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Leaf Mold Resistance in the Tomato

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LEAF MOLD RESISTANCE IN THE TOMATO[1]

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INTRODUCTION

There are approximately 600 acres under glass in Ohio devoted to vegetable culture, representing an investment of about $15,000,000. Of this amount, about 250 acres are located in the vicinity of Cleveland, and the remainder is distributed among areas surrounding Toledo, Ashtabula, Cincinnati, and Columbus. Between 60 and 75 per cent of the total acreage is devoted to tomato culture.

The most serious fungous disease of tomatoes under glass in these districts is leaf mold, caused by the fungus *Cladosporium fulvum* Cooke. Although the disease occurs occasionally on out-of-door tomatoes, it is usually found only on the crop growing in close proximity to greenhouses devoted to this crop, where an abundance of spores of the fungus are produced on the spring crop under glass.

Practical control of leaf mold in the greenhouse depends upon the maintenance of a sufficiently low relative humidity to prevent spore germination and infection. This is accomplished to a fairly satisfactory degree by leaving the ventilators open at night and keeping the temperature sufficiently high with heat. The critical periods are during the early part of the fall-crop season and the latter part of the spring-crop season. The additional firing required adds from $300 to $500 per acre to the annual cost of heating. Furthermore, complete protection is not assured, since during warm, rainy periods it is impossible to maintain a sufficiently low relative humidity to preclude infection.

Spraying is generally unsatisfactory. In the first place, the fungicides more commonly used are not sufficiently toxic to the fungus; secondly, it is almost impossible to cover the dense foliage of greenhouse-grown tomatoes adequately; and, thirdly, the cost of spraying a crop of greenhouse tomatoes thoroughly is between $125 and $200 per acre per crop. The most hopeful solution of the control of leaf mold lies in the development of strains of tomato resistant to the disease. The writer started a selection and breeding program with this aim in mind in 1930. The present paper is a report of progress to date.

HISTORY OF THE DISEASE

The fungus was first described by the English mycologist, M. C. Cooke, in 1883 on the basis of specimens sent to him from South Carolina (7). It is possible that the organism came originally from South America, where the tomato is indigenous. During the next 13 years it was reported on greenhouse tomatoes by Galloway from New Jersey in 1887 (8), by Bailey from New York in 1892 (3), and by Selby from Ohio in 1896 (20). The disease is now common in many greenhouse tomato sections throughout the world. It has been reported from the following countries: Australia, Austria, Belgium, Canada, Denmark, England, France, Germany, Holland, India, Italy, Jamaica, New Zealand, Russia, Spain, and the United States.

[1]Submitted to the Graduate School of the University of Wisconsin as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Numerous workers (2, 9, 15, 16, 17, 23, 26, 27) have shown that the optimum temperature for the disease is between 20° and 25° C. (69° and 78° F.) and that a high relative humidity is necessary for infection. Wilson and Alexander (27) in a survey of Ohio greenhouses found that leaf mold was least severe in those houses which were so constructed or so managed as to facilitate maximum aeration. This includes such factors as the long dimension of the houses in a north to south direction, ridge-hinged ventilators, a relatively large amount of ridge ventilation in proportion to house width, and maintenance of heat during the latter part of the spring-crop season. Attempts have been made to control leaf mold by reducing the humidity. The most successful method is that of prolonging the period when artificial heating is maintained. Forced air circulation has been tried with some success but as yet it has not been established as an economically sound practice in Ohio greenhouses.

The results of attempts to control the disease by means of fungicides are summarized in several papers (10, 15, 19, 24). In general, fungicides are not commercially successful. Bewley and Orchard (5) have recently reported excellent control with a proprietary compound, Shirlan, the active principle in which is salicylanilide.

The possibility of control of leaf mold through varietal resistance has been studied by several workers. Jagger (11) tested 96 tomato varieties and found Stirling Castle, Up-to-Date, and Norduke partially resistant. Small (22) tested 200 varieties for resistance. All were very susceptible except Stirling Castle, Up-to-Date, Norduke, Main Crop, Satisfaction, and Frogmore Selected; these varieties showed only a partial resistance. Newhall (18) reported partial resistance in two varieties, Satisfaction and Main Crop, which he crossed with Bonny Best and Marhio.

