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STUDIES ON THE INHERITANCE OF STEMPHYLIUM RESISTANCE IN TOMATOES

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ABSTRACT

Gray leaf spot of tomatoes, caused by *Stemphylium solani* Weber, is widespread and highly destructive in Hawaii. Control by application of fungicides is expensive and, in many instances, only partially successful. All the locally adapted, commercial varieties are susceptible.

In a program to develop gray leaf spot resistant commercial varieties, tiny-fruited, resistant tomato lines *(Lycopersicon pimpinellifolium* and Targinnie Red–*L. esculentum)* were introduced. These were crossed with locally adapted susceptible varieties. Seed from such crosses was further propagated and backcrossed to the two parents. First, second, and third generation seedlings, as well as backcross generations, were examined in greenhouse tests to determine the mode of inheritance of resistance.

A program of testing was employed in which 12- to 14-day-old plants were inoculated with a spore suspension of the pathogen, incubated 3 to 5 days under high humidity, and examined for individual seedling reaction. The validity of this procedure was demonstrated by a perfect correlation between cotyledon and mature plant reactions. The mono-conidial isolate No. 419 was used throughout the study. Copious sporulation was secured *in vitro* by passing the pathogen through a susceptible host and then treating the reisolated fungus with ultraviolet light.

First generation hybrids from Susceptible × Resistant crosses were represented by 987 plants, 983 of which were resistant. In the second generation 701 plants out of a total of 943 were resistant and the remaining 242 were susceptible. This conforms closely to a 3:1 ratio. Third generation hybrids were represented by 120 families. Of this number, 36 families were homozygously resistant, 54 segregated for resistance, and 30 were homozygously susceptible. The deviation from a 1: 2: 1 ratio was not marked. Backcross populations of (Susceptible × Resistant) × Susceptible segregated in a 1:1 ratio.

The data obtained indicate that resistance is governed by a single dominant genetic factor pair. This factor pair is assigned the symbol "Sm-sm."

THE AUTHORS

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STUDIES ON THE INHERITANCE OF STEMPHYLIUM RESISTANCE IN TOMATOES

INTRODUCTION

Gray leaf spot caused by *Stemphylium solani* Weber has, since about 1941, been one of the most common and destructive foliage diseases of tomatoes in Hawaii. It reduces tomato yields at all seasons of the year and during the fall, winter, and spring at the lower elevations of Oahu is capable of causing complete defoliation. The common attempts at control have involved the application of fungicides at frequent intervals from the time the plants go in the field until the fruits are mature. Such control has been expensive and, in many instances, where weather conditions have prevented entry into fields with machinery, or where the choice of fungicides has been poor, or where suitable implements for spraying or dusting have been wanting, successful control has not been achieved.

The discovery by Andrus, Reynard, and Wade (*3*) in 1942 of resistance to the gray leaf spot disease in the *Lycopersicon* genus opened a new approach to the control problem. The Hawaii Agricultural Experiment Station, upon learning of this discovery, secured lines of tomatoes bearing resistance to the *Stemphylium* pathogen and a breeding project was initiated to develop for the farmers of Hawaii commercially acceptable, resistant tomatoes. An earlier paper (*7*) records the progress made from 1943 to 1945 in the development of such varieties.

At the beginning of the breeding project, little information was available on breeding procedures for developing varieties resistant to this disease. Thus as an aid in determining the most appropriate procedure to follow, one of the original phases of the breeding program was to determine the manner in which resistance to gray leaf spot was inherited. Initial progress was slow. The growing of test plants in the field required greater land area than was conveniently available; the presence of other leaf spot diseases on field-grown plants at times interfered with the correct grading of individual plants; and the methods available at the outset of testing for *Stemphylium* resistance in the greenhouse did not permit a sufficiently high degree of precision in grading individual plants to establish the manner of inheritance of resistance. This bulletin describes certain findings on the manner in which resistance to *Stemphylium solani* is inherited and describes the development of a method of conveniently testing large numbers of plants for resistance to gray leaf spot.

[1]Portions of this report, including the greenhouse and certain field phases of the work, were included in a thesis submitted by the senior author to the Graduate School of the University of Minnesota as partial fulfillment of requirements for the Ph.D. degree in July, 1947.

REVIEW OF THE LITERATURE

Gray leaf spot of tomatoes was first described from Florida by Weber in 1929 (*20*), and its causal agent, *Stemphylium solani,* was described and named by him in the following year (*21*). In 1932 Weber *et al.* (*22*) described the spread of the disease in Florida and estimated losses of 2 to 15 percent to the tomato growers of Florida for each of the years from 1925 to 1931, inclusive. Instances were cited in which individual fields sustained total loss. In 1936 what appears to have been the same disease was reported in Georgia (*15*) and by 1941 it had spread westward to Texas (*1*). In 1948 Samson (*18*) reported the occurrence of gray leaf spot on tomatoes in Indiana for the first time, but he pointed out that it had been observed there for at least 12 years previous to the report. Andrus *et al.* (*3*) reported that *Stemphylium solani* was of importance in the Charleston, South Carolina, area in 1938 and that in the following year it was one of the predominant leaf-spotting pathogens of tomatoes. The disease attracted atention of Experiment Station workers in Hawaii in 1941 (*7*).

Weber *et al.* (*22*) studied the host range of *Stemphylium solani* in Florida and found among its susceptible hosts *Capsicum annuum* L., *C. frutescens* L., *Physalis pubescens* L., *Lycopersicon lycopersicon* (L.) Karst., *L. esculentum* Mill., and numerous species of *Solanum.* They observed the behavior of approximately 200 commercial tomato varieties and strains in experimental plots but did not find resistance among them. In other susceptible species, however, they observed, after inoculations, flecking of the leaf blades under certain conditions and stated that unfavorable environmental conditions for infection and variations in susceptibliity and resistance among individual plants within these species may have been the explanation for such a phenomenon. This seems to have been the first suggestion that resistance to *Stemphylium solani* was to be found within an otherwise susceptible species. Andrus *et al.* (*3*) grew plants of numerous commercial *Lycopersicon esculentum* varieties and non-commercial introductions in the field at the United States Vegetable Breeding Laboratory, Charleston, South Carolina. They observed tolerance to defoliation diseases in progenies of selections of *Lycopersicon pimpinellifolium,* notably P. I. 79532,[2] and in Targinnie Red, a variety of *L. esculentum*[3] from Australia.

MATERIALS AND METHODS

PARENTAL MATERIAL

In 1943 Hawaii accession lines 1398, 1682, and 1683 were found on the basis of field reaction and controlled greenhouse testing to resist *Stemphylium* infection at University Farm, Honolulu, T.H. These lines, together with the Accessions 1687 and 1688, which were added to the collection of resistant germ plasm at the Hawaii Station in 1944, have been the source of gray leaf spot resistance for the breeding program and for the inheritance studies. Accession 1398, a selection of *Lycopersicon pimpinellifolium,* was received from Dr. L. J. Alexander of the Ohio Station as line P.I. 79532 and is the same line that Andrus *et al.* (*3*) found resistant to *Stemphylium* infection at Charleston, South Carolina. Accessions

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[2]P.I. refers to the accession numbers of the United States Department of Agriculture, Division of Plant Exploration and Introduction.

