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Combining Ability Studies in Tomato (*Lycopersicon esculentum* Mill.)

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Summary. Diallel analysis was carried out involving eight diverse varieties of tomato, namely Pusa Early Dwarf, Sl-1, S-12, Punjab Tropics, Sl-120, HS-101, Pusa Ruby and Sl-73-1, to characterize the gene action involved in the inheritance of some of the quantitative traits and to correlate array mean and *per se* performance with general combining ability (gca) and specific combining ability (sca) effects, respectively.

The results indicated that the variance component due to general combining ability was higher than that due to specific combining ability for yield and number of fruits, showing preponderance of an additive type of gene action. On the other hand, all other characters — height, number of branches, locule number, T.S.S., acidity and ascorbic acid content — were found to have a high variance component due to specific combining ability, which means excess of non-additive type gene action. In such cases, heterosis breeding, or any other breeding plan which makes use of specific combining ability effects, would be more effective. High correlation between parental array means and gca effects and between *per se* performance of the crosses and the sca effects was observed. The implications of the results are discussed.

Combining ability analysis, following the diallel technique, is frequently being used for testing the performance of lines in hybrid combination and also for characterizing the nature and magnitude of gene action involved in controlling a quantitative trait. With these objectives, many workers have used this technique in the tomato (Ahuja, 1968; Armstrong, 1968; Ibarbia et al. 1969). Their work has, however, been confined to the analysis of morphological characters and very few have considered the analysis of chemical components related to the quality aspect of this important vegetable crop. Furthermore, the estimation of general and specific combining ability effects has become routine in diallel analysis, but no-one has tried to correlate the gca and sca effects with the array means of the parents and the *per se* performance of the crosses, respectively. The array means and the *per se* performance, being direct estimates based on no assumptions, provide more accurate information regarding general and specific combining ability. Keeping these points in mind the present investigation was planned and the experiments were conducted involving eight varieties of tomato at the Research Farm of Haryana Agricultural University, Hissar (India). The results are presented here.

Materials and Methods

Eight different varieties of tomato, namely Pusa Early Dwarf, Sl-1, S-12, Punjab Tropics, Sl-120, HS-101, Pusa Ruby and Sl-73-1 were randomly selected and F_1s were produced by making all possible one-way crosses among them. Eight parents and 28 F_1s were planted in randomized block design with two replications spaced 60 cm apart. Each net plot had 10 plants and spacing between rows was 90 cm. Normal recommended cultural practices were followed. On eight randomly selected plants from each plot the following characters were recorded: height, number of branches, number of fruits, locule number, T.S.S., acidity, ascorbic acid content and yield.

The first step in the statistical analysis was to test the 'Null hypothesis' that there were no genotypic differences among the progenies under study. These tests involved the randomized block analysis of variance. This analysis followed the combining ability analysis assuming the following mathematical model:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + \frac{1}{bc} \sum_k \sum_l e_{ijkl} \, . \quad \begin{cases} i, j = 1, 2 \ldots p \\ k \quad = 1, 2 \ldots b \\ l \quad = 1, 2 \ldots c \end{cases}$$

where μ is the population mean, $g_i(g_j)$ is the gca effect, s_{ij} is the sca effect and e_{ijkl} is the effect peculiar to $ijkl^{th}$ observation; p is the number of parents (8), b is the number of replications (2) and c is the number of plants per plot (8).

Using this mathematical model as a base, the combining ability analysis was performed according to Griffing's method 2 (model 2) and the components of variance, such as δ_g^2 (component of variance due to general combining ability) and δ_s^2 (component of variance due to specific combining ability), and their effects were estimated.

Results

To test the significant differences among the progenies consisting of both parents and the crosses a simple variance analysis was done and the results are summarised in Table 1. Except for the number

Table 1. *Analysis of variance*

Source of variation	Mean sum of squares df	Height of the plant (cm)	Number of branches	Number of fruit per plant	Number of locule/fruit	T.S.S.	Acidity	Ascorbic acid content	Yield (kg/plant)
Replication	1	11.30	274.80	1395.00	2.360	28.42	0.52	593.74	0.19
Treatment	35	1206.83*	11.97*	703.50*	0.276	2.10*	0.052*	33.121*	0.582
Error	35	113.36	1.338	314.69	0.177	1.065	0.023	14.909	0.535

* Significant at 5% level.