SCOPE OF THE PRESENT INVESTIGATION

In order to control leaf mold adequately through disease resistance under Ohio conditions it is necessary to acquire strains of a desirable type which remain free from infection during optimum conditions for the disease. These varieties which are reported partially resistant are not suitable types for Ohio culture. It became necessary, therefore, to determine (a) whether this degree of resistance was suitable for hybridization with susceptible varieties of desirable type; (b) whether more highly resistant varieties or individuals could be found; and (c) what the possibilities were for combining highest resistance with desired type. All these questions are considered in this report.

METHOD OF EXPERIMENTATION

Plants to be tested for resistance were transplanted from seed flats, about 2 weeks after sowing, into 3-inch clay pots, where they remained until discarded or transplanted into permanent beds. When the fifth true leaf began to unfold, the plants were inoculated, placed in an infection chamber for 48 hours, and then removed to benches or ground beds for 14 days.

Since pure cultures of the fungus sporulate rather sparingly, severely infected leaves were collected in commercial greenhouses and the spores were either used immediately or the leaves stored for future use. Spores were collected in a 12-inch evaporating dish by the use of an adapted DeVilbiss No. 15 atomizer, operated with compressed air (Figure 1A). A piece of tubing connected with a compressed air line was attached to the atomizer in place of the hand bulb. A continuous water supply was secured by replacing the short, glass, liquid intake-tube with a piece of small rubber tubing attached to a large container of distilled water. The same apparatus was used to spray plants with spore suspensions.

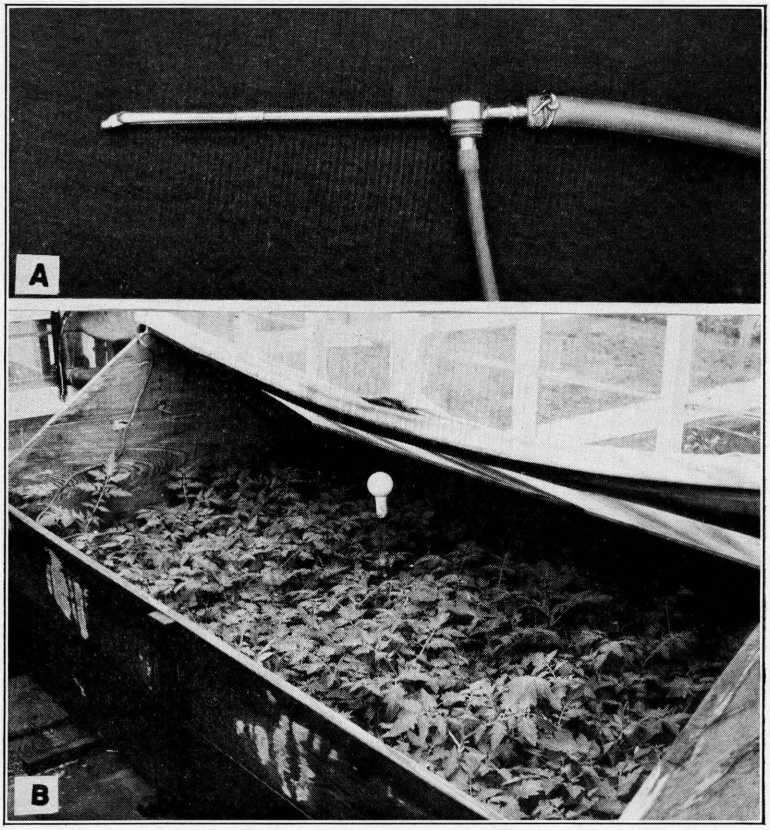

Fig. 1.—A. Atomizer adapted for use in collecting spores and making inoculations.
B. An interior view of the infection chamber.

