12 cross combinations in the reciprocal crosses (**Tables 7A, 7B**).

6. Acidity

Positive and significant GCA was observed in 6 lines. Among the testers, GCA was highly significant and positive (0.023) in SL 120 (T_4). The SCA effect of acidity was also positive and significant in 6 cross combinations (**Tables 8A, 8B**).

7. Ascorbic acid

In the direct crosses, a positive and significant GCA effect was observed in CLN 2026C, CLN 2026E, CLN 1466J and LE 812 (L_1, L_2, L_3 and L_9). The tester SL 120 (T_4) recorded the highest positive and significant GCA effect of 1.160. The tester Arka Ahuti (T_{10}) recorded the highest positive significant SCA effect (2.225) and the highest positive SCA (5.200) was observed in Hisar N_1 × CLN 2026E ($L_1 \times T_2$) (**Tables 9A, 9B**).

8. Lycopene

The GCA effect for this trait was recorded with LE 812 (L_9) as 1.298. The GCA effect was positive and significant in CLN 2026E, CLN 1464A, CO 3, LE 812 and Arka Ahuti (L_2, L_5, L_8, L_9 and L_{10}) (**Tables 10A, 10B**).

Table 8A Estimates of general and specific combining ability for acidity (%) under (direct crosses).

Testers **Lines**	T_1	T_2	T_3	T_4	*gca* **(Lines)**
L_1	-0.041**	-0.101**	-0.161**	0.102**	0.079**
L_2	0.045**	-0.103**	-0.060**	0.118**	0.057**
L_3	0.061**	-0.011	0.041**	-0.090**	0.041**
L_4	0.055**	0.002	0.024	-0.081**	-0.013
L_5	-0.025	0.027	-0.045**	0.043**	0.082**
L_6	0.037*	0.014	0.022	-0.074**	-0.140*
L_7	-0.008	0.038**	0.045**	-0.075**	-0.164**
L_8	-0.007	-0.065**	0.057**	0.015	0.100**
L_9	-0.036*	-0.064**	0.053**	0.047**	0.024**
L_{10}	-0.081**	0.061**	0.023	-0.003	-0.066**
gca (Testers)	0.016**	-0.011*	-0.028**	0.023**	

SE (gi) = 0.007; SE (gj) = 0.005; SE (Sij) = 0.014; * Significant at 5% level; ** Significant at 1% level

Table 8B Estimates of general and specific combining ability for acidity (%) under (reciprocal crosses).

Testers **Lines**	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	*gca* **(Lines)**
L_1	-0.018	-0.038	-0.017	0.005	0.093**	0.039	-0.008	-0.011	0.040*	-0.086**	-0.043**
L_2	0.051*	0.056**	-0.007	-0.025	0.017	0.034	-0.059**	0.009	-0.020	-0.056**	-0.043**
L_3	-0.026	0.064**	0.050*	0.028	-0.054**	-0.033	0.039	-0.013	-0.077**	0.022	-0.021**
L_4	-0.007	-0.082**	-0.026	-0.008	-0.056**	-0.040	0.028	0.015	0.056**	0.120	0.106**
gca (Testers)	-0.005	-0.030**	0.009	-0.024**	-0.036**	0.018	0.040**	0.028**	0.002	-0.002	

SE (gi) = 0.006; SE (gj) = 0.010; SE(Sij) = 0.020; * Significant at 5% level; ** Significant at 1% level

Table 9A Estimates of general and specific combining ability for ascorbic acid (mg/100 g) (direct crosses).

Testers **Lines**	T_1	T_2	T_3	T_4	*gca* **(Lines)**
L_1	1.773**	-0.629	1.650*	-2.794**	2.459**
L_2	-1.276*	1.742**	-1.238	0.772	2.898**
L_3	-0.326	1.302**	-1.923**	0.947	2.778**
L_4	-0.428	-2.015**	1.834**	0.610	-0.780*
L_5	-1.407**	0.701	2.215**	1.509*	0.219
L_6	4.394**	2.932**	0.322	7.648**	-2.697**
L_7	-3.295**	1.648**	-2.65**7	4.303**	-7.473**
L_8	0.950	-3.237**	-0.872	3.158**	0.502
L_9	-0.561	-1.078	1.007	0.632	4.688**
L_{10}	0.175	-1.367**	-0.337	1.528*	-2.593**
gca (Testers)	-0.657**	-0.280	-0.224	1.160**	

SE (gi) = 0.312; SE (gj) = 0.197; SE (Sij) = 0.624; * Significant at 5% level; ** Significant at 1% level

Table 9B Estimates of general and specific combining ability for ascorbic acid (mg/100 g) (reciprocal crosses).