Table 2. *Analysis of variance for combining ability*

Source of variation	d.f.	Height of the plant (cm)	Number of branches	Number of fruit per plant	Number of locule per plant	T.S.S.	Acidity	Ascorbic acid content	Yield (kg/plant)
g.c.a.	7	1680.87*	10.38*	973.62*	0.19*	0.36*	0.03	16.72	0.68*
s.c.a.	28	335.06*	4.75*	196.28	0.12*	1.21*	0.24	15.27	0.19
Error (M'e)		52.20	0.66	144.91	0.09	0.80	0.12	7.45	0.267
σ^2g		134.581	0.563	77.734	0.007	−0.085	−0.0210	0.145	+0.0495
σ^2s		282.86	4.09	51.37	0.03	0.41	0.12	7.82	−0.75
σ^2e		52.20	0.66	144.91	0.09	0.80	0.12	7.45	0.267

* Significant at 5%

Table 3. *General combining ability (gca) effects and the rankings of parents*

Characters/Parents	Height of the plant (cm)	Number of branches	Number of fruit per plant	Number of locule per fruit	T.S.S.	Acidity	Ascorbic acid	Yield kg/plant	Ranks array means	Ranks gca effects
Pusa Early Dwarf	−61.287	−8.199	−45.134	−2.653	−1.568	−0.780	−18.725	−1.954	5	5
Selection-1	−67.087	−9.692	−60.358	−2.520	−1.935	−0.745	−15.189	−2.334	6	6
S-12	−57.792	−8.208	−35.619	−2.753	−1.945	−0.787	−17.838	−1.994	4	4
Punjab Tropics	−33.957	−7.087	−62.673	−2.448	−1.776	−0.790	−15.199	−1.578	1	1
Sel-120	−42.570	−7.770	−43.428	−2.726	−2.129	−0.821	−16.229	−1.587	2	2
HS-101	−61.742	−9.230	−43.687	−2.663	−2.106	−0.871	−17.864	−1.641	5	5
Pusa Ruby	−37.788	−6.592	−52.939	−2.465	−2.042	−0.706	−17.132	−2.012	3	3
No. 73-1	−63.380	−8.292	−38.520	−2.818	−2.053	−0.703	−16.358	−1.949	7	7
S.E. for gca	± 2.14	±0.076	± 3.56	±0.027	±0.0264	±0.10	± 0.807	±0.449		
S.E. for (gi-gj)	± 3.18	±0.37	± 5.38	±0.13	±0.4	±0.16	± 1.22	±0.230		

of locules per fruit and the yield, significant differences were observed for all the characters. Significant differences among the progenies, especially for quality characters such as T.S.S. and acidity, indicated enough scope for selection.

In the analysis of variance for combining ability (Table 2) the variances due to gca were significant for all the characters except acidity and ascorbic acid content. The variances due to sca effect were also significant for most of the characters except acidity, ascorbic acid and yield. This indicated the importance of both additive and non-additive gene action in the inheritance of these characters. With the exception of acidity and T.S.S., the variances due to gca were larger than those due to sca. However, the estimated components of variance such as σ_g^2 and σ_s^2 did not show the same relationship as the total variances due to gca and sca. It is evident from the data in Table 2 that σ_s^2 was greater than σ_g^2 in most of the cases — plant height, number of branches, number of locule per fruit, T.S.S., acidity and ascorbic acid content. A preponderance of non-additive gene action was thus evident in the control of these characters. σ_g^2 was higher than σ_s^2 for yield and number of fruits, indicating the dominant role of additive-type gene action in these cases.

Table 3 gives the gca effects of the parents. In order to facilitate comparison, the lines were ranked on the basis of their gca effects with respect to each trait and finally these ranks were pooled to get an overall ranking of the parents for all the traits simultaneously. Similarly, the ranking of the parents was