The infection chamber was rectangular in shape, 4 x 6 feet with 18-inch sides, and was covered with a medium grade of muslin (Figure 1B). The air in the chamber was kept saturated by sprinkling water on the muslin cover. No attempt was made to control the temperature inside the chamber except that the room was kept at 20° to 25° C. (69° to 78° F.) during the winter. In the warm summer months the temperature of the chamber was kept favorable for infection by shading the inside of the greenhouse with whiting and by the water spray which was about 22° C. (72° F.). Numerous tests within the chamber with a standard Livingston atmometer showed less than 1 c. c. loss of water in 48 hours.

Notes for resistance were taken 10 and 14 days after inoculation. The five arbitrary classes which were used to record the degree of resistance or susceptibility are illustrated in Figure 5A and are as follows:

CLASS	DESCRIPTION
Excellent	No visible infection with reflected light but may show pin-point spots with transmitted light.
Good	Minute lesions up to 2 mm. in diameter. Fungous fruiting structures have never been observed, and certain of these lesions may be due to oedema.
Fair	Yellow, slowly enlarging lesions which bear fungous fruiting structures after a prolonged incubation period.
Poor	Slightly prolonged incubation period.
None	Complete susceptibility.

Plants for breeding purposes were grown to maturity in the experimental greenhouse in ground beds or in the experimental field. In order to grow as many plants as possible on a limited amount of greenhouse space, the plants were spaced 1 foot apart in 2-foot rows and pruned to a single stem.

It was necessary to shake the vines to secure a set of fruit. Self-pollinated clusters were not bagged, but those which were emasculated for hybridization were covered with glassine bags.

EXPERIMENTAL RESULTS

RESISTANCE IN COMMERCIAL VARIETIES

The reports of other investigators who have studied relative resistance and susceptibility to leaf mold in commercial varieties of tomato have already been cited. In the course of this investigation, the following varieties of the common tomato, *Lycopersicum esculentum* Mill., and one lot of *L. pimpinellifolium* Dunal, commonly referred to as Red Currant tomato, were tested for resistance. Seed for a large portion of the varieties of common tomato was secured from Dr. S. P. Doolittle of the United States Department of Agriculture.

Abundance
Ailsa Craig
Alice Roosevelt
Alliance
American Beauty
Atlantic Prize
Australian Dwarf Red
Australian Large Red
Avon Early
Beatall
Beauty
Beefsteak
Best-of-all
Bides Recruit
Bonny Best
Border Wonderful
Bountiful
Break O'Day
Brimmer
Buckeye State
Bunting's No. 1
Burbank
Chalk's Early Jewel
Cherry-shaped Yellow
Chiswick Peach
Clark's Early
C. O. I.
Colossal
Columbia
Comet
Conqueror
Cooper's First
Cooper's Luscious
Cooper's Special
Coreless
Danish Export
Danish Extra Early
Devon Special
Duke-of-York
Dwarf Yellow Prince
Earliana
Earliest of All
Earliest Open Ground
Earliest Shipper
Early Dawn

Early Detroit
Early Dwarf Red
Early Eclipse
Early Harbinger
Early Marvel
Early Paris Market
Early Sunrise
Early Winner
Enormous
E. S. I.
Every Day
Excelsior
Favorite
Ficcarazzi
Fillbasket
First Crop
Florida Special
Fruit Tomato
Garden Giant
Gold Ball
Golden Gem
Golden Perfection
Golden Ponderosa
Golden Queen
Golden Sunrise
Golden Trophy
Greater Baltimore
Heterosis
Homes Supreme
Hudson Valley Maid
Ideal
Imperial Ficcarazzi
Italia
Johnnisfeuer
Jubilee Blumen-Schmidt
June Pink
Kelway's Eldorado
Kelway's Sunshine Improved
Kilgore's Special
King Humbert
King Humbert Improved
King George
Kondine Red
Langportonian
La Preferee
Large Red
Large Yellow
Lieby's Export
Louisiana Red
Lucullus
McGee
Magnum Banum
Magnus
Main Crop
Marglobe
Market Favorite (Godber's)
Market King
Marmande
Marvel-of-Italy
Marvel of the Market
Marvelosa
Matchless
Mauthner's
Mikado
Money Maker
Nonsuch
New Invincible
New King
New Yellow Oxheart
Norduke
Norton
Open Air
Orange Sunrise
Owen's Topper
Oxheart
Peach Blow
Peach Tomato (yellow)
Perdrigeon
Perfection
Phenomenon
Pierette
Ponderosa
President Garfield
Princess-of-Wales
Profusion
Purple Mikado
Queen of the Purple
Queen Mary
Radio
Radio Large Red
Recordschlager
Red Cherry
Red Head
Red Currant
Red Pear
Redfield Beauty
Reynold's No. 2
Riverside Favorite
Rosy Morn
Rotkäppchen
San Marzano
Sutton's A-1
Satisfaction
Scarlet Champion
Schöne von Lathringer
Sieger (Victor)
Starks Table Dainty
Stirling Castle
St. John's Day
Stone (Norton's Improved)
Stoner
Success
Sunrise
Targinnie Blue
Table Dainty
The Toogood
The Kid
Tiptop
Triumph
Trucker's Favorite
Tuckwood
Up-to-Date
Victor
Victory
Walker's Recruit
Westlandria
White Tomato
Winter Beauty
Wonderful
Wright's V. C.
Yates Express
Yellow Cherry
Yellow Peach
Yellow Pear
Yellow Plum

