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Combining Ability of Tomato Lines for Fruit Quality Traits

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INTRODUCTION

In demand for the tomato processing industry are tomato lines having fruit of high acidity and high soluble solids content. A significant step in a comprehensive breeding program to develop better processing varieties was the identification and characterization of germ-plasm possessing these desirable traits (12, 13, 21).

Genetic studies are currently underway at the Missouri Agricultural Experiment Station to study the mode of inheritance of these traits and to determine the combining potential for fruit quality attributes of several breeding lines and varieties in hybrid combinations. Generally, in a hybridization program it is desirable to test inbred lines for general combining ability before testing them in specific hybrid combinations. After the more promising inbreds have been selected on the basis of high general combining ability, single, three-way, or double crosses are identified that will give the highest performance for the traits of interest. The following research was conducted to investigate the potentials of several promising breeding lines.

REVIEW OF LITERATURE

Quality Traits

A search of the literature on the inheritance of quality attributes revealed only the study of soluble solids by Stoner and Thompson (20). In that study, four of the parents had small fruits and four had large fruits. The investigators found differences in specific and general combining ability for soluble solids. Stoner's unpublished work (19), from which the published report was taken, reported significant genetic variation among parents, dominance effects, and reciprocal differences among the diallel crosses.

Yield Traits

Earlier studies of combining ability in the tomato pertained primarily to yield characters. Currence *et al.* (3) reported close agreement between the yield of a particular variety and its general combining ability. They suggested that

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varieties with good general combining ability may be used to test with other varieties for parents of hybrid combinations. It was indicated that the general combining ability of a variety can be determined by averaging its performance in several combinations, preferably with varieties known to have good combining ability. Powers (15) showed that inbred lines of high combining ability for eleven characteristics were also superior in the characteristics in comparison with other inbreds.

Moore and Currence (14), in their evaluation of 27 tomato varieties for yield, reported that three-way cross performance gave a "fair approximation" of general combining ability as estimated from the means of varieties in single crosses. However, the 3-way crosses were not superior to varietal performance in predicting early fruit yield, total fruit yield, yield of grade 1 fruit, and, possibly, fruit size. Also the three-way cross was not generally useful as an indicator of general combining ability for fruit size. They pointed out this may have been due to biases resulting from unfavorable climatic conditions.

In a different genetic scheme, Honma and Currence (7) used individual plants of four established varieties as testers to measure the combining ability of backcross selections with the recurrent and non-recurrent parents, and the original cross for early yield, total yield, and fruit size. They averaged the test cross means to estimate general combining ability and used the means of the different backcross generations in crosses with individual testers to estimate the specific combining ability of the backcross selections.

In a three-year study of general and specific combining ability for yield traits of tomatoes, Horner and Lana (8) showed that the effects of specific combining ability were not stable from year to year.

The top cross test using a variety, a single cross, or a double cross as testers, has been used widely on agronomic crops since it was first reported by Davis (4). It has been suggested that the choice of tester depends on the use of the lines in a breeding program (6). For corn indications are that the single cross is the most desirable tester when one or more of the lines to be used are on the opposite side of the double cross. Beard (1), among others, recommended using the single cross rather than an open-pollinated variety as tester. Sprague and Tatum (18) suggested that the top cross be used primarily for screening lines on the basis of their general combining ability. Other workers, (6, 10, 11, 18) agreed that top cross tests could be used safely to discard poor combining lines.

MATERIALS AND METHODS

Parental lines

Eleven tomato lines representing a wide range for soluble solids (Brix), pH, and titratable acidity were selected for this study, using two inbred lines and their F_1 single cross as tester parents. Brief descriptions of the lines, their accession number, and origin are in Table 1. Figure 1 illustrates the morphological characteristics and relative fruit size for these lines. The inbred testers were Mo Acces-

Table 1 IDENTITY, SEED ORIGIN AND FRUIT CHARACTERISTICS OF 13 TOMATO LINES AND VARIETIES

Mo. Acc.	P.I. No.	Seed Origin*	Variety	Approx. Fruit Weight(g.)	Fruit Color	Fruit Shape
2	91458	India	Primrose Gage	48	Yellow	Globe
31	118785	Venezuela	---	38	Red	Globe
90	127810	Peru	---	37	Red	Pear
98	128223	Bolivia	---	40	Red	Globe
117	128886	France	Merveille de Merches	68	Red	Pear
197	270246	South Carolina	Stemless Penn Orange	134	Yellow	Globe
223	272689	El Salvador	---	23	Red	Oval (egg)
235	272709	Guatemala	---	69	Red	Flat Globe
---	---	H.J. Heinz Co.	H 1370	107	Red	Globe
---	---	Mo. AES	Tomboy	191	Pink	Globe
---	---	Commercial Source	Improved Garden State	265	Red	Globe
---	---	Commercial Source	Orange Jubilee	167	Orange	Globe
I-417-1	---	Mo. AES	---	174	Pink	Globe

* Seed of all P.I. lines were obtained from the USDA Plant Introduction Station at Ames, Iowa.

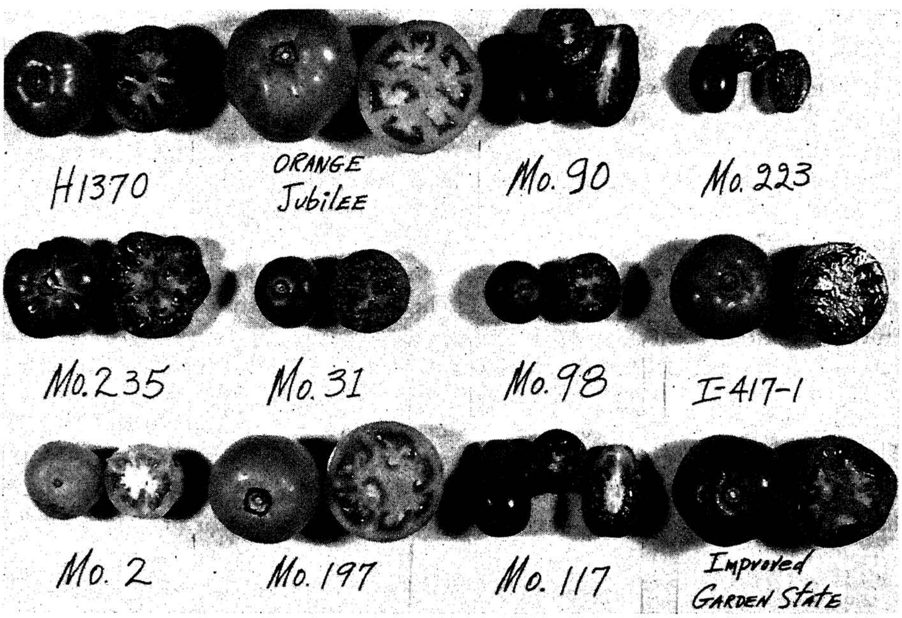

Fig. 1.—Morphological characteristics of fruit of tomatoes used in this study.

sion 223 and I-417-1. Mo. Accession 223, a selection of USDA PI 272689 has a small fruit (ca 24g.), high acidity, and high sugar. I-417-1 has a large fruit (ca 175g.), low acidity, and low sugar.

Hybridization

During the fall and winter of 1967, each line was crossed to each of the three testers to produce seed for the 22 possible single crosses and the 11 3-way crosses. It was assumed that reciprocal differences were not present, and whether crossed seed was produced on either parent was not considered a source of error.

Seeding and Culture

All test cross and three-way cross hybrids plus the 13 inbreds (including the two inbred testers) were seeded in flats containing vermiculite April 18, 1968. Upon reaching the first true leaf stage, the seedlings were transferred to peat pots. May 25, the seedlings were transplanted to the field at the Horticultural Research Facility at New Franklin, Mo. The field design was a randomized complete block with seven replications. A replication consisted of 46 plots of three plants. The single-row plots were spaced about 3 feet and the plants within the plot about 2½ feet apart.