[3]C. F. Andrus and G. B. Reynard in their article, "Resistance to Septoria Leaf Spot and Its Inheritance in Tomatoes," *Phytopathology* 35:19, 1945, stated that many non-*esculentum* types appeared as segregates in this variety and concluded that the variety had become admixed with natural out-crosses.

1682 and 1683 are selections of Targinnie Red (an *esculentum* variety from Australia) and were received as possible sources of resistance from Dr. C. F. Andrus and his co-workers under code numbers VBL[4] 42.8 and VBL 42.19, respectively. Accessions 1687 and 1688 are complex hybrids of Michigan State Forcing—*L. peruvianum* × Home Garden crossed with German Sugar × *L. pimpinellifolium*—and were furnished to the Hawaii Station by the Experiment Station of the Hawaiian Sugar Planters' Association as selections T.H. 1168 and T.H. 1178, respectively. Horticulturally, accession lines 1398, 1682, and 1683 were tiny-fruited, indeterminate tomatoes and the remaining two were determinate types of intermediate fruit size. All proved to be completely fertile in crosses with commercial tomatoes.

As an early step in utilizing the resistance of accessions 1398, 1682, and 1683 in developing large-fruited, resistant varieties, crosses were made between them and some of the more adapted susceptible commercial ones on hand at the Hawaii Station. Among the resistant derivatives from such crosses which have been used in these studies are lines HES[5] 1930, 1931, 1941, and 1942. HES 1930 is an F_3 selection of the three-way cross (HES 657 × HES 523—VBL 42.19) crossed with HES 1191. HES 1931 is an F_3 single plant selection from a double cross of Bounty—VBL 42.8 × Pearl Harbor—Bounty crossed with HES 917. HES 1941 and HES 1942 are F_4 sister selections from the double cross HES 823—Bounty × Pritchard—P. I. 79532. HES 1884 and HES 1903 are F_4 selections from accessions 1687 (T. H. 1178) and 1688 (T. H. 1168), respectively.

The commercial varieties Bounty (Acc. 749), Pearl Harbor (HES 1516), Pritchard (Acc. 700), and the Station selections HES 1863 and 1864 and others were selected as susceptible parents in the genetic studies because of their extreme susceptibility to *Stemphylium* infection.

BREEDING PROCEDURE

In the fall of 1944 seed was harvested from the resistant selections HES 1930, 1931, 1941, 1942, 1884, and 1903 and was planted the following spring in a greenhouse crop to provide further inbred seed and to obtain crosses between them and the susceptible lines Acc. 749 (Bounty), HES 1516 (Pearl Harbor), Acc. 700 (Pritchard), HES 1863, and HES 1864. In a few instances reciprocal crosses were made, but in most cases crosses were made on the susceptible commercial parent because of the greater ease in emasculating the flowers on these large-fruited types. In the case of HES 1884 (from T. H. 1178) and HES 1903 (from T. H. 1168), emasculation was accomplished with about the same facility as in Bounty or the other commercial parents; but for the sake of conformity, the susceptible variety was used as the female parent.

First-generation seed of Susceptible × Resistant hybrids was seeded in the greenhouse, tested for disease reaction, and planted in two lots—one in the field for observational purposes and for inclusion in the breeding project for commercial resistant varieties, and the other in the greenhouse for further propagation of the hybrid and for backcrossing to its two parents.

Second-generation and backcross material was planted and tested in the same manner as was the preceding generation. After disease readings were made the Susceptible Parent × F_1 seedlings (backcross) were transplanted to

[4]VBL refers to the accession numbers of the United States Vegetable Breeding Laboratory.
[5]HES refers to the selection numbers of the Hawaii Agricultural Experiment Station.

the field only, no further attempts being made to continue the lines for genetic studies. Backcrosses of $F_1 \times$ Resistant Parent were discarded after testing. The F_2 plants were propagated in the greenhouse to provide seed for analysis of the behavior of the F_3 generation.

CULTURE OF THE PATHOGEN USED

Single conidial cultures were obtained from naturally infected plant material collected at a number of scattered points on Oahu and were tested for pathogenicity in controlled greenhouse experiments. Isolate No. 419 proved highly pathogenic and was subsequently used in the preliminary stages of the breeding program to inoculate hybrid populations for resistance determinations. This isolate remained to all appearances unchanged in cultural and pathogenic characters during the investigation and was therefore used in the greenhouse phases of the inheritance studies.

GREENHOUSE TESTING FOR RESISTANCE

Mycelial Suspension Method

In the initial stages of the breeding program, inoculum was prepared in the manner described by Andrus *et al.* (*3*). It involved growing the fungus pathogen on a liquid medium in Erlenmeyer flasks held at room temperature, macerating the fungus pelts in a high-speed mechanical blender (Waring blender), and

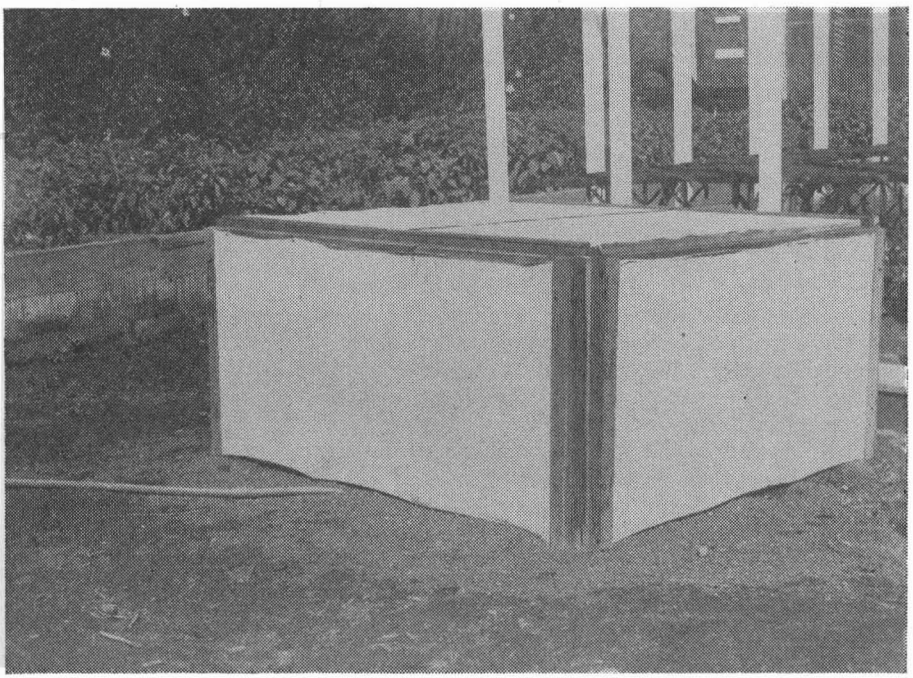

Figure 1. Muslin frames used as incubators in controlled inoculation experiments. The relative humidity is maintained at a high level by the use of two atomizing nozzles (capacity, 5 quarts per hour) attached to the water main.

adjusting the richness of the inoculum (mycelial suspension) to the required level by the addition of measured quantities of distilled water. Inoculation was accomplished by dipping the seedling tops into a basin of inoculum or by applying the mycelial suspension in spray form to the upper and lower leaf surfaces of seedling plants. After inoculation, the plants were incubated 2 days under muslin chambers (figure 1) in which a relative humidity of nearly 100 percent was maintained. The plants were then moved to outside benches to permit fullest development of the disease.

