Tomato Anthracnose: Inheritance of Reaction to *Colletotrichum coccodes* in *Lycopersicon* spp.[1]

M. LeRon Robbins[2] and Fred F. Angell[3]
University of Maryland, College Park

Abstract. Resistant plant introduction (P.I.) 129027 was hybridized with susceptible 'Roma' and 'Heinz 1350', and P.I. 127833 was hybridized with 'Heinz 1350'. Plants of 6 populations (P_1, P_2, F_1, F_2, B_1P_1, and B_1P_2) of each of 3 crosses (127833 × 'Roma', 127833 × 'H-1350', 129027 × 'Roma') were field-grown and fruits were inoculated in a laboratory. Genetic analysis indicated presence of a leading factor and that 6 genes might be involved in anthracnose reaction. Resistance was partially dominant to susceptibility, and genetic variance was non-additive.

Tomato anthracnose, caused by the fungus *Colletotrichum coccodes* (Wall.) Hughes (6), occurs widely in the world. Cultural practices have not been an effective control.

Tomato cultivars are differentially susceptible to anthracnose (9), but none is known to have an appreciable amount of resistance. The genetics of resistance has not been defined, although Hoadley (4, 5) stated that resistance appeared to be inherited in a complex manner. Genetic information would be valuable to plant breeders by indicating the possibilities of breeding for resistance and suggesting effective breeding methods for developing resistant cultivars. This paper reports an investigation of the inheritance of resistance to tomato anthracnose.

Materials and Methods

Parental plant material. 'Roma' and 'Heinz 1350' were used as susceptible parents because they are highly susceptible to anthracnose and they have many horticultural characteristics desired in resistant cultivars. Plant Introductions (P.I.) 127833 and 129027, previously reported resistant to anthracnose (1), were used as the resistant parents. P.I. 127833 is *Lycopersicon pimpinellifolium,* and P.I. 129027 is a species cross *(L. esculentum* × *L. pimpinellifolium).* An individual plant selection from P.I. 127833 and one from P.I. 129027 were hybridized with 'Roma', and one from P.I. 127833 was hybridized with 'H-1350'. The 3 individual plant selections from the P.I. lines and their selfed progenies are hereafter referred to as 641-9, 640-1 and 641-1, respectively. Fruits of the P. I. lines are much smaller than those of 'Roma' and 'H-1350', but preliminary tests indicated little relationship between fruit size and anthracnose reaction as measured in this study.

Inoculation. The pathogen was grown on V-8 agar (8) under continuous light (2) at 23° C. Each week for 7 weeks, 1 ripe fruit was harvested from each plant and inoculated by the hypodermic method (8). This method consists of placing a droplet of spore suspension from a hypodermic syringe onto each fruit and pricking the fruit skin through the droplet. One site was inoculated on each fruit; inoculated fruits were kept in a laboratory at approximately 23° C, and lesion diameter was measured 5, 9, and 12 days later. Preliminary examination indicated that 5 days after inoculation was not enough time to allow for separation of susceptible and resistant reactions of fruits. Nine days was sufficient, and the data presented are those obtained 9 days after inoculation.

Experimental design. The genetic design consisted of 6 populations of each of the 3 families. They were P_1, P_2, F_1, F_2, B_1P_1, and B_1P_2 where P_1 represents the resistant parent, P_2 the susceptible parent, and B_1P_1 and B_1P_2 refer to the backcross of the F_1 to P_1 and P_2 respectively.

The environmental design was a modified split plot of 4 replications with families occupying whole plots, and generations within families occupying split plots, each subplot containing 5 plants. Each non-segregating generation occurred once in each replication but there were 2 plots of each backcross and 5 plots of each F_2 generation.

Data analysis. Data were analyzed by Chi-square and by the components of variance methods proposed by Mather (7). The following formulae were used:

$$\text{Environmental variance (E)} = (S^2P_1 + S^2P_2 + S^2F_1)/3$$

$$\text{Dominance variance (D)} = 4(S^2B_1 + S^2B_2 - S^2F_2 - E)$$

$$\text{Additive variance (A)} = 2(S^2F_2 - \tfrac{1}{4}D - E)$$

$$\text{Genetic variability (V)} = A + D/A + D + E$$

$$\text{Dominance} = \bar{F}_1 - \frac{\bar{P}_1 + \bar{P}_2}{2}$$

$$\text{Potence ratio} = \bar{F}_1 - [(\bar{P}_1 + \bar{P}_2)/(\bar{P}_2 - \bar{P}_1)]$$

These formulae require the mean and variance of each population. Scaling tests indicated that transformation of the data would not be worthwhile.