Harvesting and storage

Firm ripe fruits were harvested from individual plants on August 15 and placed in transparent plastic bags and immediately frozen at temperatures ranging from –4 to 0°F. Each sample consisted of 1-15 fruits.

Chemical assay

Chemical analyses were started September 2 and completed October 14. Fruit samples were allowed to thaw in plastic beakers and macerated with a porcelain pestle. The juice was strained through a double layer of muslin cloth, then centrifuged. Soluble solids were then determined with a Bausch and Lomb Abbe refractometer and the readings were corrected for temperature. Ten-ml aliquots of juice from each sample were pipetted into disposable, aluminum-lined paper cups and diluted to 100 ml with demineralized water. The pH and titratable acidity were determined on this sample with a Fischer automatic/manual titrimeter. The solution was titrated with a .0657N NaOH solution and the titratable acidity was expressed as percent citric acid equivalent.

Statistical analyses

Analysis of variance and linear regression analyses were made on individual plant data with an IBM 7040 computer. Rank correlation coefficients were computed manually by Spearman's method as described by Snedecor (17).

RESULTS AND DISCUSSION

Soluble Solids (Brix)

1. Tests of Significance.

F-tests from the analysis of variance showed highly significant differences in soluble solids content within and between groups of inbreds and top/test crosses (Table 2). The mean square of inbreds was about 3 times as large as that of the $F_1{}^2$ group which had the largest mean square of the 3 hybrid groups. The 3-way crosses had the smallest mean square of the three hybrid groups of progenies.

An orthogonal set of group comparisons indicated that the average Brix of the two single (test) cross groups (5.53) was significantly higher than that of the inbreds (5.14), as shown in Table 3. The $F_1{}^1$ group had a significantly higher Brix (6.07) than the average Brix (4.99) of the $F_1{}^2$ group. The average of these two test cross groups (5.53) closely proximate that of the three-way cross (5.58).

2. Combining Performance.

Three-way (top) cross performance (Table 3, line 4) was used as a measure of general combining ability and the average (Brix) of the two test crosses, designated $F_1{}^1$ and $F_1{}^2$ (Table 3, line 5) was used as a measure of average combining ability. However either measure of combining ability may reflect general and specific effects. Use of both procedures should screen the inbred lines for breeding worth on the inbred and moderate base single cross testers. Significant regressions discussed later indicated important additive gene effects. The measures would thus also effectively screen lines for general combining ability. The means (Table 3, line 6) were used as indicators of over-all combining ability.

Mo. 98, Mo. 235, Mo. 31 and Mo. 2 showed superior general combining ability for Brix, and their means (Table 3, line 4) were not significantly different. These lines are all comparatively small-fruited, ranging in fruit weight from 40 to 70 gms. The general combining ability for soluble solids of Orange Jubilee, a large fruited line, was significantly lower than that of Mo. 98 only. The general combining ability of the other large fruited varieties, H 1370, Improved Garden State (IGS), and Tomboy was not different but it was significantly lower than that of Mo. 235 and Mo. 98.

In terms of average combining ability for Brix, all large-fruited lines except Orange Jubilee were significantly lower in Brix than Mo. 235, Mo. 98 and Mo. 2. Missouri 31, Mo. 90 and Orange Jubilee showed good average combining ability, their Brix values being significantly lower only from Mo. 235.

The over-all performance data (Table 3, line 6) indicate that Mo. 235; Mo. 98; Mo. 2; and Orange Jubilee have good potential for high Brix. The performance of Mo. 31 is of particular interest. Although it was significantly lower in Brix than the other lines in inbred performance (Table 3, line 1), it differed significantly only from Mo. 235 in the top group for over-all combining ability.

Table 2 MEAN SQUARES AND DEGREES OF FREEDOM FROM ANALYSES OF VARIANCE OF BRIX, pH AND TITRATABLE ACIDITY BETWEEN AND AMONG GROUPS OF INBREDS AND TOP/TEST CROSSES

Source	d.f.	Mean Squares		
		Brix	pH	Titratable Acidity
Reps	6	1.9907**	0.6744**	0.2890*
Entries	43	6.4489**	0.1224**	2.0559**
Groups	3	54.3780**	0.0227	2.3892**
Inbreds vs. Average of F_1's	1	23.2185**	0.0659	0.5316*
F_1^1 vs. F_1^2	1	134.2121**	0.0003	6.2719**
3-way vs. Average of inbreds and F_1's	1	5.7037**	0.0019	0.3640
Among inbreds (P)	10	6.0411**	0.3299**	4.5918**
Among F_1^1 (P x Mo. 223)	10	1.8279**	0.0319	0.7140**
Among F_1^2 (P x I-417-1)	10	2.2474**	0.0502*	1.3007**
Among 3-way cross	10	1.3004**	0.1075**	1.5170**
Experimental Error	258	0.3212	0.0249	0.1074
Sampling Error	616	0.1979	0.0149	0.0759
Total	923	--	--	--

* Significant at 5% level.
** Significant at 1% level.

Table 3 MEANS OF INBREDS AND THEIR TOP CROSSES FOR BRIX (%)

Combination	Inbreds (P)											Group Mean
	H 1370	117	IGS	31	197	Tomboy	90	OJ	235	98	2	
(1) P x P	4.08	4.67	4.70	4.79	4.98	5.26	5.52	5.55	5.55	5.60	5.84	5.14
(2) P x Mo. 223* (F_1^{1})	5.76	5.99	5.76	6.33	5.91	5.82	6.15	5.79	6.50	6.21	6.55	6.07
(3) P x I-417-1* (F_1^{2})	4.63	4.50	4.93	4.79	4.83	4.93	4.94	5.24	5.57	5.45	5.09	4.99
(4) P x (Mo. 223 x I-417-F_1) 3-way	5.49	5.12	5.48	5.73	5.39	5.43	5.54	5.62	5.90	6.01	5.68	5.58
(5) Average (2, 3)	5.20	5.25	5.35	5.56	5.37	5.38	5.55	5.52	6.04	5.83	5.82	5.53
(6) Average (2, 3, 4)	5.29	5,20	5.39	5.62	5.38	5.39	5.54	5.55	5.99	5.89	5.77	5.55

* Means of Mo. 223 = 6.78
I-417-1 = 5.92

$LSD^{.05}$ = .341 for lines 1, 2, 3, and 4.

Table 4 SUMMARY OF CORRELATION (r) AND REGRESSION COEFFICIENTS (b) FOR COMPARISONS OF PAIRED VARIATES FOR BRIX

Comparisons	r	b	Rank correlation coefficients (r_s)
Average of test crosses vs. Inbreds	.781**	.386 ± .174**	.862**
Average of test crosses vs. Top cross	.844**	.906 ± .149**	.855**
Top cross vs. Inbreds	.539	.248 ± .219	.655*
Inbreds vs. F_1^1	--	--	.618*
Inbreds vs. F_1^2	--	--	.882**
F_1^1 vs. F_1^2	--	--	.407
F_1^1 vs. Top cross	--	--	.598*
F_1^2 vs. Top cross	--	--	.707**

* Significant at 5% level.
** Significant at 1% level.

3. Correlation and Regression Analyses.

Highly significant correlations (Table 4) were observed between average single (test) cross performance and inbred productivity for Brix (r=.781**) and between top cross and average Brix of single (test) crosses (r=.844**). The correlation (r = .539) between Brix productivity of inbreds and top crosses was not significant at the 5 percent level.

The regressions of the Brix values for the average of the test crosses on their respective inbreds and on top crosses were highly significant (Table 5). The regression of top cross on inbreds was not significant. The regression coefficients (b) are summarized in Table 4.

