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GENETIC VARIABILITY AND CORRELATIONS OF YIELDS COMPONENTS AND
RESISTANCE TO PHYTOPHTHORA INFESTANS, ALTERNARIA SOLANI,
AND MELOIDOGYNE SPP. IN TOMATO

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ABSTRACT

Experiments were conducted to determine genetic variability, heritabilities, and genetic correlations of yield components, resistance to Phytophthora infestans, Alternaria solani, and Meloidogyne in eight F₂ and five F₃ tomato (Lycopersicon esculentum) populations. Three methods were utilized to calculate heritability: (1) Parent-Offspring Regression, (2) Variation among F₃ Families, and (3) Components of variance. In the F₂ and evaluation for late blight (P. infestans) indicated that all eight populations were susceptible to this disease. In the F₃ populations were moderately resistant to susceptible to the rootknot nematode (Meloidogyne) but there was no statistical differences among families. The populations were also quite susceptible to A. solani. The amount of genetic variation for yield components varied depending on the population and trait. Although heritabilities varied according to method of calculation, in general, total and commercial yields had low heritabilities across all populations. Number of fruits was often associated with intermediate heritabilities and weight per fruit with intermediate to high heritabilities. The two variance component methods gave similar results while the parent-offspring regression technique resulted in low and non-significant heritabilities. Commercial yield was significantly and positively correlated with most of its components and negatively correlated with nodule number, per cent defoliation, and rate of defoliation. In view of the low heritabilities Single Seed Descent is suggested as a useful breeding technique for selection of the traits discussed.

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INTRODUCTION

The tomato (Lycopersicon esculentum) has been widely studied due to both its popularity as a vegetable and the ease by which it can be crossed and used in genetic studies. As a subject in genetic studies it is second only to maize. Traditionally a qualitative approach to inheritance studies has been used in tomato rather than the quantitative approach common in cross pollinators. Although much is known about the inheritance of single genes for disease resistance in tomato (Walter, 1966), little is known about multigenic or quantitative disease resistance.

Pedigree selection and backcrossing are still widely used selection methods in tomato breeding. However, these methods are only useful for highly heritable traits, especially those controlled by one or few genes (Allard, 1960). Methods such as single seed descent may be more useful in situations where the above methods result in relatively little progress for the amount of work required, as is the case with lowly heritable traits (Casali and Titchelaar, 1975). Methods such as recurrent selection may even be adapted to tomato for traits that require replicated progeny testing. Recurrent selection has the advantage of maintaining genetic variability and increasing frequencies of favorable alleles rather than eliminating variability and fixing gene frequencies as is done in inbreeding.

Tomato production in Puerto Rico is plagued by high temperatures and rainfall that favor diseases and reduce yields. Three common disease problems are early blight (Alternaria solani), late blight (Phytophthora infestans), and root knot nematode (Meloidogyne spp.). Single genes have usually been used as sources of resistance to these diseases (Barksdale, 1969; Gallegly, 1960; Dropkin and Webb, 1967). However, little is known about quantitative resistance to these diseases.

The objectives of this study were to (1) measure genetic variability and heritability for yield components and the above mentioned diseases, (2) compare different heritability estimation methods, (3) determine correlations between traits, and to (4) use this information to choose appropriate selection methods for these traits in tomato.

MATERIALS AND METHODS

Eight F₂ populations (crosses) were planted at the Center of Research and Development, Isabelá, Puerto Rico in January, 1982. The station is located 128 m above sea level with an annual average precipitation of 165 cm, a mean temperature of 25.1 °C.

The eight populations originate from crosses of station experimental lines and standard varieties. Many of the experimental lines have southern US germplasm (Table 1). The crosses were planted in a randomized complete block design with two replications. The experimental unit was six 5.5 m rows of a cross, 1.2 m apart, with 0.6 m between plants. Seed was planted in the greenhouse and transplanted to the field at about five weeks. Two 85g applications of 10-10-10 fertilizer per plant were applied, one at transplanting, the second at flowering. Applications of diazinon were made as needed for insect control. Overhead irrigation and cultivation was carried out as needed.