Results

Cross 641-9 × 'Roma'. 'Roma' was much more susceptible than the resistant parent, 641-9, as shown by its larger mean lesion size (Table 1). Dominance for resistance is indicated in that the F_1 mean is close to the resistant parent; the F_2 mean falls between the backcross means; and B_1P_2 is between F_1 and P_2. However, B_1P_1 is not between P_1 and F_1.

Table 1. Mean lesion diameters in mm, and variances of the 6 populations (cross 641-9 × Roma)[x].

Population	n	$\bar{X}$ ± S.E.	S^2
P_1	19	4.72 ± 1.26	30.52
P_2	20	28.39 ± 1.55	48.27
F_1	20	5.25 ± 0.53	5.85
F_2	100	7.35 ± 0.48	22.55
B_1P_1	40	6.03 ± 0.73	21.32
B_1P_2	40	13.04 ± 1.11	49.52

[x]One site was inoculated on each fruit, and lesion diameter was measured 9 days later. Seven fruits from each plant were inoculated over a 7 week harvest period.

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[2]Present address: Department of Horticulture, Iowa State University, Ames.
[3]Department of Horticulture, University of Maryland.

Table 2. Frequency distribution for tomato anthracnose reaction of 6 populations (crosses 641-9 × Roma)[a].

Population	Upper class limit (mm)[b]															
	3	6	9	12	15	18	21	24	27	30	33	36	39	42	45	48
	Number of plants															
P_1	10	6			1	1	1									
P_2					1			3	5	5	4			1		1
F_1	3	10	6	1												
F_2	23	22	26	13	7	5	3	1								
B_1P_1	11	13	8	2	2	2	1									
B_1P_2	3	2	8	5	7	9	3			3						

[a]One site was inoculated on each fruit, and lesion diameter was measured after 9 days.
[b]The lesion size for each plant is the mean for 7 fruits, with one inoculated site per fruit.

Frequency distributions for the 6 populations further emphasize the dominance pattern (Table 2). The F_1 generation has no plants outside the range of the resistant parent, and all the segregating populations are skewed, with most classes falling in the range of the resistant parent. The F_1 generation was less variable than either parent, but uniformity of F_1 organisms is common. 'Roma' was more variable than 641-9, possibly because the 'Roma' population was not from a single plant selection as was the 641-9 population.

The hypothesis that a single gene is involved in anthracnose reaction was investigated with the Chi-square test for goodness of fit. Distributions were so continuous that discrete classes could not be recognized. A point of separation between "resistant" and "susceptible" was designated as 11.5 mm. Under this restriction the data substantiated the hypothesis (Table 3).

Table 3. Chi-square test for a dominant gene controlling anthracnose resistance (cross 641-9 × Roma).

Generation	No. plants				
	Expected		Observed		
	Res	Sus	Res[a]	Sus	P
P_1	19	0	16	3	
P_2	0	20	0	20	
F_1	20	0	20	0	
F_2	75	25	81	19	.10–.20
B_1P_1	40	0	34	5	
B_1P_2	19.5	19.5	17	25	.20–.50

[a]Mean lesion diameter 11.5 mm or less.

The data were also analyzed by quantitative genetic methods because of their continuous nature. The high dominance variance and the negative additive variance (considered zero) indicate that gene action is mostly dominant or nonadditive (Table 4). Genetic variability (heritability in the broad sense) was 81%.

Partial dominance for resistance over susceptibility is shown by the negative value for dominance. The low potence ratio indicates that the F_1 mean is close to the resistant parent and that gene action is mostly in one direction. The Wright-Burton formula (3) for estimating number of genetic factors or blocks of closely linked factors when dominance exists, indicated that at least 6 genes differentiate anthracnose reaction of the 2 parents.

Table 4. Summary of the statistics calculated in quantitative genetic analysis of anthracnose reaction (cross 641-9 × Roma).

Statistic	Value
Environmental variance	23.15
Dominance variance	100.56
Additive variance	$-51.48 = 0^x$
Genetic variability	81%
Dominance	−11.31
Potence ratio	3.85
No. genetic factors	6.0

[x]In statistical genetics, a negative variance is given the value of zero.

Cross 640-1 × 'Roma'. Data from this cross were similar to those in cross 641-9 × 'Roma' discussed earlier, in that dominant gene action occurred. The data gave no additional information concerning genetic control of resistance; therefore, we do not include them here.

Cross 641-4 × 'H-1350'. Parent 641-4, resistant when inoculated with non-wounding methods, was very susceptible when inoculated with the hypodermic method (8). The cross was included in the study, but the data, which indicated the susceptibility of both parents, are not included here.

Discussion

The genetic data obtained in this study indicate either monogenic or multigenic control of anthracnose resistance, depending upon whether data are analyzed by Chi-square or by components of variance analysis. In the Chi-square test for monogenic inheritance the data fit the hypothesis, but only when "resistant" and "susceptible" classes were discriminately designated.