Table 5 ANALYSES OF VARIANCES OF Y FOR BRIX INVOLVING 22 SINGLE (TEST) CROSSES AND 11 3-WAY (TOP) CROSSES

	d.f.	x = Inbreds y = Test Cross Ave.		x = Top Cross y = Test Cross Ave.		x = Inbred y = Top Cross	
		S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Total	10	0.7033	--	0.7033	--	0.6113	--
Regressions	1	0.4284	0.4284**	0.5019	0.5019**	0.1777	0.1777
Deviations from Regressions	9	0.2749		0.2014	0.2014	0.4336	0.0482

** Significant at 1%.

Figures 2, 3, and 4 show the linear relationships for Brix between the paired variates. Regression lines have been drawn through the scatter of observed points. Points in Figures 2 and 3 show closer fits to the regression lines than those in Figure 4. In Figure 2, the regression line indicates a .386 unit increase in average Brix of test crosses for each unit increase in inbred productivity for Brix. The regression line in Figure 3 slopes at a far greater rate of .906x.

These relationships indicate that inbred performance for Brix can be used reliably to predict average combining ability but not general combining potential. However, an inbred that has shown good general combining ability can be expected to show good average combining performance.

Rank correlations (Table 4) indicated that the rankings of respective F_1^1 and F_1^2 progenies of the 11 lines tested were not in accord statistically but rank pairings of all other lines and progenies were significantly correlated. These rank correlations, however, can not be used as substitutes for r obtained from product-moment computations (17) and are presented only to give non-parametric evidence for dependence or independence of rankings of paired values.

4. Dominance and Potence

The F_1^1 and F_1^2 test cross groups present striking contrasts in dominance relation of gene sets (Table 6). In the F_1^1 group the F_1 was, on the average, .11 units higher in Brix than the midparental (MP) value; however, this difference

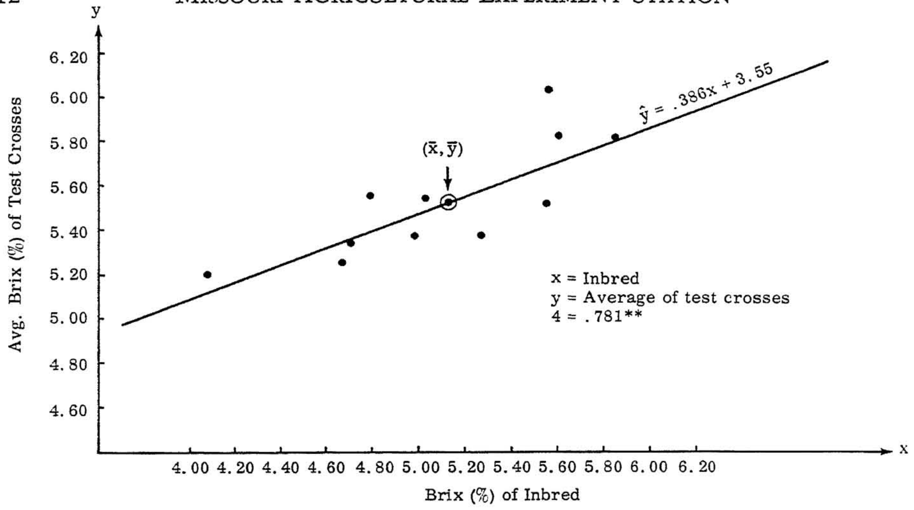

Figure 2. Regression of average test cross performance on productivity of eleven tomato inbreds for Brix. Group means (x̄, ȳ) of variates (Table 3, lines 1 and 5) denote origin.

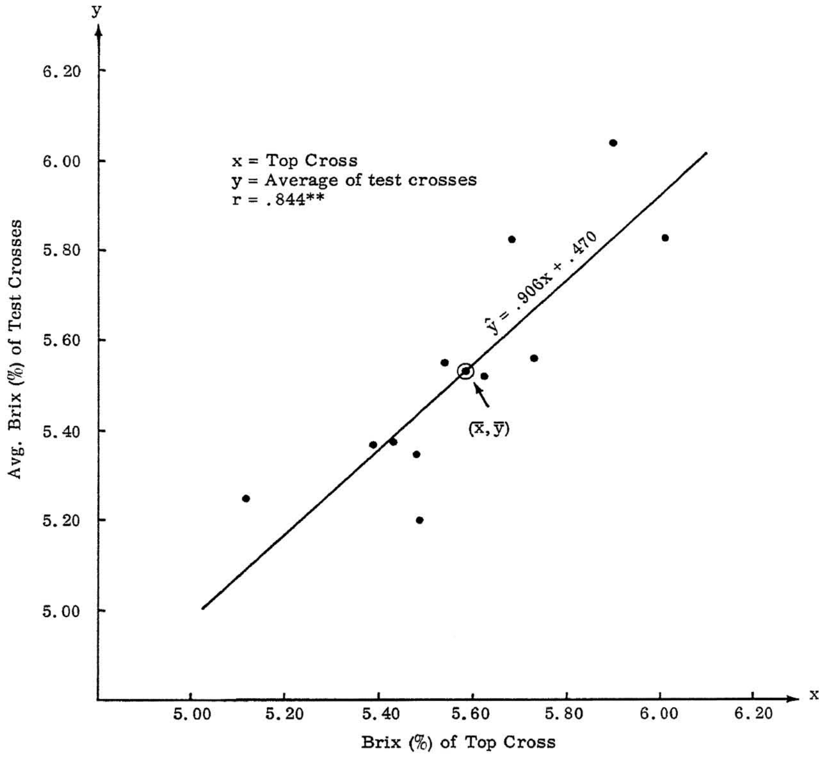

Figure 3. Regression of average test cross performance on productivity of top crosses of eleven tomato inbreds for Brix. Group means (x̄, ȳ) of variates (Table 3, lines 4 and 5) denote origin.