Testers **Lines**	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	*gca* **(Lines)**
L_1	-0.657	5.200**	-2.232**	-1.240	-0.863	-1.107	-1.387	-2.007*	1.250	3.046**	-6.134**
L_2	-2.576**	-3.539**	-0.196	0.176	1.382	0.758	1.698	3.218**	0.231	-1.153	0.180
L_3	2.372**	-1.010	2.152**	2.799**	1.040	-0.978	-1.633	-0.883	-1.835*	-2.024**	1.542**
L_4	0.862	-0.650	0.277	-1.735	-1.559	1.327	1.322	-0.328	0.354	0.131	4.412**
gca (Testers)	-2.061**	1.332**	-0.596	-2.294**	-0.735	-0.311	1.399**	-0.791	1.832**	2.225**	

SE (gi) = 0.275; SE (gj) = 0.435; SE (Sij) = 0.869; * Significant at 5% level; ** Significant at 1% level

Table 10A Estimates of general and specific combining ability for lycopene (mg/100 g) (direct crosses).

Testers **Lines**	T_1	T_2	T_3	T_4	*gca* **(Lines)**
L_1	-0.414**	-0.621**	0.969**	0.065	-0.348**
L_2	-0.454**	-0.001	0.239*	0.215*	1.008**
L_3	0.261**	0.629**	-0.245*	-0.644**	-1.408**
L_4	0.276**	-0.011	0.484**	-0.749**	-0.308**
L_5	0.250*	0.158	-0.577**	0.169	0.134**
L_6	0.611**	0.189	-0.035	-0.764**	-1.263**
L_7	-0.831**	-0.513**	-0.973**	2.318**	-1.540**
L_8	-0.215*	0.033	0.723**	-0.541**	1.159**
L_9	0.516**	0.194	-0.770**	0.060	1.298**
L_{10}	0.001	-0.056	0.184	-0.129	1.268**
gca (Testers)	-0.171**	-0.239**	0.121**	0.290**	

SE (gi) = 0.049; SE (gj) = 0.031; SE (Sij) = 0.098; * Significant at 5% level; ** Significant at 1% level

Table 10B Estimates of general and specific combining ability for lycopene (mg/100 g) (reciprocal crosses).

Testers **Lines**	T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	*gca* **(Lines)**
L_1	-0.121	-0.683**	-0.157	-0.359*	0.356**	0.820**	0.958**	0.405*	-0.542**	-0.677**	0.022
L_2	-0.825**	-0.367*	0.314**	0.871**	-0.472**	0.141	0.169	-0.108	-0.001	0.279	-0.364**
L_3	1.062	0.380*	0.471**	-0.271	-0.310*	0.254	0.031	-0.841**	-0.523**	-0.253	0.094
L_4	-0.117	0.670**	-0.628**	-0.240	0.425**	-1.215**	-1.158**	0.544**	1.067**	0.652**	0.248**
gca (Testers)	0.253**	0.590**	0.184*	0.087	0.025	-0.343**	-0.971**	0.082	-0.201**	0.294**	

SE (gi) = 0.048; SE (gj) = 0.076; SE (Sij) = 0.153; * Significant at 5% level; ** Significant at 1% level

Evaluation of parents and hybrids through *per se* performance and combining ability

The line × tester analysis provides information about the GCA of parents and SCA of the hybrids and is also helpful in estimating the various types of gene effects. This design to study the combining ability of parents besides heterosis in tomato has also been employed earlier in tomato (Srivastava *et al*. 1998; Sharma *et al*. 1999; Bhatt *et al*. 2001; Chandha *et al*. 2001; Dhaliwal *et al*. 2003, 2004; Barar *et al*. 2005; Saleem *et al*. 2009). Sprague and Tatum (1942) defined GCA to indicate the performance of a line in several hybrid combinations and SCA was used to designate close effects in certain combinations which significantly departed from what would have been expected on the basis of the average performance of lines involved. The variance components due to GCA and SCA may be genetically interpreted under certain assumptions and therefore useful in framing the most suitable breeding methods.