The mycelial suspension method was employed frequently in the general tomato improvement program but because of certain factors over which the investigators were unable to gain control, it was not used in the genetic studies. Segregating populations inoculated by this method showed all degrees of reaction from complete absence of any symptom of disease to complete defoliation or killing of the plant. Further observations on these groups revealed that plants falling near the outer limits of the range responded similarly to natural field infection, i.e., those plants which failed to develop symptoms of injury in inoculation tests remained free of disease in the field, and those that were defoliated or were heavily marked with *Stemphylium* spots proved susceptible to natural infection. However, the group that was characterized by occasional lesions, irregular blotches, ill-defined lesions, or that otherwise fell near the center of the range, segregated in field trials into definite resistant and susceptible types without necessary correlation with their symptoms in the greenhouse test.

Andrus *et al.* (*3*) pointed out that the richness of inoculum influenced the severity of disease; also, that in the dipping process the first plants dipped had a tendency to screen out a high portion of the mycelial fragments from the inoculum and that without frequent replenishment, the stock suspension grew progressively weaker. Hendrix *et al.* (*7*) observed that hairiness of leaves influenced the amount of inoculum retained by individual plants. These variables may explain why potentially susceptible plants may appear resistant on the basis of this manner of testing. Further, it has been observed that the size of mycelial particle is capable of influencing the nature and severity of reaction; very large particles may cause leaf flecking or localized necrosis on plants known to be resistant to natural infection. Such lesions are sometimes mistaken for the susceptible reaction type.

Spore Suspension Method

Induced Sporulation.—The weaknesses described in the foregoing method necessitated turning to the use of conidial suspensions as a source of inoculum. In testing large numbers of plants at irregular intervals, however, it was necessary to have at hand an easily available and ample supply of viable spores. But because of the low conidia-producing ability of *Stemphylium solani* in pure culture, such a supply was at first not available. Frazier *et al.* (*6*) overcame this obstacle in their work on combining resistance to gray leaf spot with resistance to spotted wilt and Fusarium wilt by securing conidia from naturally infected leaf material, and Weber (*21*) successfully collected and used similar inoculum in inoculation tests in Florida. When this source was explored it was found that sufficient inoculum was difficult to obtain and that the interfering presence of other organisms, including *Alternaria solani* and *Septoria lycopersici*, was unavoidable.

By drastically wounding the mycelium of certain cultures of *Macrosporium solani*, a fungus which like *Stemphylium solani* often produced relatively few

or no spores *in vitro*, Kunkel (*10*) secured a copious production of conidia. Rands (*16*) obtained similar results when he shredded the medium on which *Alternaria solani* was growing and exposed the culture to sunlight for 24 to 48 hours. McCallan and Chan (*14*) were able to induce heavy sporulation of *A. solani* by scraping the fungus colony and exposing it to ultraviolet irradiation. When these devices were tried with the present pathogen, the increased number of sports obtained was inconsequential. Modifications of these methods were also tried in which various levels of pH from 4.8 to 8.0 and various temperatures from 14°C. to 30°C. were maintained. None of these conditions or combinations of them gave noticeable increases in spore production. Likewise, no difference could be detected between the number of spores produced by colonies grown on standard potato dextrose agar and those grown on a large variety of other media, even when subjected to the varying conditions of pH and temperature mentioned above.

In culturing *Stemphylium solani* from field-grown tomato vines, it was repeatedly observed that tissue isolates yielded more spores than single-spore isolates or isolates that had been held in culture through repeated transfers. On occasion such spores were included in pathogenicity tests and were found to be equally as infective as the vegetative portions of the fungus used in earlier trials. Conidia thus obtained seemed to answer the needs for the genetic study, except that they were obtained from naturally infected material and no assurance could be had that individual spore lots were identical.

The matter of spore uniformity was later solved by making tissue platings from plants inoculated with mycelial suspensions of the mono-conidial isolate,

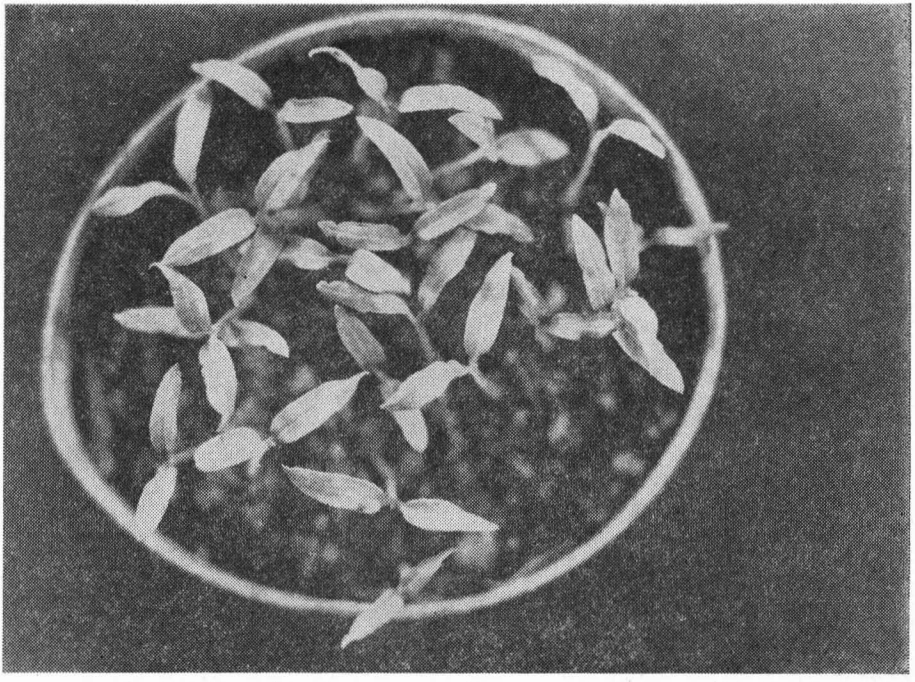

Figure 2. Tomato seedlings, after thinning, ready for inoculation. Photograph made 12 days after seeding.