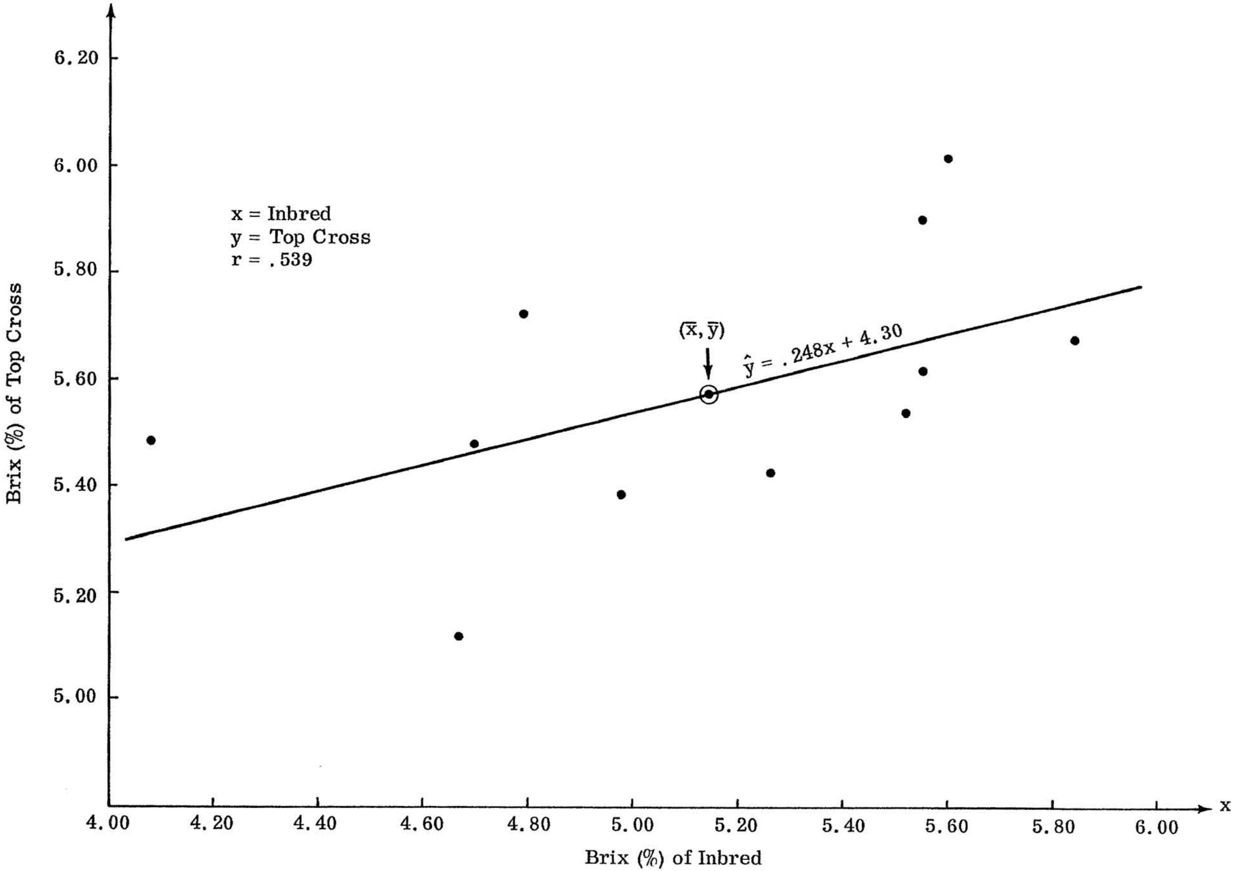

Figure 4. Regression of top cross performance on productivity of eleven tomato inbreds for Brix. Group means ($\bar{x}$, $\bar{y}$) of variates (Table 3, lines 1 and 4) denote origin.

Table 6 RELATIVE POTENCE[1] OF GENE SETS FOR BRIX CONTENT IN TWO SETS OF SINGLE (TEST) CROSSES

Lines	Means	$F_1^1 - \overline{MP}^1$	Potence	$F_1^2 - \overline{MP}^2$	Potence
H 1370	4.08	.33	.24	-.37	- .40
Mo. 117	4.67	.26	.25	-.80	- 1.29
IGS	4.70	.02	.02	-.38	- .62
Mo. 31	4.79	.54	.55	-.57	- 1.02
Mo. 197	4.98	.03	.03	-.62	- 1.32
Tomboy	5.26	- .20	- .26	-.66	- 2.00
Mo. 90	5.52	0.0	0.0	-.78	- 3.90
O.J.	5.55	- .38	- .62	-.50	- 2.78
Mo. 235	5.55	.33	.54	-.17	- .94
Mo. 98	5.60	.02	.03	-.31	- 1.94
Mo. 2	5.84	.24	.51	-.79	-19.75
Average	5.14	.11	.12	-.54	- 3.27
Mo. 223 (Tester 1)	6.78				
I-417-1 (Tester 2)	5.92				

1 Obtained from the ratio $\frac{\overline{F_1} - \overline{MP}}{\overline{P} - \overline{MP}}$ (after Griffing) where $\overline{P}$ = greater parent mean.

may not be statistically significant. The average potence of .12 suggests a preponderance of plus genes for Brix.

In the F_1^2 group, the F_1 was, on the average, .54 units lower than the MP Brix value. This appears to be a significant deviation from the MP origin and indicates negative dominance. An average potence of –3.27 suggests a preponderance of plus genes for lower Brix.

Some crosses also showed partial dominance for high Brix. These data give further support to a previous report (15) on the presence of dominant genes for both low and high solids.

5. Heritability Estimates

Heritability estimates were obtained for Brix of each cross from regressions of individual F_1 plant values on their respective MP values. These estimates, presented in Table 7, should proximate the additive gene effects. Exceptionally high or low values may indicate profound dominance or possible genotype-environment interactions. Negative estimates were considered meaningless.

The preponderance of positive estimates in the F_1^1 group indicates that Mo. 223 may be the more efficient tester (8) for Brix of the two inbreds. Most heritability estimates in both F_1 groups are sufficiently high, indicating appreciable additive gene effects which could play a prominent role in a selection program.

Table 7 HERITABILITY OF SOLUBLE SOLIDS CONTENT EXPRESSED AS THE REGRESSION OF F_1 ON MIDPARENTAL VALUES

Lines	Mean[1]	F_1^1 Group Heritability (%)	F_1^2 Group Heritability (%)
H 1370	4.08	3.2	-42.5*
O.J.	5.55	63.4	-30.5
Mo. 90	5.52	6.3	20.5
IGS	4.70	- 4.7	- 0.2
Mo. 235	5.55	50.3	-20.4
Mo. 31	4.79	32.1	8.7
Mo. 98	5.60	8.0	-23.9
Mo. 197	4.98	90.0*	- 6.3
Mo. 2	5.84	84.2*	0.2
Tomboy	5.26	39.6	15.3
Mo. 117	4.67	16.3	20.9

1/ Mo. 223 = 6.78; I-417-1 = 5.92
* Significantly different from zero at 5% level.

Acidity (pH)

1. Tests of Significance

Variance analysis and orthogonal comparisons of group means indicated no significant statistical differences in pH between groups (Table 2).

However, significant differences in fruit pH were found between inbreds, among F_1^2 single (test) crosses, and among three-way (top) crosses. Fruit pH's of F_1^1 single (test) crosses did not differ significantly from each other.

The variance of the inbred parents was about three times as great as that of the three-way crosses. Variances of the two F_1 groups were less than half those of the three-way crosses.

The pH means of inbreds and their test or top crosses are summarized in Table 8. The most acidic lines, as indicated by low pH values, were Mo. 235, Mo. 98, and Mo. 31. Although these lines did not differ significantly among themselves, all three had significantly lower pH's than the other inbred lines (except IGS), including the tester inbreds.

2. Combining Performance.

From a comparison of the means of the three-way crosses, Mo. 98, Mo. 31, Mo. 2, and Orange Jubilee had significantly higher general combining ability than Improved Garden State, Mo. 197, and Mo. 90 (Table 8, line 4). Mo. 98 also showed significantly higher general combining potential for low pH than Tomboy and Mo. 117. The top lines in general combining ability were also high in average combining ability (Table 8, line 5); however, their means for average combining ability did not differ significantly. Of the top lines, Mo. 31 was the most consistent performer in all of its top and test crosses. The over-all performance data (Table 8, line 6) suggest that lines Mo. 235, Mo. 98, and Mo. 31 should give specific hybrid combinations having low fruit pH's.

Table 8 MEANS OF INBREDS AND TOP CROSSES FOR FRUIT pH

Combination	Inbreds (P)											Group Mean
	235	98	31	IGS	Tomboy	OJ	117	197	H 1370	90	2	
(1) P x P	4.24	4.28	4.31	4.40	4.41	4.48	4.50	4.53	4.53	4.59	4.61	4.45
(2) P x Mo. 223* ($F_1^{\ 1}$)	4.35	4.40	4.38	4.46	4.41	4.46	4.47	4.41	4.46	4.45	4.42	4.42
(3) P x I-417-1* ($F_1^{\ 2}$)	4.38	4.34	4.37	4.45	4.44	4.43	4.42	4.51	4.47	4.46	4.42	4.43
(4) P x (Mo. 223 x I-417-1)F_1 3-way	4.40	4.32	4.37	4.49	4.44	4.38	4.45	4.49	4.41	4.58	4.38	4.43
(5) Average (2, 3)	4.37	4.37	4.38	4.46	4.43	4.45	4.45	4.46	4.47	4.46	4.42	4.43
(6) Average (2, 3, 4)	4.38	4.35	4.38	4.47	4.43	4.41	4.45	4.47	4.45	4.50	4.41	4.43

* Means of Mo. 223 = 4.40
I-417-1 = 4.46

$LSD^{.05}$ = .10 for mean comparisons in lines 1, 2, 3, 4, only.

3. *Correlation and Regression Analyses*

Paired comparisons were made to analyze relationships between inbreds, test crosses and top crosses (Table 9).

Average test cross performance was highly correlated ($r=.782^{**}$) with inbred performance. A significant correlation ($r=.666^{*}$) was also observed between three-way (top) cross and average test cross performance. The correlation ($r=.502$) between inbred and top cross performance was not significant at the 5 percent level.