The analysis of variance showed highly significant differences among the genotypes indicating the existence of greater variability among the genotypes selected for all the economic traits (Hannan *et al*. 2007). The variance due to lines was highly significant for all the traits in the direct crosses. Among the reciprocal crosses, highly significant values were recorded for all the traits except plant height. The GCA represented additive type of gene action and SCA represents dominance and non additive type of gene action such as epistasis (Sprague and Tatum 1942).

The variance due to testers was non significant for most of the traits suggesting that there is less variation among the testers. The variances due to interaction between lines x testers were significant for all the characters among both direct and reciprocal crosses revealing considerable variation for SCA effects.

The variance due to GCA and SCA were prominent for all the characters in the present investigation. The variance due to SCA was higher than that of GCA suggesting the preponderance of non additive gene action in the expression of characters. This observation is in conformity with earlier findings in tomato for plant height by Aruna (1992), fruit weight, number of fruits per plant and TSS by Lakshmanan (1996).

In general, all the characters are under the influence of non additive gene action and thus offer scope for improvement through heterosis breeding.

With respect of plant height, the parent PT 4716A was the tallest and the parent CLN 1464A was the shortest. The hybrids PT 4716A × SL 120 ($L_7 \times T_4$) among the direct crosses and SL 120 × PT 4716A ($L_4 \times T_7$) among the reciprocal crosses recorded the highest plant height. The tallest parent PT 4716A which recorded highly significant GCA effects could produce taller hybrids. The parents with higher positive GCA estimates were able to produce hybrids with high positive SCA estimates suggesting additive × additive gene interaction among the direct and reciprocal crosses.

The number of fruits per plant has considerable influence on total yield of fruits. In the present investigation, the variance due to SCA was much greater than that of GCA for this trait indicating the preponderance of non additive gene action. This is in accordance with the results of Kurian (1990) and Anbu *et al*. (1980). The preponderance of non additive genetic variance and availability of good combiners suggested that improvement for this trait could be achieved effectively by heterosis breeding. The highest *per se* for this trait was recorded by the hybrids PT 4716A × SL 120 ($L_7 \times T_4$) and Patriot × PT 4716A ($L_3 \times T_7$) among the direct and reciprocal crosses respectively. The former represents high x low GCA parental combination exhibiting high SCA while the later high x high GCA parental combination with high SCA suggesting additive × dominant gene interaction in the first and additive x additive gene interaction in the second (**Table 11**).

Highest significant positive SCA effect was noticed in the hybrids CLN 1466J × Hisar N_2 ($L_3 \times T_2$) and Patriot × PT 4716A ($L_3 \times T_7$) among the direct and reciprocal crosses respectively. The parental performance and GCA were in agreement for number of fruits per plant. PT 4716A with more *per se* also had higher GCA. The hybrids such as, CLN 2026C × Hisar N_2 ($L_1 \times T_2$), CLN 2026E × Hisar N_2 ($L_2 \times T_2$) and CLN 1466J × Hisar N_2 ($L_3 \times T_2$) were of low × high GCA combinations suggesting dominance x additive gene interaction among the direct crosses. Among reciprocal crosses Hisar N_2 × PT 4716A ($L_2 \times T_7$), a combination with low × low GCA resulting in high SCA suggested the role of non-additive gene interaction such as epistasis. These combinations can also be exploited in breeding for development of hybrids with more number of fruits per plant.

Fruit yield in tomato is determined by fruit weight and number of fruits (Dudi and Kalloo 1982). The parents which exhibited higher *per se* for fruit weight were SL 120 and CLN 1466S and they also had high positive GCA effects. Among the hybrids of direct and reciprocal crosses, CLN 2026C × SL 120 ($L_1 \times T_4$) and SL 120 × LE 812 ($L_4 \times T_9$) recorded the highest mean for fruit weight and had high SCA effects, respectively. The hybrids CLN 1464A × SL 120 ($L_5 \times T_4$) and SL 120 × CLN 1464A ($L_4 \times T_5$) also had the highest significant positive SCA effect among the direct and reciprocal crosses respectively. Hybrids with high SCA included low × high GCA, high × low GCA parents suggesting additive × dominance type of interactions. The SCA variance was greater than GCA variance suggesting the better role of non additive genetic factors than that of additive genes. The crosses having at least one good combiner as parent should be exploited in heterosis breeding and this view is shared by Aruna (1992) and Sankari (2000) in tomato.