Table 4. Per se *performance (means) of the twenty-eight crosses*

Crosses	Height	No. of branches	Fruit number	Locule number	T.S.S.	Acidity	Ascorbic acid	Yield
1 × 2	53.70	10.20	94.25	4.16	1.25	1.13	18.17	3.25
2 × 3	50.95	10.80	59.50	3.46	2.79	1.25	20.46	2.12
1 × 4	118.75	10.40	55.17	3.77	3.89	1.05	24.00	2.93
1 × 5	70.60	12.70	86.97	3.65	3.36	1.21	21.35	3.12
1 × 6	55.00	11.00	16.50	3.80	4.38	0.90	24.95	2.87
1 × 7	58.00	13.60	65.00	4.10	3.50	1.00	20.00	2.11
1 × 8	78.60	11.80	81.92	3.29	3.89	1.37	31.17	2.89
2 × 3	57.25	12.00	58.40	3.81	1.88	1.22	24.60	2.08
2 × 4	72.00	10.37	56.70	3.49	3.63	0.91	26.25	2.36
2 × 5	48.25	6.97	59.62	3.75	3.22	1.10	26.71	1.97
2 × 6	72.33	11.00	49.90	3.72	4.42	1.13	33.28	2.62
2 × 7	70.00	7.32	45.30	4.73	1.95	0.96	22.84	1.90
2 × 8	84.80	15.05	52.10	3.90	1.80	1.56	23.47	1.87
3 × 4	118.25	14.25	58.20	4.18	3.15	1.03	22.22	2.72
3 × 5	66.70	11.10	89.80	3.75	3.90	1.02	21.60	2.89
3 × 6	55.00	6.60	93.50	3.24	1.40	0.93	20.96	2.51
3 × 7	103.00	13.70	77.50	3.66	4.99	1.25	25.34	2.64
3 × 8	55.20	12.20	77.10	3.29	1.42	1.26	23.39	2.15
4 × 5	114.00	13.75	66.25	3.50	1.84	1.16	28.16	3.72
4 × 6	61.50	11.80	56.00	4.20	2.40	1.05	26.50	2.90
4 × 7	106.50	14.65	41.80	4.02	2.10	1.36	29.47	2.88
4 × 8	68.00	12.80	40.00	3.90	2.25	1.11	23.70	2.60
5 × 6	94.50	9.80	77.33	4.36	1.85	0.86	24.26	3.70
5 × 7	124.62	13.12	75.00	3.05	1.56	1.04	27.56	2.91
5 × 8	73.70	11.75	82.00	3.68	3.02	0.93	22.88	3.30
6 × 7	103.25	14.07	73.80	4.13	3.34	1.25	18.84	3.46
6 × 8	43.07	12.32	99.55	3.00	2.61	0.90	24.22	2.90
7 × 8	50.50	10.25	62.66	2.50	2.92	1.13	16.32	1.79

1 = Pusa Early Dwarf; 2 = Sl-1; 3 = S-12; 4 = Punjab Tropics; 5 = Sl-120; 6 = HS-101; 7 = Pusa Ruby; 8 = Sl-73-1.

also done on the basis of their array means. These rankings are presented in the last two columns of Table 3. It is interesting that the positions occupied by the parents under these two criteria of comparison were almost the same. Punjab Tropics occupied the first position, followed by Sl-120, Pusa Ruby and S-12 etc. Sl-73-1 proved to be the poorest general combiner among the lines studied. It is, however, worth mentioning that although Punjab Tropics was ranked best for general combining ability considering all the traits simultaneously, Sl-120 occupied the first position when yield was the only criterion. If yield potential only was considered for the parents in their various combinations, the order of the varieties was Sl-120, HS-101, Punjab Tropics, Pusa Early Dwarf and so on.

Two criteria, the *per se* performance (Table 4) and the sca effects (Table 5), were used to study the performance of the lines in their specific cross combinations. Here again the crosses were ranked once on the basis of *per se* performance and secondly on the basis of the sca effects. Rank correlation was applied to test the degree of association between these two rankings. As the rank correlation was very high ($r_s = 0.99$), it was concluded that any of these criteria may be used to select the best cross combinations. In order to confirm whether the crosses selected on the basis of the high sca effects were really the best performing crosses, the five best crosses were selected firstly on the basis of *per se* performance of the hybrids and secondly on the basis of sca effects. These crosses are presented in the following list.

Characters	*per se* performance	sca effects
Height	5×7	2×8
	1×4	3×4
	3×4	1×4
	4×5	5×7
	4×7	1×8
Number of branches	2×8	2×8
	4×7	2×6
	3×4	2×3
	6×7	6×7
	4×5	6×8
Number of fruits	6×8	1×2
	1×2	6×8
	3×6	2×4
	3×5	1×5
	1×5	3×6

Number of locules	2×7	2×7
	5×6	5×6
	4×6	1×2
	3×4	4×6
	1×2	5×7
T.S.S.	3×7	3×7
	2×6	2×6
	1×6	1×6
	3×5	3×5
	1×4	1×8
Acidity	5×6	1×7
	1×6 and 6×8	2×4 and 5×8
	2×4	6×8
	3×6 and 5×8	1×7
	2×7	7×8
Ascorbic acid	2×8	2×7
	1×8	2×4
	4×7	5×8
	3×8	6×8
	1×3	1×7
Yield	4×5	1×2
	5×6	6×7
	6×7	5×6
	5×8	4×5
	1×2	5×8

From the list the following points were evident:

i) It was only for yield that all the five crosses were common for *per se* performance and sca effects. It may, however, be mentioned that these crosses occupied different positions under these two comparisons. For other traits like height, number of branches, number of fruits, locule number, T.S.S. and acidity, only a few crosses were common to both comparisons. None of the crosses selected for ascorbic acid content on the basis of *per se* performance tallied with those selected on the basis of sca effects.