419. This involved removing small squares of leaf tissue containing in the center a gray leaf spot lesion and plating the squares on acid potato–dextrose agar. By scraping these cultures in the manner described by Kunkel (*10*) and exposing them to ultraviolet irradiation as described by McCallan and Chan (*14*), approximately 5 million spores per plate were obtained. These cultures, while they sporulated profusely up to the time they were about 3 weeks old, gradually lost this ability on further aging of the culture and on succeeding transfers. Thus for the inoculation of succeeding groups of seedlings, fresh cultures were required.

Inoculation and Incubation.—In original trials, tomato lots to be tested were seeded in flats filled with a steam-sterilized soil composed of two parts of field loam and one part of volcanic black sand. The seedlings were transplanted to 4-inch clay pots or size 2½ tin cans approximately 12 days after seeding and were held in the greenhouse for 2 weeks, or until inoculations were made. In subsequent trials, a simpler method was used. Seeds of hybrid lots were seeded directly into each of five No. 2½ tin cans at a rate of approximately 50 seeds per can. When the cotyledons were fully expanded and before true leaves were formed, overpopulated stands were thinned to about 25 uniform seedlings per can (figure 2). Slow-developing and ill-formed seedlings were removed from all cans, the thought being that unfolded cotyledons or cotyledons protected from above by the cotyledons of stronger neighbors might possibly escape inoculation and thereby introduce error into the disease tally. Following this thinning the cans were removed to infection chambers. Either a cloth-covered chamber (figure 1) as described by Hendrix *et al.* (7) or a fog-room incubator was

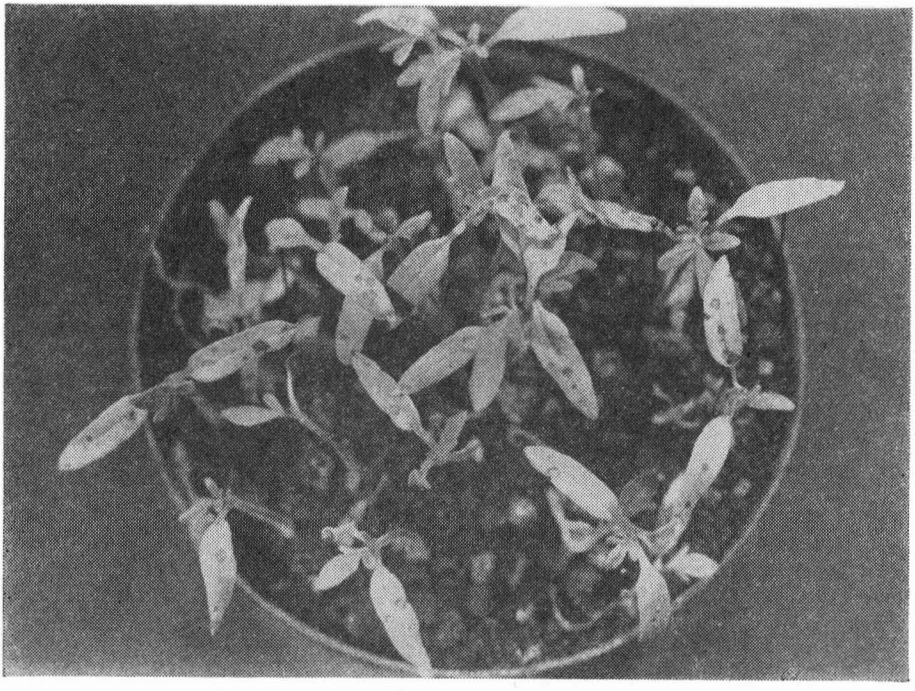

Figure 3. *Stemphylium solani* lesions on tomato cotyledonary leaves. Note that some cotyledons have become detached. Photograph made 4 days after inoculation.

used. The latter was a room designed to accommodate large numbers of plants and was equipped with adjustable valves in which jets of water were permitted to strike against baffle plates and so become dispersed as a fine mist. The atmosphere of fog thus produced was sufficient to maintain the humidity near the point of saturation. The room, with approximately ten times the capacity of the cloth chamber, was used in larger operations; for limited numbers of seedlings the cloth type was used. Both gave equal degrees of infection in comparative tests.

Inoculations were made in the infection chamber by atomizing the cotyledonary leaves with an inoculum adjusted to contain 20,000 spores per cubic centimeter of water. For assurance of adequate dosage and thorough leaf coverage a second application was made 6 hours after the first. In each series of plants tested, check plants of susceptible Bounty, Pearl Harbor, or Pritchard were included to show irregularities in infection and/or loss in pathogenicity of the organism if such existed.

Evaluation of Disease Reaction

Symptoms of infection normally appeared on the third day after inoculation, at which time the plants were removed from the incubator. The disease gradually developed until on the fifth or sixth day (figure 3), depending on weather conditions, the cotyledons of heavily infected plants began to fall. The determination of the reaction of individual plants was made at a time when the disease was most pronounced and before the evidence was destroyed by leaf casting.

At the outset, each plant received a score under the following system of grading: 0, no lesions or other symptoms of disease; 1, from 1 to 3 lesions per plant; 2, from 4 to 6 lesions; 3, 7 to 9 lesions; 4, 10 to 12 lesions; 5, 13 to 15 lesions; and 6, 16 or more lesions per plant. In later phases this detail was omitted because further testing showed that plants exhibiting only one or two lesions in the cotyledon test were as susceptible in field tests as the plants having higher numbers of lesions. Thus only those plants with a complete absence of symptoms were considered resistant and the presence of one or more lesions was considered as signifying susceptibility.

CORRELATION OF GREENHOUSE AND FIELD REACTION

To determine the validity of the above method of testing, segregating populations were tested in the cotyledon stage and the reaction of individual plants was compared with the reaction of the same plants at later stages of plant development. Three lots of F_2 Susceptible $\times$ Resistant seed were sown and inoculated in the manner employed for the genetic studies. Each plant was individually graded, transplanted, and held on outside benches until true leaves were formed and until the plants were approximately 5 weeks old. A second inoculation was administered at this stage and again each plant was individually graded. When the plants were sufficiently recovered from the shock of the second inoculation, the infected leaves of susceptible plants were removed and the plants were transplanted to the field. In the field, observations on the gray leaf spot reaction were made at periodic intervals. Such observations ceased when about half the fruits on the plants were ripe. It was believed that by this time the susceptible segregates would have had ample opportunity to become inoculated and that the disease would have developed.

The gray leaf spot reaction of individual plants in these three stages of development is presented in table 1.