Although the Chi-square test indicated monogenic inheritance of anthracnose resistance, the data were continuous, suggesting multigenic control. Quantitative analysis indicated that a minimum of 6 genes differentiate anthracnose reaction of the 2 parents, and that gene action is nonadditive. Therefore, heritability in the narrow sense and expected advance under selection could not be calculated.

It could be that monogenic inheritance is the case, and that the hypodermic inoculation technique is so severe that resistance in a fruit is sometimes overcome. It is more likely, however, that a leading factor is involved, with minor genes contributing to anthracnose reaction.

The resistance mechanism in 641-9 functions both to prevent infection and to inhibit lesion development in fruits which become infected. While 96% of inoculated 'Roma' fruits developed detectable lesions, only 41% of 641-9 fruits did.

Susceptibility of a cultivar varies in degree throughout the season, depending upon the physiological condition of the plants at a given time. In addition, cultivars differ in the time of the season at which they are most susceptible (5). Such variation may prevent accurate interpretation of genetic data. If one wishes to reduce variation, he could inoculate fruits harvested at only one date. This, however, would confound genetic reaction with the physiological condition of the plants. In the present study we were interested in determining the average reaction of the various genotypes throughout the

season. This should give a more nearly accurate indication of the true genetic reaction.

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Furrow Irrigation of Lettuce Resulting in Water and Nitrogen Loss[1,2]

F. D. Moore, III[3]

Colorado State University, Fort Collins

Abstract. Water and nitrogen loss from field soil cropped to head lettuce with furrow irrigation was measured during three seasons in a semi-arid region. Water applications were reduced during the latter ⅓ of the growth period in an attempt to conserve N and water in the root zone.

Approximately 5 acre feet of water was applied to grow the crop. One-fifth of the applied water drained off and one-half percolated below the root zone. Eighty-nine lb./acre of NO_3-N was leached. Two-thirds of the water and three-fourths of the N (soil and applied) which were lost below the root zone were lost during germination. Reducing the total volume of water applied by 1½ acre feet did not reduce water or N loss appreciably and had a deleterious effect on the crop.

Very little N was lost as a result of runoff, but much was moved to the bed tops after the first irrigation. Implications of these findings are discussed.

THE major method of supplying water to lettuce in the West is by furrow irrigation. In some areas sprinklers are being used to a limited extent to germinate the crop. Reports from Arizona and California indicate that from 6 to 41 acre inches of water are applied by furrow irrigation for germination alone (8, 10, 13).

Lettuce removes little N (18) in relation to the large amount applied. It is well documented that a highly mobile anion such as nitrate would leach (1, 2, 16) during periods of heavy furrow irrigation and also move to the bed surface (7, 12) between irrigations. When one considers a shallow rooted crop such as head lettuce growing on porous soils in semi-arid regions, N leaching and movement become extremely important in the growth of the crop.

It was the purpose of this experiment to measure the volume of water applied, surface drainage (runoff), internal drainage (percolation), as well as the disposition of NO_3-N relative to this water during furrow irrigation of a head lettuce crop. It was also the purpose of this experiment to determine the effect of water conservation on the parameters above as well as the crop. Such quantitative information may be useful as an aid in decision making when contemplating a shift to sprinkler irrigation, at least for early growth.

MATERIALS AND METHODS

Field experiments were conducted from June through August during 1965, 1966, and 1967 at Colorado State University's San Luis Valley Experiment Station. Each year a half-acre site was selected. Soils from two of the sites were San Acacio. Soil from the third site belonged to the Del Norte soil series. The texture of these three calcareous soils is a sandy loam. Organic matter content averaged 0.8 percent. Permeability rate is classified as moderate to moderately rapid,[4] and depth to a gravel horizon is 30–35 inches. Moisture and particle size characteristics are presented in Table 1. Slope of the sites ranged from 0.29–0.34 per cent. These soils are repre-

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[3]Associate Professor, Department of Horticulture.

[4]Personal communication, J. P. Pannell. 1967. Soil Scientist, SCS, Alamosa, Colorado.

Table 1. Average moisture and particle size characteristics of the three experimental soils.[a]

Moisture tension	Plow layer 0–12 inches	Root zone 0–24 inches
Bars	Moisture %	Moisture %
0.10	17.1	16.3
0.33	11.9	11.9
1.00	8.7	8.7
7.50	7.4	7.6
15.00	7.0	7.3

Particle size	Plow layer 0–12 inches	Root zone 0–24 inches
	Weight %	Weight %
Gravel	—	15
Sand	74	63
Silt	14	12
Clay	12	10

[a]Average of 6 samples, 2 from Del Norte site and 2 from each San Acacio site.