(ii) With regard to plant height, locule number, T.S.S., ascorbic acid content and yield, the crosses selected on the basis of their actual performance were superior to the best parent. For number of branches and for number of fruits the crosses were inferior to the best parent. With the exception of number of branches, number of locules, T.S.S. and ascorbic acid content, the specific combining ability effects

Table 5. *Specific combining ability (sca) effects of twenty-eight crosses and their ranks*

Characters/ crosses	Height of plant	Number of branches	Number of fruit per plant	Number of locule per plant	T.S.S.	Acidity	Ascorbic acid content	Yield kg/plant	Ranks Performance	sca effects
(1 × 2)	47.40	7.22	78.42	2.68	0.01	0.71	9.71	2.78	18	8
(1 × 3)	35.36	6.33	18.94	2.21	1.54	0.87	14.65	1.32	24	21
(1 × 4)	79.32	4.81	41.66	2.22	2.47	0.67	15.55	1.71	10	10
(1 × 5)	39.79	7.80	54.22	2.37	2.30	0.86	13.93	1.91	14	8
(1 × 6)	43.36	7.56	44.01	2.43	3.29	0.60	19.17	1.71	7	1
(1 × 7)	22.41	7.52	41.76	2.56	2.35	0.54	19.49	1.32	16	13
(1 × 8)	68.60	7.42	44.31	2.11	2.75	0.90	23.88	2.04	11	5
(2 × 3)	47.46	9.03	33.06	2.43	1.00	0.81	15.26	1.66	20	12
(2 × 4)	38.37	6.28	58.42	1.80	2.58	0.50	14.26	1.50	17	11
(2 × 5)	23.24	3.56	42.09	2.34	2.52	0.73	15.76	1.14	21	17
(2 × 6)	66.49	9.05	32.63	2.22	3.70	0.81	23.96	1.91	15	2
(2 × 7)	40.21	2.73	37.28	3.06	1.17	0.47	12.79	1.50	20	15
(2 × 8)	80.60	12.16	29.71	2.56	1.03	1.07	12.65	1.40	19	16
(3 × 4)	75.33	8.67	35.18	2.73	2.11	0.66	12.88	1.54	2	7
(3 × 5)	32.39	7.20	47.53	2.57	3.21	0.68	13.30	1.72	9	10
(3 × 6)	39.86	3.16	51.47	1.97	0.69	0.64	14.29	1.40	22	18
(3 × 7)	63.91	7.63	44.74	2.22	4.22	0.79	16.95	1.90	3	3
(3 × 8)	41.70	7.83	29.97	2.21	0.66	0.80	15.21	1.34	23	20
(4 × 5)	55.86	7.73	51.04	2.02	0.99	0.82	17.22	2.13	4	8
(4 × 6)	22.53	7.24	41.04	2.63	1.52	0.76	17.19	1.36	13	15
(4 × 7)	43.58	7.46	36.10	2.28	1.16	0.91	19.43	1.73	12	14
(4 × 8)	30.67	7.31	19.93	2.51	1.32	0.65	12.89	1.37	17	19
(5 × 6)	64.14	5.93	43.13	3.06	1.33	0.60	15.98	2.18	1	3
(5 × 7)	70.31	6.61	50.05	1.59	0.97	0.62	18.55	1.75	8	9
(5 × 8)	44.98	6.94	42.68	2.59	2.44	0.50	13.10	2.08	5	4
(6 × 7)	68.11	8.99	49.11	2.57	2.73	0.88	11.46	2.36	16	3
(6 × 8)	33.52	8.97	60.49	1.80	2.01	0.52	16.07	1.73	15	6
(7 × 8)	17.00	4.26	32.85	2.13	2.26	0.59	7.51	0.99	25	22
S.E.	±6.55	±0.73	±10.92	±0.265	±0.81	±0.315	±2.47	±0.468	$r = 0.977$	
S.E. for (Sij-Skl)	±9.14	±1.02	±15.23	±0.12	±1.13	±0.44	±3.45	±0.654		

did not predict the best performing cross combination.