TABLE 1.—Reaction of Individual F_2 Susceptible × Resistant plants in cotyledon, 5-week-old, and mature plant stages.*

PLANT NO.	COTYLEDON STAGE	5-WEEK STAGE	MATURE PLANT	PLANT NO.	COTYLEDON STAGE	5-WEEK STAGE	MATURE PLANT	PLANT NO.	COTYLEDON STAGE	5-WEEK STAGE	MATURE PLANT
Line P-244				52	R	R	R	103	R	R	R
1	S	S	S	53	R	R	R	104	S	S	S
2	R	R	R	54	R	R	R	105	R	R	R
3	R	R	R	55	R	R	R	106	S	S	S
4	R	R	R	56	R	R	R	107	R	R	R
5	R	R	R	57	R	R	R	108	S	S	S
6	S	S	D	58	R	R	R	109	S	S	S
7	R	R	R	59	R	R	R	110	S	S	S
8	R	R	R	*Line P-134*				111	R	R	R
9	R	R	R	60	R	R	R	112	R	R	R
10	R	R	R	61	R	R	R	113	S	S	S
11	S	S	S	62	R	R	R	114	R	R	R
12	S	S	S	63	S	S	S	115	R	R	R
13	R	R	R	64	R	R	R	116	R	R	R
14	R	R	R	65	R	R	R	117	R	R	R
15	R	R	R	66	S	S	S	118	S	S	S
16	S	S	S	67	R	R	R	119	R	R	R
17	S	S	S	68	R	R	R	120	R	R	R
18	R	S	S	69	R	R	R	121	R	S	S
19	R	R	R	70	R	R	R	*Line P-138*			
20	R	R	R	71	R	R	R	122	R	R	R
21	R	R	R	72	R	R	R	123	R	R	R
22	S	S	S	73	S	S	S	124	R	R	R
23	R	R	R	74	R	R	R	125	S	S	S
24	R	R	R	75	S	S	S	126	R	R	R
25	R	R	R	76	R	R	R	127	R	R	R
26	S	S	S	77	R	R	R	128	R	R	R
27	R	R	R	78	R	R	R	129	R	R	R
28	R	R	R	79	R	R	R	130	R	R	R
29	R	R	R	80	S	S	S	131	R	R	R
30	R	R	R	81	R	R	R	132	S	S	S
31	R	R	R	82	S	S	S	133	S	S	S
32	S	S	S	83	S	S	S	134	R	R	R
33	S	S	S	84	R	R	R	135	R	R	R
34	R	R	R	85	R	R	R	136	R	R	R
35	R	R	R	86	R	R	R	137	R	R	R
36	S	S	S	87	R	R	R	138	R	R	R
37	R	R	R	88	R	R	R	139	S	S	S
38	R	R	R	89	S	S	S	140	R	R	R
39	R	R	R	90	R	R	R	141	S	S	S
40	S	S	S	91	S	S	S	142	S	S	S
41	R	R	R	92	R	R	R	143	S	S	S
42	S	S	S	93	R	R	R	144	S	S	S
43	R	R	R	94	R	R	R	145	S	S	S
44	R	R	R	95	S	S	S	146	R	R	R
45	R	R	R	96	R	R	R	147	S	S	S
46	R	R	R	97	R	R	R	148	R	R	R
47	R	R	R	98	R	R	R	149	R	R	R
48	R	R	R	99	R	R	R	150	R	R	R
49	R	R	R	100	R	R	R	151	R	R	R
50	R	R	R	101	R	R	R	152	R	R	R
51	R	R	R	102	R	R	R	153	R	R	R

*The letter "S" is used to denote susceptibility; "R" denotes resistance; and "D" indicates that plant died.

Continued on following page

TABLE 1.—*Continued*

PLANT NO.	COTYLEDON STAGE	5-WEEK STAGE	MATURE PLANT	PLANT NO.	COTYLEDON STAGE	5-WEEK STAGE	MATURE PLANT	PLANT NO.	COTYLEDON STAGE	5-WEEK STAGE	MATURE PLANT
154	S	S	S	166	R	R	R	178	R	R	D
155	R	R	R	167	R	R	R	179	R	R	R
156	S	S	S	168	S	S	S	180	R	R	R
157	R	R	R	169	R	R	R	181	R	R	R
158	R	R	R	170	S	S	S	182	S	S	S
159	S	S	S	171	R	R	R	183	R	R	R
160	R	R	R	172	R	R	R	184	S	S	S
161	R	R	R	173	R	R	R	185	R	R	R
162	S	S	S	174	R	R	R	186	R	R	R
163	R	R	R	175	S	S	S	187	S	S	S
164	R	R	R	176	S	S	S	188	S	S	S
165	S	S	S	177	S	S	S				

It was significant that the plants judged resistant on the basis of cotyledon response were almost invariably resistant in later stages. This was true whether inoculation was accomplished by the deliberate application of *Stemphylium* spores in controlled tests or whether infection resulted from natural means in field plantings. In a total of 188 plants observed for disease reaction in these three stages, viz., cotyledon stage, 5-week-old plants, and mature plants, only two cases of reversal of reaction to *Stemphylium* infection were found. Plants 18 and 121 (table 1) were regarded as resistant in the cotyledon stage but were susceptible in later tests. This may be explained by the failure of these plants to become inoculated in the initial test. In addition, from many hundreds of plants selected for resistance on the basis of cotyledon tests and later transplanted to the field for breeding purposes, only a negligible number of susceptible plants have been observed.

VARIATION IN THE PATHOGEN

Studies from the standpoint of differences in pathogenic properties were made on approximately 50 single-conidial isolates of *Stemphylium solani* derived from random points on Oahu. Mycelial suspensions were made of each culture and were used to inoculate 20 plants of each of three *Lycopersicon esculentum* varieties—Pan America, Pritchard, and Bounty—and one line of *L. pimpinellifolium* —P. I. 79532. Inoculation was accomplished in the manner described by Andrus, Reynard, and Wade (*3*) and the method of grading individual plants was identical with that used by these authors. Typical gray leaf spot symptoms were produced by all of the isolates tested, and, while no evidence of host specificity was found, a slight variation in degree of pathogenicity was found among the isolates. Among the isolates of highest pathogenicity was culture No. 419, which was discussed earlier in the paper.

INHERITANCE OF RESISTANCE

SUSCEPTIBLE × SUSCEPTIBLE CROSSES

Eight crosses were made between commercial varieties and Hawaii Station selections classified as susceptible. The results of the inoculations of the progenies

of these crosses are given in table 2. All the parents represented in the crosses had been observed to be susceptible in field and controlled tests, but adequate notes on their hybrid reaction had not been kept. In one previous lot of F_1 Pearl Harbor × Rutgers seedlings, resistant plants had appeared. These were thought to have been the result of natural outcrossing with resistant material growing in close proximity to these lines. The crosses considered here were made in the greenhouse and covered with paper bags immediately after pollination so as to avoid the activity of bees and other agents that might possibly be associated with natural pollination or with mixing of pollen. From the eight crosses combined, approximately 3,500 F_1 seeds were obtained. When seeded in the greenhouse in the manner adopted for these studies, about 2,800 seedlings emerged. Damping-off killed a small number of plants in the humid chambers during inoculation and incubation, but gray leaf spot reaction was observed for the 2,548 seedlings that survived. As is apparent from the figures presented in table 2, not one of the 2,548 hybrid seedlings was resistant.

TABLE 2.—Gray leaf spot reaction of F_1 seedlings from eight intervarietal crosses between susceptible tomatoes.