The rank correlations show that the $F_1^{\,1}$ group does not have significant r_s with respect to the other variate compared. On the other hand, the $F_1^{\,2}$ group had significant concordance with ranks of inbreds and top cross but not with those of the $F_1^{\,1}$ group. The lack of significance of $r=.502$ between top cross and inbreds is confirmed by the low r_s value of .438.

The regressions of average test cross performance on inbred and top cross productivities were statistically significant; however, the regression of top cross on inbred performance was not significantly different from zero (Table 10). Regression coefficients are given in Table 10.

The linear relationships between the paired variates are shown in Figures 5, 6, and 7.

The regression lines in Figures 5 and 6 fit well the observed points while that of Figure 7 does not. The slope, however, in the latter figure is steep as a result of the high regression coefficient of 1.590; nevertheless, values as great or greater than this could occur largely due to chance.

The linear regressions suggest that inbred performance for low fruit pH can be used to predict average combining ability but would be tenuous in predicting general combining ability. A line that has shown good general combining ability, however, can be expected to show good average combining ability.

4. *Dominance and Potence*

On the average, the pH's of the $F_1^{\,1}$'s fell midway between those of their parents, showing general lack of dominance (Table 11). Slight deviations of the F_1 from the midparent (MP) in individual crosses were of no statistical significance. An average negative potence value of -0.01 indicates a very slight preponderance of dominant genes for low pH.

In like manner, the deviations of F_1's in the $F_1^{\,2}$ group from MP values were not statistically significant, the deviation being on the average -0.03. An average negative potence of -0.93 suggests a preponderance of plus genes for low pH.

5. *Heritability Estimates*

The heritability of fruit pH in each cross was obtained from regressions of individual F_1 plant values on their respective MP values. These are given in Table 12 for the $F_1^{\,1}$ and $F_1^{\,2}$ groups of single (test) crosses. These values estimate the additive genetic effects. Only H 1370 gave significant high estimates

Table 9 SUMMARY OF CORRELATION (r) AND REGRESSION (b) COEFFICIENTS FOR COMPARISON OF PAIRED VARIATES FOR FRUIT pH

Comparison	r	b	Rank Correlation Coefficient (r_s)
Average of test crosses vs. Inbreds	.782**	.240 ± .024**	.625*
Top cross vs. Inbreds	.502	1.590 ± .065	.438
Average of test crosses vs. Top cross	.666*	.356 ± .030*	.736**
Inbreds vs. F_1^1	--	--	.498
Inbreds vs. F_1^2	--	--	.619*
Inbreds vs. Top cross	--	--	.437
F_1^1 vs. F_1^2	--	--	.466
F_1^1 vs. Top cross	--	--	.482
F_1^2 vs. Top cross	--	--	.782**

* Significant at 5% level.
** Significant at 1% level.

Table 10 ANALYSES OF VARIANCES OF Y FOR pH INVOLVING 22 SINGLE (TEST) AND 11 3-WAY (TOP) CROSSES

		x = Inbred y = Test Cross Ave.		x = Inbred y = Top Cross		x = Top Cross y = Test Cross Ave.	
S.V.	D.f.	S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Total	10	.0149	--	.0522	--	.0149	--
Regression	1	.0091	.0091**	.0132	.0132	.0066	.0066*
Deviation from Regression	9	.0058	.0006	.0390	.0043	.0082	.0009

* Significant at 5% level.
** Significant at 5% and 1% levels.

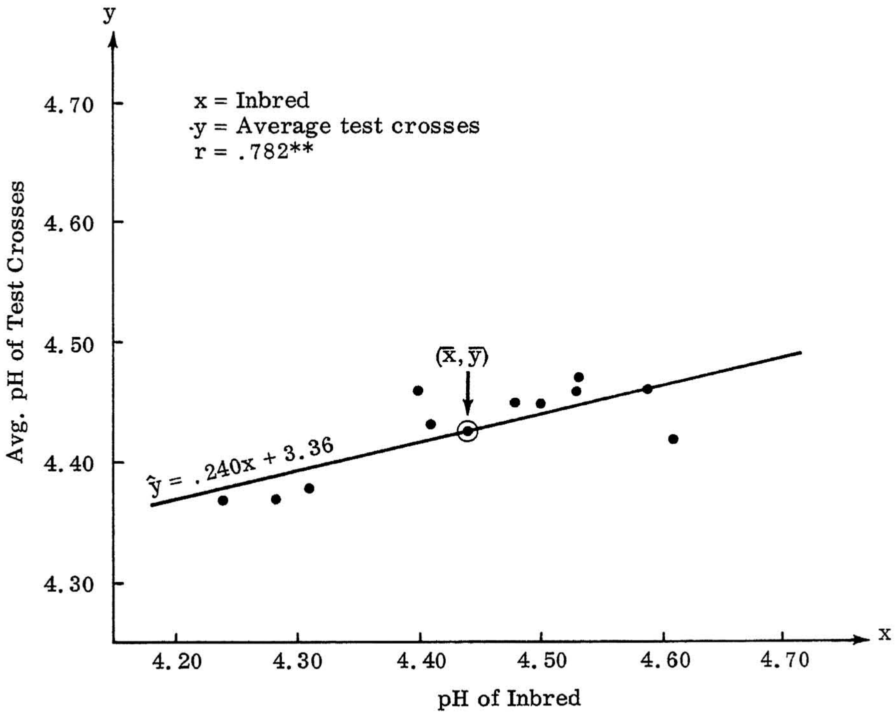

Figure 5. Regression of average test cross performance on productivity of eleven tomato inbreds for pH. Group means ($\bar{x}$, $\bar{y}$) of variates (Table 8, lines 1 and 5) denote origin.

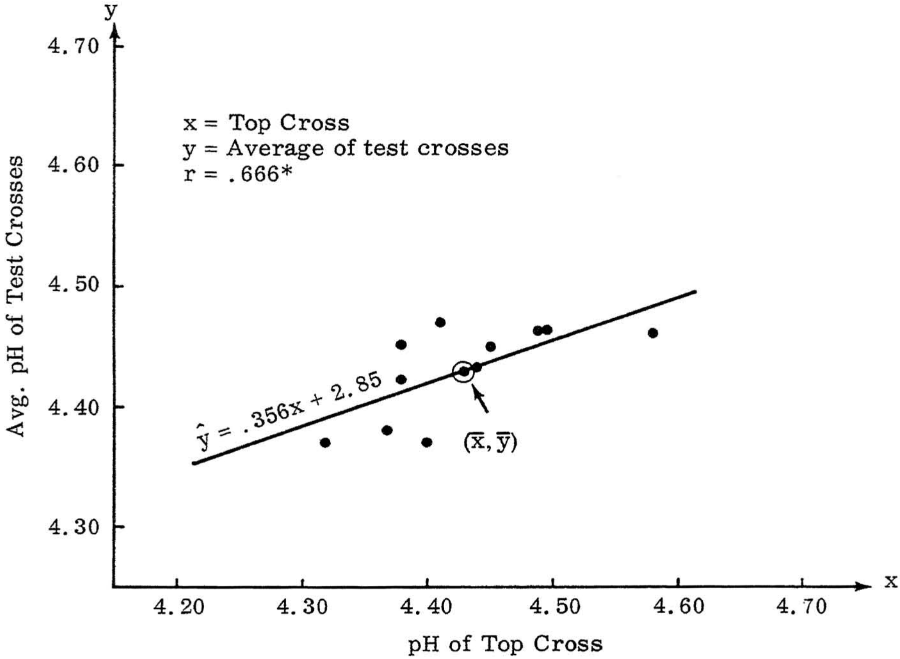

Figure 6. Regression of average test cross performance on productivity of top crosses of eleven tomato inbreds for pH. Group means ($\bar{x}$, $\bar{y}$) of variates (Table 8, lines 4 and 5) denote origin.