(iii) It was evident from the above comparison that the ranking of best crosses on the basis of *per se* performance was not necessarily reflected by the ranking based on sca effects.

iv) The crosses showing high mean performance for yield did not show high sca effects or high mean performance for other characters also including yield components.

Critical analysis of Table 5 would give an idea of the type of parent involved in the best crosses. This analysis would provide information on the correlation between general combining ability and specific combining ability. The crosses which produced maximum yield were Punjab Tropics × Sl-120 (3.728 kg/plant), Sl-120 × HS-101 (3.709 kg/plot) and Sl-120 × Sl-73-1 (3.309 kg/plot). One of the parents involved in these cases was Sl-120 which had been rated as best general combiner with regard to yield and was judged second when overall performance was considered. The other parents, Punjab Tropics, Sl-120 and Sl-73-1, were also among the good general combiners. This means that high heterotic performance was shown by the crosses involving parents with high general combining ability effects. This indicates the presence of the additive × additive type of gene interaction.

Taking height, the cross which had the maximum height was Sl-120 × Pusa Ruby (124.62 cm), followed by Pusa Early Dwarf × Punjab Tropics (118.75) and S-12 × Punjab Tropics (118.25). On the other hand, the best general combiner with regard to height was Punjab Tropics (94.13 cm), followed by Pusa Ruby (88.0 cm) and Sl-120 with an array mean of 84.53 cm. This clearly indicates that in these cases at least one of the parents was a good general combiner.

Discussion

The purpose of diallel analysis is (i) to spot the best combiners for general and specific purposes and (ii) to provide estimates for gca and sca variances. The variance components due to gca and sca may be genetically interpreted under certain assumptions and are, therefore, useful in framing the most suitable breeding plans. In the present study it was demonstrated that the variance component due to gca (σ_g^2) was higher than due to sca (σ_s^2) in the case of yield and number of fruits, indicating the preponderance of the additive type of gene action. This means that simple selection schemes would suffice to bring about desired changes in yield and fruit number in the population. On the other hand, all the other characters were seen to have high variance component due to specific combining ability, which means an excess of non-additive type gene action. In such cases heterosis breeding, or any other breeding plan which makes use of specific combining ability effects, would be more effective.

The estimates for general and specific combining ability effects provide a basis for selecting the parents with high general and specific combining ability. Again, the gca and sca effects are the estimates and may be estimated only under certain sets of assumptions (Griffing 1956). In the present investigation, it has been demonstrated that the ranking pattern of the parents based on the array means remained unaltered when it was compared with the ranking on the basis of gca effects. Similar observations were also made by Singh *et al.* (1974) in a line × tester analysis in pearl millet. These results indicate that suitable combiners may be selected on the basis of the array mean itself and it does not seem to be necessary to estimate the gca effects as generally done in diallel analysis.

When all the characters were considered simultaneously, the ranking pattern of the crosses based on their *per se* performance was also reflected in that based on the sca effects. The rank correlation was found to be very high ($r_s = 0.99$), but when the crosses were examined for the individual characters separately, the best crosses selected on the basis of sca effects were not always the same as those selected on the basis of their real performances. The five best crosses selected on the basis of these two criteria were the same with respect to yield, but the positions occupied by these crosses under the two comparisons were not the same. For other traits, such as number of branches, only 3 out of 5 crosses were common to both these criteria. If we analyse these results critically, keeping in view the objectives of heterosis breeding, the selection of crosses on the basis of *per se* performance seems to be more reliable than selection based on sca effects. The latter, being an estimate, may be biased through non-fulfilment of any of the assumptions involved in the model. The *per se* performance is the true realized mean of the crosses and hence the question of being wrong does not arise. In addition, the calculation of sca effects is complicated and time consuming. High specific combining ability denotes, undoubtedly, a high heterotic response; this, however, does not mean high performance of the hybrid as well. It is easy to conceive of a situation where high heterotic response may result due to poor performance of the parents in relation to their hybrid combination. On the other hand, even with the same amount of heterotic response, the sca effect may be lower provided that the parental performance is relatively high. This suggests that sometimes the estimates of sca effects may not lead to the correct choice of hybrid combination. It is, therefore, advisable to put more emphasis on the *per se* performance than on the estimates of specific combining ability. It was also observed that the best hybrid combinations with respect to yield were given by the crosses between those genotypes which had relatively high gca effects. This shows an additive type of epistatic interaction. In other cases, only one of the parents involved in the crosses was a good general combiner.

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