CROSS NUMBER	PARENTAGE	GRAY LEAF SPOT REACTION		
		Total No. Plants	Resistant	Susceptible
S–1	Bounty × Pritchard	321	0	321
S–2	Bounty × Rutgers	339	0	339
S–3	Bounty × HES 1863	307	0	307
S–4	Pearl Harbor × Bounty	364	0	364
S–5	Pearl Harbor × Rutgers	298	0	298
S–6	Pritchard × Pearl Harbor	338	0	338
S–7	Pritchard × HES 1863	255	0	255
S–8	HES 1863 × Marglobe	326	0	326
Total		2,548	0	2,548

RESISTANT × RESISTANT CROSSES

Crosses were made in all possible combinations between resistant selections HES 1903, 1930, 1931, and 1941. The results of the inoculations of the progeny of these crosses are listed in table 3. Because there were few seeds of cross S-23 as compared with the other crosses, hybrid seed of a cross (S-24) involving parents of the same descent as cross S-23 were included also. The disease reaction of cross S-24 was identical with that of cross S-23; the reaction of the group as a whole, as contrasted with the behavior of F_1 progenies of Susceptible × Susceptible crosses (table 2), was one of complete resistance. Not one of the 1,293 F_1 plants tested developed gray leaf spot symptoms whereas 100 percent of the Bounty seedlings included as checks were susceptible.

TABLE 3.—Gray leaf spot reaction of F_1 seedlings from inter-selection crosses, Resistant × Resistant.

CROSS NUMBER	PARENTAGE	GRAY LEAF SPOT REACTION		
		Total No. Plants	Resistant	Susceptible
S–21	HES 1930 × HES 1931	211	211	0
S–22	HES 1930 × HES 1930	236	236	0
S–23	HES 1930 × HES 1941	92	92	0
S–24	HES 1884 × HES 1942	114	114	0
S–25	HES 1931 × HES 1903	193	193	0
S–26	HES 1931 × HES 1941	207	207	0
S–27	HES 1903 × HES 1942	240	240	0
Total		1,293	1,293	0
Check	Bounty	92	0	92

SUSCEPTIBLE × RESISTANT CROSSES

In the fall of 1945 crosses were made between each of the resistant selections HES 1884, 1903, 1930, 1931, 1941, and 1942 and one or more of the susceptible varieties (or selections) Bounty, Pearl Harbor, Pritchard, HES 1863, and HES 1864. In making the crosses, the parent plants were grown in 5-gallon metal drums in adjoining rows in the greenhouse. The individual resistant plants used as parents in these crosses were the same plants used for making the crosses listed in table 3; the susceptible plants were the same as those used for making the crosses listed in table 2.

Six F_1 lines from these crosses were chosen for backcrossing to the parental lines and for propagation through the F_3 generation. For each cross, seed lots of the first, second, and third filial generations and backcrosses of the F_1 with each of the resistant and susceptible parents were tested for reaction to gray leaf spot infection. The reaction of these groups is given in table 4.

TABLE 4.—Gray leaf spot reaction of F_1, F_2, and backcross progenies and of F_3 families from six crosses, Susceptible × Resistant.

Susceptible		Resistant	
HES 1863—	×	—HES 1930	
P–100 (21:22)			P–106 (95:1)*
F_1 T–2685		F_1	
(183:0)			
F_2 P–103			
(113:35)			
F_3 Family 1 –	90	:	29
2 –	137	:	43
3 –	0	:	30
4 –	0	:	74
5 –	63	:	16
6 –	50	:	20
7 –	28	:	12
8 –	82	:	37
9 –	0	:	116
10 –	90	:	0
11 –	96	:	0
12 –	81	:	0
13 –	0	:	105
14 –	61	:	22
15 –	56	:	0
16 –	139	:	0
17 –	36	:	12
18 –	125	:	0
19 –	136	:	40
20 –	0	:	62

Susceptible		Resistant	
HES 2032 (PH)—	×	—HES 1931	
P–120 (28:38)			P–121 (76:0)
F_1 T–2693		F_1	
(213:0)			
F_2 P–119			
(95:28)			
F_3 Family 1 –	0	:	114
2 –	0	:	134
3 –	0	:	98
4 –	0	:	122
5 –	131	:	0
6 –	141	:	45
7 –	78	:	29
8 –	91	:	0
9 –	111	:	0
10 –	127	:	0
11 –	69	:	20
12 –	85	:	25
13 –	63	:	19
14 –	56	:	20
15 –	83	:	26
16 –	62	:	18
17 –	143	:	46
18 –	84	:	25
19 –	130	:	48
20 –	0	:	109

Susceptible		Resistant	
Bounty—	×	—HES 1941	
P–135 (65:71)			P–140 (31:0)
F_1 T–2696		F_1	
(194:0)			
F_2 P–134			
(159:59)			
Family 1 –	0	:	171
2 –	0	:	29
3 –	0	:	120
4 –	0	:	224
5 –	21	:	0
6 –	88	:	27
7 –	24	:	0
8 –	94	:	34
9 –	58	:	0
10 –	104	:	28
11 –	27	:	9
12 –	39	:	23
13 –	80	:	0
14 –	60	:	0
15 –	45	:	16
16 –	75	:	31
17 –	118	:	24
18 –	115	:	0
19 –	129	:	0
20 –	0	:	119

Susceptible		Resistant	
Pritchard—	×	—HES 1941	
P–147 (44:47)			P–145 (58:0)
F_1 T–2696–A		F_1	
(109:0)			
F_2 P–146			
(121:42)			
Family 1 –	0	:	65
2 –	0	:	49
3 –	0	:	165
4 –	0	:	90
5 –	121	:	47
6 –	121	:	0
7 –	110	:	0
8 –	36	:	16
9 –	106	:	0
10 –	37	:	0
11 –	117	:	38
12 –	110	:	38
13 –	184	:	67
14 –	70	:	27
15 –	104	:	40
16 –	64	:	0
17 –	130	:	48
18 –	116	:	0
19 –	50	:	23
20 –	0	:	94

*First number indicates resistant plants.