Table 11. RELATIVE POTENCE[1/] OF GENE SETS OF pH IN TWO SETS OF SINGLE (TOP) CROSSES

Lines	Means	$\overline{F}_1^1 - \overline{MP}^1$	Potence	$F_1^2 - \overline{MP}^2$	Potence
Mo. 235	4.24	.03	.35	.03	.27
Mo. 98	4.28	.06	.50	- .03	- .33
Mo. 31	4.31	.02	.75	- .02	- .29
IGS	4.40	.06	0.0	.02	.69
Tomboy	4.41	0.0	0.0	0.0	0.0
O.J.	4.48	.02	.50	- .04	-4.00
Mo. 117	4.50	.02	.40	- .06	-3.00
Mo. 197	4.53	- .06	-1.00	.01	.33
H 1370	4.53	- .01	- .17	- .03	-1.00
Mo. 90	4.59	- .05	- .56	- .07	-1.16
Mo. 2	4.61	- .09	- .90	- .12	-1.71
Average	4.45	0.0	- .01	- .03	- .93
Mo. 223	4.40				
I-417-1	4.46				

1/ Obtained from the ratio $\frac{\overline{F}_1 - \overline{MP}}{\overline{P} - \overline{MP}}$ (Griffing) where P is extreme parent.

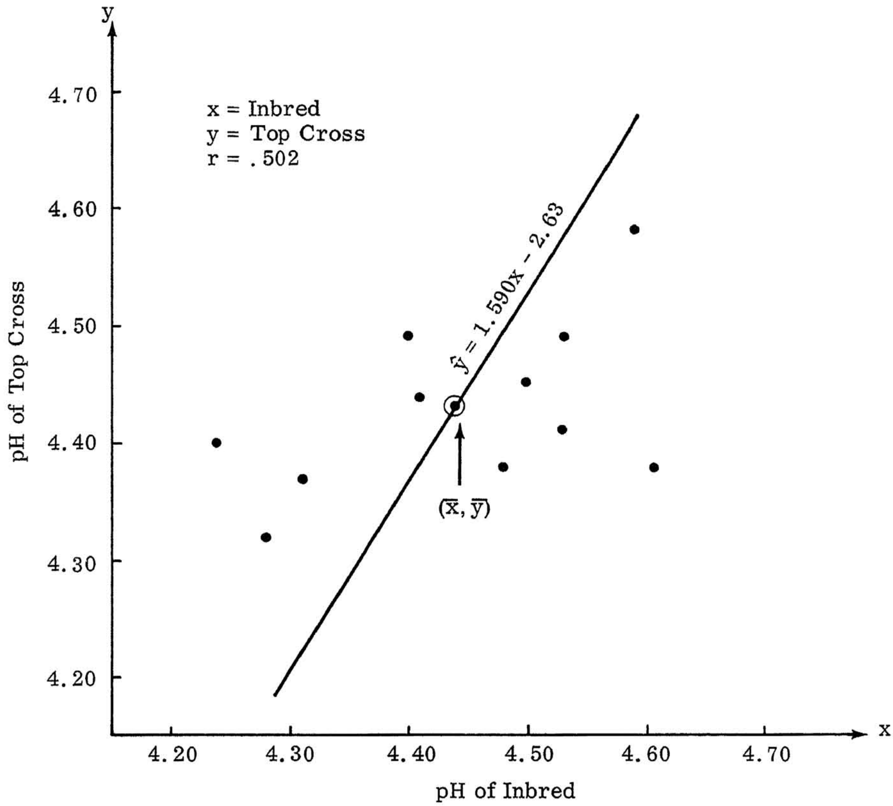

Figure 7. Regression of top cross performance on productivity of eleven tomato inbreds for pH. Group means ($\bar{x}$, $\bar{y}$) of variates (Table 8, lines 1 and 4) denote origin.

Table 12 HERITABILITIES (%) OF FRUIT pH IN SINGLE (TEST) CROSSES OF ELEVEN LINES OF TOMATOES BASED ON REGRESSIONS OF F_1 ON MIDPARENTS

	F_1 [1] Group	F_1 [2] Group
Lines	Heritability (%)	Heritability (%)
H 1370	41.1*	89.0*
O.J.	8.2	10.4
Mo. 90	30.9	- 4.2
IGS	1.0	- 4.2
Mo. 235	15.0	63.9
Mo. 31	56.1*	39.4
Mo. 98	18.9	-26.4
Mo. 197	9.4	28.9
Mo. 2	13.0	17.0
Tomboy	25.9	- 0.3
Mo. 117	6.5	47.8

* Significant at 5% level.

consistently. The more acidic lines Mo. 235 and Mo. 31 had high estimates also, in the range of 55 to 60 percent. Individual values with negative signs are meaningless. Most of the individual heritabilities, however, are of sufficiently high magnitude to justify individual plant selection for low pH.

Titratable Acidity

1. Tests of Significance

Significant differences in titratable acidity between and among groups of inbreds and top crosses were observed (Table 2). The variance of inbreds was about 3 times as great as that of the top crosses. The M.S. of $F_1{}^1$ group was about half that of the $F_1{}^2$ group. Variances of the top crosses and $F_1{}^2$ group appeared to be of the same magnitude.

The means of inbreds and top crosses for titratable acidity are presented in Table 13. The three-way (top) cross mean (.403) was not significantly higher than the averages of the inbreds (.386) and the two F_1 groups (.398). The titratable acidity of the $F_1{}^1$ group (.422) was significantly higher than that of the $F_1{}^2$ group (.372), but their average (.398) was not different from that of the inbred lines (.386).

2. Combining Performance

Mo. 98, Mo. 31, and Mo. 235 were among the top lines for general combining ability for titratable acidity and their citric acid equivalents did not differ significantly (Table 13, line 4). Mo. 2 and Orange Jubilee did not differ in titratable acidity from Mo. 31 and Mo. 235. The top three lines in general combining ability also did not differ in average combining ability among themselves or from Mo. 2 (Table 13, line 5). Mo. 98 showed identical performance in its two test crosses (Table 13, lines 2 and 3). Similarly, Mo. 31 also had consistent test cross performance regardless of tester inbred used. As expected, Mo. 31, Mo. 98, and Mo. 235 were equally good in over-all combining performance (Table 13, line 6). Mo. 2 also did not differ in titratable acidity from these three lines.

The large-fruited lines Mo. 197, H 1370, Improved Garden State, and Tomboy had a medium range for combining performance.

3. Correlation and Regression Analyses

Statistically significant correlations (Table 14) were obtained between the titratable acidity of the inbreds and the average titratable acidity of their test crosses (r=.655*) and between inbred and top crosses (r=.791**). Similarly, top cross performance and average titratable acidity of test crosses were highly correlated (r=.871**).

The rank correlation coefficients (r_s) of the first three comparisons confirm the significant r values. Of the three hybrid groups, only $F_1{}^1$ had non-significant r_s (.537) with the inbreds. All other possible comparisons of rankings of these three groups were highly correlated and their respective r_s values were about the same in magnitude.

Table 13 MEANS OF INBREDS AND TOP CROSSES FOR TITRATABLE ACIDITY (% CITRIC ACID)

Combination	Inbred (P)											Group Mean
	90	117	2	197	H 1370	IGS	OJ	Tomboy	31	98	235	
(1) P x P	.262	.284	.299	.320	.335	.348	.421	.457	.494	.502	.523	.386
(2) P x Mo. 223* ($F_1^{\ 1}$)	.381	.368	.488	.409	.420	.406	.421	.387	.450	.438	.473	.422
(3) P x I-417-1* ($F_1^{\ 2}$)	.340	.301	.394	.366	.321	.347	.369	.344	.450	.438	.444	.372
(4) P x (Mo. 223 x I-417-1)F_1 3-way	.317	.321	.433	.359	.398	.399	.424	.385	.456	.488	.455	.403
(5) Average (2, 3)	.360	.335	.441	.388	.371	.376	.395	.365	.450	.438	.459	.398
(6) Average (2, 3, 4)	.346	.330	.438	.378	.380	.384	.404	.372	.452	.455	.457	.400

* Mean of Mo. 223 = .467%
I-417-1 = .374%

Table 14 SUMMARY OF CORRELATION (r) AND REGRESSION (b) COEFFICIENTS FOR COMPARISON OF PAIRED VARIATES FOR TITRATABLE ACIDITY

Comparison	r	b	Rank Correlation Coefficient (r_s)
Average of test crosses vs. Inbreds	.655**	.288 ± .003*	.664*
Average of test crosses vs. Top cross	.871**	.644 ± .020**	.873**
Top cross vs. Inbreds	.791**	.456 ± .036**	.782**
Inbreds vs. $F_1^{\ 1}$	--	--	.537
Inbreds vs. $F_1^{\ 2}$	--	--	.700**
Inbreds vs. Top cross	--	--	.769**
$F_1^{\ 1}$ vs. $F_1^{\ 2}$	--	--	.846**
$F_1^{\ 1}$ vs. Top cross	--	--	.855**
$F_1^{\ 2}$ vs. Top cross	--	--	.864**

* Significant at 5% level.
** Significant at 1% level.