Yield is a complex character and is dependent on its component traits and their inheritance. Any change in these would reflect on total yield. Considering the yield, the mean expression of the parent LE 812 was high with high significant positive GCA effect. The components of variance due to GCA and SCA pointed out the importance of both

Table 11 Best performing hybrids with their mean and *gca* of their parents.

Character	Hybrids	Mean	*gca* of parents
Plant height	PT 4716A × SL 120	118.80	High × Low
Number of fruits per plant	PT 4716A × SL 120	90.64	High × Low
Fruit weight	CLN 1464A × SL 120	67.19	Low × High
	CLN 2026C × SL 120	67.13	High × High
Yield per plant	CLN 2026C × SL 120	2.45	Medium × Low
TSS	PT 4716A × SL 120	5.33	Low × High
	LE 812 × SL 120	5.33	Low × Low
Acidity	CLN 2026C × SL 120	0.69	Low × Low
Ascorbic acid	LE 812 × SL 120	32.70	Low × High
	CLN 2026C × SL 120	32.60	Low × High
Lycopene	CLN 2026C × SL 120	7.68	High × High
	CO 3 × Patriot	6.75	High × Low
	CLN 1464A × SL 120	6.68	High × High

additive and non-additive gene effects with predominance of later. The predominant role of non-additive gene action for fruit yield in tomato was reported by Anbu *et al.* (1980), Kurian (1990) and Sankari (2000). The predominance of non-additive gene action for fruit yield observed in the present study suggests that improvement of yield could be achieved by development of F_1 hybrids. Among the parents CLN 2026C, CLN 1464A, CO 3, LE 812 and SL 120 showed high positive and significant GCA effects. CLN 2026C × SL 120 ($L_1 \times T_4$), CLN 1464A × SL 120 ($L_5 \times T_4$) among the direct crosses and Patriot × CLN 2026E ($L_3 \times T_2$) among the reciprocal crosses, showed highest SCA effect. In these crosses one of the parents involved was a good general combiner for yield. It is clearly seen that in unique combination of parental lines for high productivity, SCA was expressed although the GCA was probably more important in identifying parents for such unique combinations. Non-additive gene effects would seem to be small in some other situations but they might be important to identify superior hybrids for direct use.

Total soluble solids increases from mature green stage to red ripe stage. Wide variations in TSS occur as a result of both genetic and environmental factors. The main objective of the breeder in quality improvement programme would be to evolve a better hybrid combination which has got heterosis for yield as well as TSS which is rare phenomenon to arrive at. Processors are interested in soluble solids content primarily because paste yields of products which are sold on solid basis. Yield potential is reduced as high solids are selected and solid level is reduced as yield potential is selected. One of the likely reasons for this adverse relationship between solids and yield can be that a high yielding cultivar having a heavy concentrated fruit set on compact vine do not have any photosynthates available to give high solids in the fruits. So, attempts were made to have genotypes with high yield and high solids content. In the present study, the parent PT 4716A recorded the highest TSS followed by Arka Ahuti. Among the direct and reciprocal crosses, CO 3 × Patriot ($L_8 \times T_3$) and Hisar N_1 × Arka Ahuti ($L_1 \times T_{10}$) recorded the highest significant SCA effect. One of the parents involved in these crosses was a good general combiner. High *per se* for TSS was seen in the hybrids PT 4716A × Hisar N_2 ($L_7 \times T_2$), PT 4716A × SL 120 ($L_7 \times T_4$) and LE 812 × SL 120 ($L_9 \times T_4$). One of the parents has contributed to TSS so F_1 hybrids had increased yield and TSS. Such combinations have to be selected for high yield with TSS. In such combinations soluble solids per unit area would be much higher which is normally rare in tomato genotypes. The proportion of GCA and SCA variance indicated the role of both additive and non additive gene effect for TSS content of fruits with preponderance of later, indicating the better role of non additive gene action in the expression of this trait. Crosses involving parents with good GCA would also be desirable. This is in line with the findings of Singh and Nandpuri (1975).