Thirty random plants were tagged in each population and individual plant data was recorded. Seed was harvested from each tagged plant for replicated F₃ family trials. Traits measured were (on a per plant basis): yield, number of fruit, weight/fruit and per cent defoliation. Both commercial and cull yields were measured, commercial defined as damaged or deformed fruit not considering size. Six harvests were carried out in the F₂.

F₃ families originating from F₂ parents were planted in July at the same location using the same cultural methods. The same traits were measured except that per cent defoliation was determined in six consecutive weeks following the assessment key of James (1971). Roots were sampled to score for *Meloidogyne* spp. resistance using a scale from 0 to 5 where 0 is no nodules, 1 for 1-2 nodules, 2 for 3-10, 3 for 10-30, 4 for 31-100, and 5 for more than 100 nodules.

Only five of eight populations were used in the F₃. The F₃ families were planted in separate reps-in-blocks designs, each population considered as a separate experiment. Depending on the population there were approximately 10 F₃ families assigned to each of 3 blocks or 15 families assigned to two blocks. Some families were lost so number of entries varied from experiment to experiment. The two parents of a population were included in each block. Entries within blocks were arranged in randomized complete block designs with three

replications. Sums of squares and degrees of freedom were pooled over blocks within an experiment (population). Variance components were estimated by setting mean squares from the combined analyses equal to expected mean squares. Heritability using the variance among F₃ families method (family mean basis) was estimated as: $\sigma_{F_3}^2 / (\sigma_e^2 / r + \sigma_{F_3}^2)$ where $\sigma_{F_3}^2$ is the genetic variance among F₃ family means, σ_e^2 the error variance from the combined analysis, r number of replications, and where the sum in the numerator equals the phenotypic variance. Using the variance component method, the genetic variance remains the same but environmental variance is estimated by the variance among the parents divided by the number of replications. Finally, parent offspring regression was used to calculate heritability as 2/3 of the regression coefficient (Smith and Kinmann, 1965), using the mean of F₃ families as the dependent variable. Standard errors of these estimates were calculated following Turner and Young (1969) for the first two methods, and as 2/3 of the standard error of the regression coefficient in parent-offspring regression. Phenotypic correlations between commercial yield and the other traits were calculated on F₃ data.

RESULTS AND DISCUSSION

Total yields in the F₂ averaged 25.2mt/ha with no significant differences between populations (Table 1). The mean commercial yield was 17.2mt/ha, differences among populations being significant. There were also differences among populations for per cent of total yield of commercial quality. Fruit was most often culled because of fruit rot, suggesting that there were differences among populations in resistance to the organisms responsible for fruit rots. Fruit weight in the F₂ was low and differences among populations were not significant for weight per commercial fruit. Lack of significant differences among populations can be explained in part by the lack of sufficient replication. However, the primary purpose of the F₂ planting was not to compare populations but to obtain individual plant data and seed for the F₃.

No significant differences were found among populations for per cent defoliation in the F₂ (Table 2). The primary cause of defoliation in the F₂ planting was P. infestans, the most prevalent foliar disease during the cooler winter months. A. solani was also present but the per cent defoliation data represents chiefly the late blight attack. Incidence was fairly uniform over the field, but some plants may have

escaped infection.

Yields in the F3 were considerably less than in the F2 due to time of planting (hot, rainy months), fewer harvests, and the fact that the F2 data was on individual plants and probably exaggerated. Although yields were reduced, fruit size was increased in the F3 (Table 3). Since populations represented separate experiments in the F3, statistical comparisons can be made only between families within populations and not between populations.