From the regression analyses, summarized in Table 15, the regressions of top cross and of average test cross performance on inbreds were statistically significant. Also, the regression of average test cross or top cross performance was significantly different from zero. The regression coefficients are given in Table 14.

The simple linear relationships between the paired variates are shown in Figures 8, 9 and 10.

The linear regressions indicate that the inbred means for titratable acids can be relied upon in predicting their average and general combining potentials. A high general combining ability of an inbred, would also indicate its average combining ability for titratable acids.

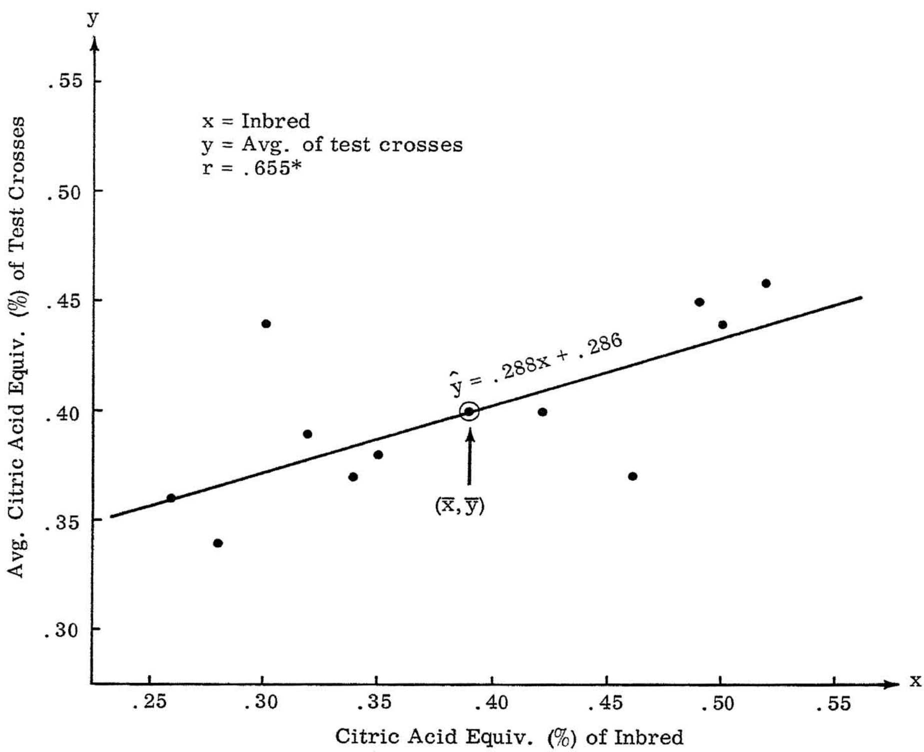

Figure 8. Regression of test cross productivity for titratable acidity on inbred performance of eleven tomato lines. Dot in circle denoting point of origin marks intersection of group means ($\bar{x}$, $\bar{y}$) of variates (Table 13, lines 1 and 5).

Table 15. ANALYSES OF VARIANCE OF REGRESSIONS OF Y FOR TITRATABLE ACIDITY IN 11 TOMATO LINES

	d.f.	x = Inbred y = Av. of test crosses		x = Top cross y = Av. of test crosses		x = Inbred y = Top cross	
		S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Total	10	0.0177	--	0.0177	--	0.0305	--
Regression	1	0.0076	.0076*	0.0134	0.0134**	0.0191	0.0191**
Deviations from Regression	9	0.0101	.0011	0.0043	0.0004	0.0114	0.0013

* Significant at 5% level.
** Significant at 1% level.

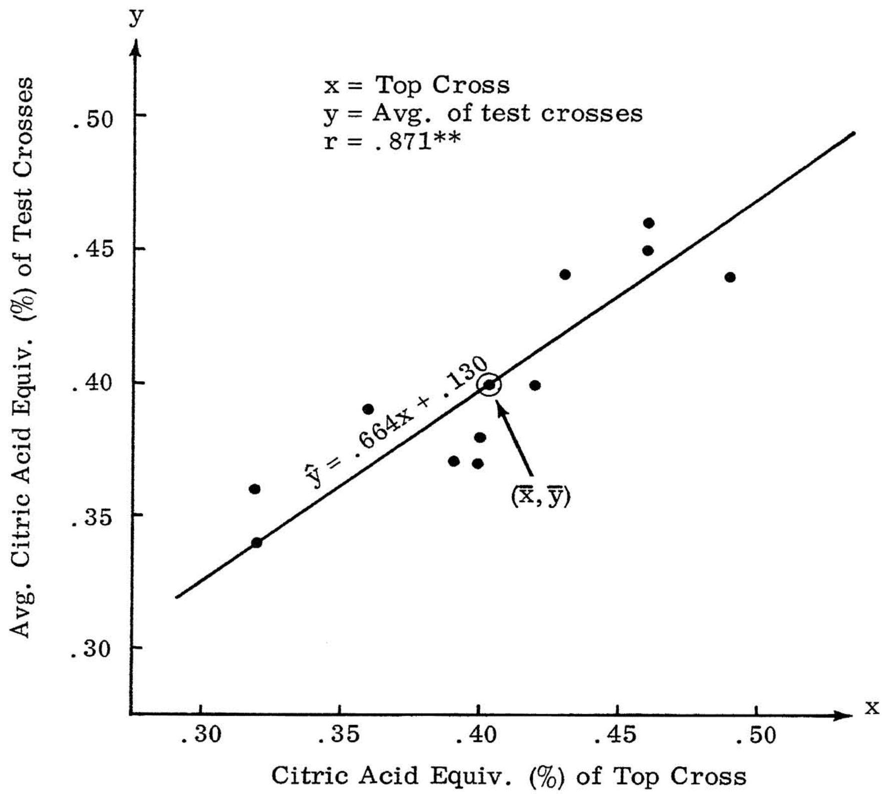

Figure 9. Regression of average test cross productivity for titratable acidity on top cross performance in eleven tomato lines. Dot in circle denoting point of origin marks intersection of group means ($\bar{x}$, $\bar{y}$) of variates (Table 13, lines 4 and 5).