Continued on following page

TABLE 4.—*Continued*

Susceptible Resistant
HES 2032 (PH) —×— HES 1884
P–262 ⟩ ⟨ P–261
(94:98) ⟨ ⟩ (29:0)
F_1 T–2716 F_1
(142:4)
F_2 P–258
(153:56)

Family				
1	–	0	:	77
2	–	0	:	141
3	–	0	:	67
4	–	0	:	25
5	–	88	:	26
6	–	31	:	11
7	–	44	:	0
8	–	109	:	0
9	–	78	:	0
10	–	136	:	0
11	–	36	:	14
12	–	125	:	47
13	–	58	:	0
14	–	123	:	0
15	–	121	:	0
16	–	81	:	32
17	–	78	:	30
18	–	76	:	28
19	–	75	:	29
20	–	0	:	61

Susceptible Resistant
HES 1864 —×— HES 1903
P–282 ⟩ ⟨ P–283
(74:68) ⟨ ⟩ (71:0)
F_1 T–2722 F_1
(142:0)
F_2 P–281
(60:22)

Family				
1	–	0	:	88
2	–	0	:	145
3	–	43	:	13
4	–	0	:	22
5	–	90	:	24
6	–	0	:	83
7	–	99	:	34
8	–	93	:	0
9	–	30	:	15
10	–	58	:	0
11	–	48	:	0
12	–	145	:	0
13	–	43	:	16
14	–	86	:	30
15	–	28	:	10
16	–	119	:	0
17	–	160	:	51
18	–	65	:	24
19	–	149	:	0
20	–	0	:	147

Behavior of the F_1

First-generation hybrids from the six Susceptible × Resistant crosses as seen in tables 4 and 5 were represented by 987 F_1 plants, 983 of which were resistant and the remaining four susceptible. In five crosses (T-2685, T-2693, T-2696, T-2696-A, and T-2722) all the plants were reisistant; in one cross (T-2716) four plants of 146 appeared as susceptible. No special significance is attached to the appearance of this small number of susceptible plants; such an occurrence might rather be explained by faulty emasculation of the flower on which the cross was made or by the mechanical mixture of seed during the seed extraction process.

TABLE 5.— Gray leaf spot reaction of F_1 seedlings from crosses, Susceptible × Resistant.

CROSS NO.	PARENTAGE	GRAY LEAF SPOT REACTION		
		Total No. Plants	Resistant	Susceptible
T–2685	HES 1863 × HES 1930	183	183	0
T–2693	Pearl Harbor × HES 1931	213	213	0
T–2696	Bounty × HES 1941	194	194	0
T–2696–A	Pritchard × HES 1941	109	109	0
T–2716	Pearl Harbor × HES 1884	146	142	4
T–2722	HES 1864 × HES 1903	142	142	0
Total		987	983	4
Check	Bounty	56	0	56

Behavior of the F_2

Second-generation hybrids of Susceptible × Resistant crosses were represented by 943 plants derived from the six crosses listed in table 4. As can be seen from the data on the reaction of the F_2 plants to *Stemphylium* infection (tables 4 and 6), a 3:1 ratio was approximated. In no single cross was the deviation from a 3:1 ratio significant and the conformity of the combined results (701 resistant plants to 242 susceptibles) to a 3:1 ratio was significant.

TABLE 6.—Gray leaf spot reaction of F_2 seedlings from crosses, Susceptible × Resistant.

CROSS NO.	PARENTAGE	GRAY LEAF SPOT REACTION			CHI^2 3:1
		Total No. Plants	Resistant	Susceptible	
P–258	T–2716 (P. H. × HES 1884)	209	153	56	0.359
P–281	T–2722 (HES 1864 × HES 1903)	82	60	22	0.146
P–103	T–2685 (HES 1863 × HES 1930)	148	113	35	0.144
P–134	T–2696 (Bounty × HES 1941)	218	159	59	0.495
P–146	T–2696–A (Pr. × HES 1941)	163	121	42	0.051
P–119	T–2693 (P. H. × HES 1931)	123	95	28	0.328
					1.523
					0.221
Total		943	701	242	
Check	Bounty	61	0	61	
		Heterogeneity x^2 (5 D. F.)			1.302

Behavior of the F_3

Third-generation hybrids of Susceptible × Resistant crosses were represented by 120 families derived from the six crosses presented in table 4. Twenty F_2 plants for each of the six crosses were grown to provide the F_3 material; five of the plants were classified "susceptible" in the F_2 and 15 were classified "resistant." If, as is suggested by the approximate 3:1 ratio found in the F_2, a single dominant factor type of inheritance were actually involved, theoretically a 1:2:1 ratio should result in the F_3. An analysis of the F_3 family reactions (table 7) shows that such an expectation was approximated. In no cross was the deviation from a 1:2:1 ratio significant, and the ratio of all families combined (36R:54Seg.:30S) significantly approximated the expected 30:60:30.

TABLE 7.—Gray leaf spot reaction of 120 F_3 families, Susceptible × Resistant.

CROSS NO.	PARENTAGE	NUMBER OF F_3 FAMILIES				CHI^2 1:2:1
		Total	Resistant	Segregating	Susceptible	
P–258	T–2716	20	7	8	5	1.200
P–281	T–2722	20	6	9	5	0.300
P–103	T–2685	20	6	9	5	0.300
P–134	T–2696	20	7	8	5	1.200
P–146	T–2696–A	20	6	9	5	0.300
P–119	T–2693	20	4	11	5	0.300
						3.600
Total		120	36	54	30	1.800
		Heterogeneity x^2 (5 D. F.)				1.800

BACKCROSSES

Backcrosses were made between each of the six F_1 hybrids listed in table 4 and their respective parents. First-generation backcrosses of (Susceptible × Resistant) × Resistant were inoculated, recorded, and discarded. While an analysis of the F_2 of this backcross would have been necessary to show segregation of plants into resistant and susceptible classes and to clarify further the mode of inheritance of resistance such an analysis was not attempted. Horticulturally, little was to be gained by carrying such a backcross through additional generations. However, the reaction of the F_1 backcross is presented (table 8) further to illustrate the dominant nature of the resistant factor.

Of a total of 361 plants, one was susceptible. The appearance of a susceptible plant in a population of (Susceptible × Resistant) × Resistant plants does not conform to the single dominant factor hypothesis, but since a slight amount of what may be referred to as pollen contamination or admixture of seed has been noted on one other occasion in these studies, no special significance is attached to the phenomenon.

TABLE 8.—Gray leaf spot reaction of first-generation backcrosses, (Susceptible × Resistant) × Resistant.

CROSS NO.	PARENTAGE	TOTAL NO. PLANTS	RESISTANT	SUSCEPTIBLE
P–106	T–2685 × HES 1930	96	95	1
P–121	T–2693 × HES 1931	76	76	0
P–140	T–2696 × HES 1941	31	31	0
P–145	T–2696–A × HES 1941	58	58	0
P–261	T–2716 × HES 1884	29	29	0
P–283	T–2722 × HES 1903	71	71	0
Total		361	360	1
Check	Bounty	43	0	43

First-generation backcrosses of (Susceptible × Resistant) × Susceptible were inoculated and observed for segregation of *Stemphylium* reaction. A 1:1 ratio was closely approximated in each of the six backcrosses and the number of resistant plants for the six crosses combined was roughly equal to the number classified as susceptible. A chi-square test for goodness of fit to a 1:1 ratio showed that in no single backcross, nor in the backcrosses combined, did a significant deviation from a theoretical ratio of 1:1 occur.

TABLE 9.—Gray leaf spot reaction of first-generation backcrosses, (Susceptible × Resistant) × Susceptible.