No population studied in the F3 showed significant differences among families for either resistance to Meloidogyne spp. (as indicated by nodule score) or A. solani, (as indicated by average per cent defoliation or rate of defoliation). Thus the genetic variance and heritability estimates for these traits were zero. Some populations showed more resistance than others but all were moderately or highly susceptible to both diseases (Table 4 and Figure 1). Plausible explanations for this lack of heritable variation within populations: (1) the parents of the cross are similar in terms of resistance to these two diseases and thus there is little or no variability in the segregating generations, (2) heritability of the two diseases is very low due to little genetic variability, high environmental variability, or a combination of both, and the experimental design was not precise enough to detect the low heritability or (3) incidence of the diseases may not have been sufficiently high or uniform to detect variability.

Estimates of genetic variance among F3 families were significant in certain populations for all yield component traits (genetic variances not shown). Genetic variance among F3 families estimates all of the additive and a portion of the non-additive variance (Hallauer and Miranda, 1980) if one considers the F2 of an autogamous species as the reference population equivalent to the S₀ of a cross-pollinator, and the F3 equal to the S₁. Heritability estimates on an F3 family mean basis are in the wide sense. Heritability estimates for the variance among F3 families and variance component methods were similar (Table 5). Estimates were most often significant for weight/fruit (Table 5). Population St 642 x PR117F8 had significant heritability estimates for nearly all yield components indicating it would be a good candidate for continued selection. Populations PR111F7 x PR116F8 and PR112F7 x PR117F8 had the lowest heritability estimates for yield components. Some differences between populations could be due to differences in environmental variability in the specific locations in the field where each experiment was conducted.

Genetic coefficients of variation (GCV) measure the relative amount of genetic variation between populations or between traits. The GCV's for yield and number of fruit were high while those for weight/fruit were low (Table 6). This indicated that heritability, and thus progress from selection, could be improved for the former traits with the use of an appropriate design to control experimental error. Heritability of weight/fruit was high but the relatively low amount of genetic variability suggests that there might be a limit to selection in these populations.

Phenotypic correlations (Table 7) between commercial yield and other traits showed total yield and fruit number to be highly correlated with commercial yield. Weight/fruit was lowly correlated (both negative and positive) with commercial yield. If genetic correlations can be assumed to be similar to phenotypic correlations, then selection for total yield should improve commercial yield, and weight/fruit could be increased without changing yield. Nodule score and per cent defoliation was often not significantly correlated with yield, thus selection for these traits can be carried out independently from yield.

The low heritabilities found in this study indicate that pedigree selection or backcrossing will not be effective in the improvement of tomatoes for these traits. Single seed descent has the advantage of easily maintaining genetic variability until the F5 or F6 when replicated trials can be used for selection. For some traits that are lowly heritable with little genetic variability, recurrent selection may be useful.

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TABLE 1 AND 2 - MEANS OF YIELD COMPONENTS AND PER CENT DEFOLIATION CAUSED BY
PHYTOPTHORA INFESTANS IN THE F₂

Population	Yield (mt/ha) Commercial	% of total	No. of fruit/plt. (commercial)	Weight/ fruit (g) (Commercial)	% Defoliation
A. Homestead 24 x PR116F8	14.1	55	10.2	60	75
B. PR65F3 x PR116F8	19.2	87	15.4	58	74
C. PR11F7 x PR116F8	22.8	80	17.4	64	79
D. PR11F7 x PR117F8	16.1	71	11.2	57	66
E. PR112F7 x PR116F8	8.0	40	3.7	66	75
F. PR112F7 x PR117F8	11.2	51	5.9	66	67
G. PR115F8 x PR 116F8	26.0	85	19.3	67	61
H. St 642 x PR116F8	20.7	74	13.5	64	78
\bar{X}	17.2	68	12.1	61	72
F-LSD ¹	8.6	10.5	7.5	--	--
CV %	21.0	6.5	26.3	11.9	17.6

1/ Least significant difference at the 0.05 probability level, protected with an initial F-test. When F-test was nonsignificant no LSD was calculated.