With respect to acidity, the variance due to SCA was greater than GCA suggesting the predominant role of non additive gene action than additive gene action. These results coincide with the results of Kalloo *et al.* (1974), Aruna (1992) and Sankari (2000). Low acidity is conducive for anaerobic bacteria which cause easy spoilage. Higher acidity will therefore be beneficial for better storage of tomato fruits with least damage by microorganisms. In respect of processing quality also, high acidity reduces the processing time, temperature and allows to improve colour, flavour, texture and vitamin C retention in the final stage as reported by Leonard *et al.* (1959). The parents SL 120 and CO 3 had higher acidity percentage and showed significant positive GCA effect. High acidic hybrid combinations included low x low (negative) GCA parents with high positive SCA effects such as Arka Ahuti × Hisar N_2 ($L_{10} \times T_2$), Hisar N_1 × CLN 1464A ($L_1 \times T_5$) and Arka Ahuti × CLN 2026E ($L_3 \times T_2$) suggesting epistasis in parents or other non additive gene action such as complementary.

Ascorbic acid is the important vitamin present in tomato. The mean performance of the parents indicated that the parents CLN 1464A and CLN 2026C were superior for ascorbic acid content and they also recorded high positive GCA effects. However, when the parents are arrayed based on the GCA effect, LE 812 ranked top followed by SL 120 and CLN 2026E. This suggests that the parent without good *per se* can also be a good combiner. A high *per se* need not always reflect better combining ability and hence parents have to be chosen based on GCA and not merely by *per se.* Similar effects were also reported by Govindarasu *et al.* (1982). In the present study hybrids with high ascorbic acid included low × high GCA parents suggesting dominant × additive type of interaction for this trait.

Lycopene is a predominant pigment, which gives attractive red colour to tomato fruits. This inturn reflects on the colour and appearance of the processed products. The mean performance of the parents showed superiority in LE 812, Arka Ahuti, CO 3 and SL 120 these parents also recorded significant positive GCA effects. Among the hybrids of direct and reciprocal crosses, CO 3 × Patriot ($L_8 \times T_3$) and SL 120 × CLN 2026 E ($L_4 \times T_2$) recorded high mean performance and significant high positive SCA effects. These combinations had high × high GCA parents suggesting additive × additive type of gene interaction. The GCA/SCA ratio suggested non additive gene action is also more important for lycopene content. Lakshmanan (1996) also observed a similar trend for this trait.

In confirmation to the findings of Srivastava *et al.* (1998), Dhaliwal *et al.* (2003) and Saleem *et al.* (2009), none of the parents was the best general combiner for all the traits. The parent PT 4716A was adjudged as the best general combiner for the characters viz., plant height and number of fruits per plant. The parent SL 120 was identified the best general combiner for fruit weight, yield per plant (Saleem *et al.* 2009). Harer and Bapat (1982) and Premalatha *et al.* (2006) reported that the *per se* performance of the parents with the nature of combining ability provides the criteria to choose the parents for hybridization. These two parents may be used in multiple crossing program for the identification of superior genotypes as stated by Nadarajan and Gunasekaran (2005) with desirable trait(s) of interest.

CONCLUSIONS

The present research was aimed at estimating the GCA of parents, SCA of hybrids, gene action in eighty hybrids and fourteen parents. Combining ability analysis revealed that the parent PT 4716A was adjudged as the best general combiner for the characters viz., plant height and number of fruits per plant and SL 120 was identified the best general combiner for fruit weight and yield per plant. The hybrids CLN 2026C × SL120, CLN 2026E × SL 120, LE 812 × SL 120 and CLN 1464A × SL 120 were adjudged as the best specific combiners for yield and processing qualities they had improved processing traits like TSS, acidity, ascorbic acid and lycopene besides higher yield. SCA variance was higher than GCA variance for all the characters indicating the preponderance of non additive type of gene action for all the characters which suggests that heterosis breeding can be recommended to bring about desired improvement in F_1 hybrids.

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