CROSS NO.	PARENTAGE	TOTAL NO. PLANTS	RESISTANT	SUSCEPTIBLE	CHI² 1:1
P–100	T–2685 × HES 1863	43	21	22	0.023
P–120	T–2693 × Pearl Harbor	66	28	38	1.587
P–135	T–2696 × Bounty	136	65	71	0.265
P–147	T–2696–A × Pritchard	91	44	47	0.989
P–262	T–2716 × Pearl Harbor	192	94	98	0.983
P–282	T–2722 × HES 1864	142	74	68	0.254
					3.201
Total		670	326	344	0.484
		Heterogeneity x^2 (5 D. F.)			2.717

DISCUSSION

The data concerning the inheritance of gray leaf spot resistance reported in this paper were collected from experiments in which plants in the cotyledon stage of development were inoculated under controlled environmental conditions with the mono-conidial isolate No. 419. A study of plant disease resistance based on observations made under such circumstances may well raise the questions of (1) the degree to which the reactions of cotyledonary leaves of 12- to 14-day-old plants will agree with the reaction of true leaves of older plants, (2) the extent to which the reaction of seedlings inoculated and held under artificially controlled conditions will agree with the reaction of field-grown plants, and (3) the extent to which seedlings resistant to a single mono-conidial isolate of the gray leaf spot fungus will resist other collections of the same pathogen. From experiments made to provide answers to these questions, there is good indication that the reaction of plants tested under the conditions under discussion will conform closely with the reactions obtained from field tests. In the general tomato improvement program, the junior author has made and tested many additional hybrid and backcross lines involving resistant and susceptible parents. In these tests inoculation was achieved by spraying the plants with a suspension of conidia collected from naturally infested leaves. Many unpublished data have been compiled which agree with the results obtained in the tests reported here.

The close agreement, with respect to gray leaf spot reaction, of plants inoculated with a single isolate of *Stemphylium solani* and plants inoculated naturally in the field, is suggestive of an absence of physiologic specialization of the pathogen in the area in which the studies were made. In the case of *Cladosporium fulvum,* Langford (*11*) found distinct races, each with different pathogenic capabilities on given tomato varieties, but with the present fungus no such condition has been found. It must be borne in mind, however, that the present study of

pathogenic variability was made in a relatively restricted area and that the study was confined to 50 isolates of the organism and four lines of tomatoes. It does not therefore preclude the existence of races of different host preferences in other areas where the pathogen occurs.

While the method of testing recorded here is different from that devised by Andrus *et al.* (*3*) for rapidly evaluating large numbers of plants in greenhouse tests, the results obtained are in agreement with those of Andrus and associates who found that lines selected for resistance were decidedly more resistant in field tests than were lines selected for other reasons.

Resistance of the tomato to a number of diseases has been the subject of many recent genetic studies. It is of interest that for many of the diseases in which resistance has been determined, resistance has been reported as controlled by single dominant genetic factors. Sengbusch and Loschakowa-Hasenbusch (*19*) found that immunity to leaf mold, *Cladosporium fulvum,* in their lines of *Lycopersicon pimpinellifolium* was due to a single dominant Mendelian factor. Langford (*11*) confirmed the work of Sengbusch and Loschakowa-Hasenbusch in regard to the dominance of the "immunity" factor to leaf mold in *L. pimpinellifolium* and found, in addition, a second independently operating dominant "resistant" gene to the leaf mold disease. Langford further found in a commercial tomato variety, a dominant partially resistant factor to certain races of *C. fulvum.* Bohn and Tucker (*4*) found immunity to Fusarium wilt in certain lines of *L. pimpinellifolium* and showed in a subsequent report (*5*) that immunity was due to a single dominant genetic factor. Andrus and Reynard (*2*), using Targinnie Red *(L. esculentum)* as a *Septoria*-resistant parent, showed that a single dominant factor was responsible for conferring resistance to the progeny of crosses of this variety with susceptible lines. Kikuta *et al.* (*9*) introduced Pearl Harbor, a variety resistant to spotted wilt, and later Kikuta and Frazier (*10*) determined that the resistance in this variety was apparently due to a single dominant gene. The results of the studies reported here clearly indicate that resistance to gray leaf spot is dominant over susceptibility and in this respect confirm the findings of Andrus and his co-workers (*3*).

The clear-cut segregation of heterogeneous populations into resistant and susceptible classes with respect to gray leaf spot reaction and the ratios of resistant to susceptible plants found in such populations demonstrate that reaction of *Stemphylium* infection is governed by a single Mendelian factor pair.

Langford (*11*) has used a system of designating disease-resistant factors in the tomato. The initials of the Latin name of the pathogen are employed to represent the genes for resistance and subscript letters are used to represent the initial letters of the tomato variety in which resistance was discovered. Thus he ascribed "Cf_{pl}" to the immunity factor in *Lycopersicon pimpinellifolium* to *Cladosporium fulvum.* Reynard and Andrus (*17*) followed this pattern when they assigned the symbols "A_d-a_d" to the factor pair governing resistance to *Alternaria* collar-rot, found first in the variety Devon Suprise. Since resistance to gray leaf spot was found simultaneously in *Lycopersicon esculentum* (Targinnie Red) and *L. pimpinellifolium* (P. I. 79532), there seems little basis for a choice between these two sources. Moreover, were the symbol Ss_p *(pimpinellifolium)* employed it might be confused with Sp (self topping) used by MacArthur (*13*), and Ss_e *(esculentum)* could be easily confused with the Se *(Septoria)* gene described by Andrus and Reynard (*2*). The symbols "St-st" might seem logical designations for the factor pair controlling resistance to *Stemphylium*

leaf spot, but Lindstrom (*12*) has used a similar symbol "st" to designate a sterile plant character induced through radium treatment of tomato plants. To avoid the confusion of following the proposals of Langford, the symbols "Sm-sm"[6] *(Stemphylium)* are proposed to designate the genes governing reaction to this disease.

SUMMARY

A technique was devised to test segregating populations of tomato seedlings to gray leaf spot (*Stemphylium solani*), and a method of securing large numbers of *Stemphylium* conidia is described.

Tomato seedlings about 12 to 14 days old were inoculated in the cotyledon stage, incubated under controlled environmental conditions, and graded on the basis of gray leaf spot development.

The reaction of cotyledonary leaves to *Stemphylium* infection was identical to the reaction of true leaves when tested under artificial conditions and to the reaction of mature plants when exposed to natural field infection.

Based on an analysis of 50 mono-conidial isolates, there was no evidence of physiologic specialization in the gray leaf spot pathogen.

Inheritance studies of crosses of commercial varieties with gray leaf spot resistant lines were made on 943 F_2 plants, 670 backcross plants (Susceptible $\times$ Resistant) $\times$ Susceptible, and on 120 F_3 families.

Resistance to gray leaf spot was inherited as a single dominant Mendelian factor; the factor pair accounting for such resistance has been assigned the symbol "Sm-sm."

[6]The senior author, in the thesis previously noted, used the symbol "St-st" to designate the factor pair controlling resistance to gray leaf spot. At that time he was unaware of the work of Lindstrom (*12*) on the "sterile plant" character.

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