TABLE 3 MEANS OF YIELD COMPONENTS IN THE F3¹/₂

Population	Yield (mt/ha) Commercial % of total	No. of fruit/plt. (commercial)	Weight/fruit (g) (commercial)
B.	8.4	5.7	96
C.	9.4	6.4	100
F.	4.6	2.4	129
G.	9.7	6.7	96
H.	2.4	1.8	93
\bar{X}	6.9	4.6	103

1/ Direct comparisons cannot be made between populations since each was a separate experiment.

TABLE 5 HERITABILITY ESTIMATES AND THEIR STANDARD ERRORS FOR YIELD COMPONENTS IN FIVE TOMATO POPULATIONS USING THREE ESTIMATION METHODS

TRAIT	METHOD	B	C	F	G	H
YIELD (commercial)	F3	.42 ⁺ .29	.23 ⁺ .32	.53 ⁺ .28	.44 ⁺ .30	.76 ⁺ .27*
	P-F3	.48 ⁺ .29	.11 ⁺ .39	.29 ⁺ .44	.18 ⁺ .36	.60 ⁺ .36
	P-P	.01 ⁺ .30	.05 ⁺ .22	.02 ⁺ .23	.11 ⁺ .21	.703 ⁺ .12
	F-3	.27 ⁺ .29	.27 ⁺ .31	.31 ⁺ .29	.63 ⁺ .29*	.82 ⁺ .27*
# FRUIT (commercial)	P-F3	.48 ⁺ .31	.10 ⁺ .52	.11 ⁺ .55	.32 ⁺ .35	.65 ⁺ .36
	P-P	-.10 ⁺ .13	.05 ⁺ .13	.01 ⁺ .14	.11 ⁺ .20	-.01 ⁺ .13
WEIGHT PER FRUIT (commercial)	F3	.85 ⁺ .27*	.54 ⁺ .29	.27 ⁺ .30	.74 ⁺ .28*	.53 ⁺ .28
	P-F3	.81 ⁺ .27*	.26 ⁺ .28	.20 ⁺ .26	.65 ⁺ .28*	.07 ⁺ .11
	P-P	.10 ⁺ .56	.21 ⁺ .38	-.01 ⁺ .44	.04 ⁺ .51	.24 ⁺ .62

F3 Variance among F3 families method of estimating heritability

P-F3 Variance component method of estimating heritability.

P-P Parent-offspring regression method of estimating heritability.

* Indicates heritability estimate is significant (larger than 2 x S.E.)

TABLE 6 - GENETIC COEFFICIENTS OF VARIATION FOR YIELD COMPONENTS IN THE F3.

Trait:	Population							
	B %	C %	F %	G %	H %			
Yield	29.0	23.9	16.8	33.2	32.0			
Yield (commercial)	26.3	8.5	13.2	26.8	39.7			
No. of fruit	15.8	21.9	6.9	46.9	48.4			
No. of fruit (commercial)	15.8	7.6	3.2	36.6	45.6			
Weight/fruit	0.2	0.1	1.4	7.7	0.1			
Weight/fruit (commercial)	0.2	6.0	3.0	8.8	0.2			
% commercial of total yield	4.7	1.1	0.6	0.5	1.3			

TABLE 7 - PHENOTYPIC CORRELATIONS BETWEEN COMMERCIAL YIELD AND YIELD COMPONENTS AND DISEASE RESISTANCE IN THE F3

Trait	Commercial Yield			
	B	C	F	H
Total yield	0.79**	0.83**	0.79**	0.89**
Commercial Yield (% of total)	0.37**	0.47**	0.64**	0.23**
No. of fruit/plant	0.89**	0.79**	0.64**	0.88**
No of fruit/plant commercial)	0.90**	0.94**	0.91**	0.97**
Weight/fruit	0.46**	0.11	0.33**	-0.12
Weight/fruit (commercial)	0.48**	-0.13	0.30**	-0.06
Nodule score	-0.30**	-0.04	0.30**	0.01
% Defoliation	-0.19	-0.30**	0.09	0.19
Defoliation rate	-0.19	-0.21	-0.09	0.19

* Significantly different from zero at the 0.05 probability level.

** Significantly different from zero at the 0.01 probability level.