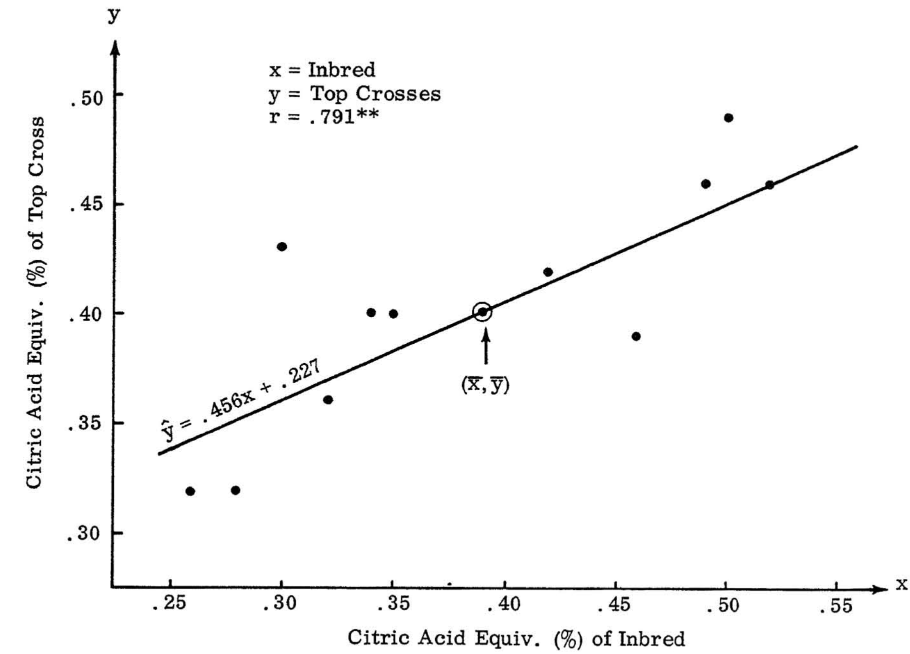

Figure 10. Regression of top cross productivity for titratable acidity on performance of eleven tomato lines. Dot in circle denoting point of origin marks intersection of group means ($\bar{x}$, $\bar{y}$) of variates (Table 13, lines 1 and 4).

4. Dominance and Potence

Generally the F_1's were lower than the midparental values but the difference had no apparent statistical significance (Table 16). The F_1^1 and F_1^2 groups, respectively, were on the average only -.003 and -.002 units from the midparental origin. This suggests a general lack of dominance. Individually, however, some crosses were observed to show some degree of dominance for high titratable acidity.

The average potence values of -1.83 and -0.33 indicate a preponderance of plus genes for lower titratable acidity.

5. Heritability estimates.

Regressions of F_1 values on those of midparents (MP) were used to estimate heritability (Table 17). Most of the estimates were negative, and thereby meaningless. Positive estimates varied widely from one cross to another. This is to be expected, considering the fact that heritability applies only to the particular population from which it was obtained. Differences in genotypic properties and in genotype-environment interactions with reference to a particular trait may affect such estimates.

Table 16 RELATIVE POTENCE[1/] OF GENE SETS FOR TITRATABLE ACIDITY IN TWO SETS OF SINGLE (TOP) CROSSES

Lines	Means	$\overline{F_1}^1 - \overline{MP}^1$	Potence	$\overline{F_1}^2 - \overline{MP}^2$	Potence
Mo. 90	.262	.02	.16	.02	.39
Mo. 117	.284	-.01	- .09	- .03	- .62
Mo. 2	.299	.11	1.25	.06	1.54
Mo. 197	.320	.02	.21	.02	.70
H 1370	.335	.02	.29	- .03	-1.79
IGS	.348	-.002	- .03	- .01	-1.08
O.J.	.421	-.02	- 1.00	- .03	-1.26
Tomboy	.457	-.08	-15.00	- .07	-1.76
Mo. 31	.494	-.03	- 2.39	.02	.27
Mo. 98	.502	-.05	- 2.77	0.0	0.0
Mo. 235	.523	-.02	- .79	- .01	- .07
Average	.386	-.003	- 1.83	- .022	- .33
Mo. 223	.467				
I-417-1	.374				

[1/] From the ratio $\frac{\overline{F_1} - \overline{MP}}{\overline{P} - \overline{MP}}$ (Griffing), where $\overline{P}$ is the mean of extreme parent.

Table 17 HERITABILITY OF TITRATABLE ACIDITY AS MEASURED BY REGRESSION OF F_1 ON MIDPARENTAL VALUES IN TWO GROUPS OF SINGLE CROSSES

Lines	F_1^1 Group	F_1^2 Group
	Heritability (%)	Heritability (%)
H 1370	2.3	57.9
O.J.	3.5	7.6
Mo. 90	- 1.4	-30.4
IGS	-24.9	-36.0
Mo. 235	-40.5	- 2.4
Mo. 31	-11.1	12.1
Mo. 98	20.8	15.4
Mo. 197	-35.1	17.8
Mo. 2	- 4.1	-32.2
Tomboy	-27.9	-24.7
Mo. 117	38.1	- 6.0

DISCUSSION

Indications of average combining ability obtained from the mean of two test crosses of 11 inbred lines were significantly correlated with measures of general combining ability obtained from respective three-way (top) crosses for all three fruit quality attributes studied. This may be interpreted to be a consequence of the fact that the single cross tester (Mo. 223 x I-417-1) was the heterozygous combination of the two inbred testers, Mo. 223 and I-417-1. This line of reasoning appears to be supported by inbred vs. top/test cross relationships for titratable acidity as shown by the significant r values of .655* and .791** (Table 14). The Brix and pH data, however, do not substantiate this contention. While inbred vs. test cross relationship for Brix was highly significant with r=.781**, top cross vs. inbred relationship, r=.539, was not (Table 4). Moreover, while inbred vs. test cross correlation (r=.782**) for pH was again highly significant, the top cross vs. inbred relationship, r=.502, was not significant (Table 9).

Some caution must be observed in the top cross evaluation of the lines since it may be influenced by specific combining effects. The single cross tester may have loci that show strong dominance and epistatic effects (18). Although there was a general lack of dominance, some F_1's showed various degrees of dominance for the traits studied. The measures of combining ability used in this study, considering the breeding scheme employed, would reflect both general and specific effects. Use of both procedures should screen the inbred lines for breeding worth on the inbred and moderate base single cross testers. Because the testers had a relatively narrow genetic base, possibly better estimates of specific combining ability were obtained than of general combining ability.

Use of more single cross testers or testers with broader genetic base would have been desirable. The 11 lines tested, however, comprised a population of lines previously untested and unselected for combining ability. In this case, genes with additive effects may be more frequent or have greater effects than genes with dominance or epistatic effects (18). Only two crosses each for Brix and titratable acidity significantly exceeded both parents in phenotypic values and this may be attributed to overdominance. No crosses were observed to show overdominance for pH. In situations where there is a general lack of overdominance, selection for general combining ability is effective (2).

The significant regressions discussed have indicated important additive genetic effects. The two measures of combining ability as used in this study would thus effectively screen lines for general combining ability for the traits considered.

Although estimates of heritability from parent-offspring regressions may be biased upwards in self-pollinated species (16), estimates from midparent-offspring regressions appeared to be generally reasonable. There was considerable variation from one estimate to another but this may have been due to differences in genotypic constitutions and genotype-environment interactions of populations sampled. If general combining ability is due largely to additive gene effects, the sizable variation in heritability estimates may also help explain the significant differences observed in general combining performance of lines tested for the three fruit quality traits.

SUMMARY AND CONCLUSIONS

1. Eleven tomato lines representing a wide range of fruit soluble solids (Brix), pH, and titratable acidity were tested for combining ability for these traits in single (test) and three-way (top) crosses.
2. Significant differences in combining ability for the traits were observed among the 11 lines.
3. Three small-fruited lines Mo. 31, Mo. 98 and Mo. 235 consistently showed superior general combining ability for high Brix, high titratable acidity, and low pH of the fruit.
4. Highly significant correlations in performance of inbreds and their respective test cross averages were observed for all traits. A significant correlation between inbred and top cross performance was observed for titratable acidity but not for Brix and pH.
5. Linear regressions indicated that average combining performance can be predicted reliably from inbred performance for Brix, pH, and titratable acidity. Inbred performance was also a reliable predictor of general combining ability for titratable acidity but not of that for Brix and pH.
6. The three-way (top) cross appeared to be effective in screening the lines for general combining ability. Top cross and average test cross performance were highly correlated for all traits studied.
7. Partial dominance of high and low solids was observed in the majority of single crosses; dominance was generally lacking for pH and titratable acidity.
8. General combining (additive) effects appeared to be more prevalent and a general lack of overdominance indicated that selection for general combining potential for the traits would be effective.
9. Sizable variation in heritability estimates obtained from midparent-offspring regression appeared to confirm the significant differences in general combining ability observed between lines.

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