Red Currant was resistant, and all but five of the tomato varieties were very susceptible. Those which showed some degree of resistance are Main Crop, Norduke, Satisfaction, Stirling Castle, and Up-to-Date. The degree of resistance of these five varieties was placed in class "fair" and is illustrated in Figure 5B. The incubation period was slightly longer in Stirling Castle and Satisfaction, and, as a consequence, these two varieties were considered to be the most resistant.

Several reciprocal crosses were made between the varieties Satisfaction and Stirling Castle and two susceptible varieties of a desirable type, Globe and Marhio. Certain of the F_1 plants were inoculated. The data in Table 1 show that the type of resistance of Stirling Castle was completely dominant in these crosses. F_1 individuals from five of the crosses were grown to maturity, and F_2 progenies therefrom were inoculated (Table 2).

TABLE 1.—Inheritance of Resistance in F_1 Progenies from Crosses Between Two Partially Resistant English Varieties and Two Susceptible American Varieties

Number of cross	Cross	Plants showing various classes of resistance			
		Good	Fair	Poor	None
		No.	*No.*	*No.*	*No.*
1	Stirling Castle x Marhio	0	0	0	15
2	Stirling Castle x Marhio	0	0	0	17
3	Stirling Castle x Marhio	0	0	0	12
4	Stirling Castle x Globe	0	0	0	25
5	Stirling Castle x Globe	0	0	0	14
6	Globe x Stirling Castle	0	0	0	5
7	Globe x Stirling Castle	0	0	0	8
8	Globe x Stirling Castle	0	0	0	26
9	Satisfaction x Marhio	0	14	0	0
10	Satisfaction x Marhio	0	15	0	0
11	Satisfaction x Marhio	0	17	0	0
12	Marhio x Satisfaction	0	2	0	0
13	Satisfaction x Globe	0	16	0	0
14	Satisfaction x Globe	0	16	0	0
15	Globe x Satisfaction	0	24	0	0

Where Stirling Castle was used as the resistant parent, only a small percentage of the F_2 plants showed as high resistance as that parent. Where Satisfaction was used as the resistant parent, slightly more than half of the F_2 plants were in the "fair" class. Plants in this class were found to defoliate seriously under commercial greenhouse conditions and their intrinsic value for commercial control of the disease was questionable. These lines were not continued beyond the F_2 generation since no individuals falling into the "excellent" or "good" classes were secured.

TABLE 2.—Inheritance of Resistance in F_2 Progenies from Crosses Between Two Partially Resistant English Varieties and Two Susceptible American Varieties

Number of cross	Resistance of F_1 parent	Plants showing various classes of resistance			
		Good	Fair	Poor	None
		No.	*No.*	*No.*	*No.*
3	None	0	1	12	25
6	None	0	1	11	22
	Total	0	2	23	47
9	Fair	0	22	10	16
15	Fair	0	24	9	4
11	Fair	0	23	2	12
	Total	0	69	21	32

RESISTANCE IN OFF-TYPE PLANTS

In the spring of 1930 Mr. Carl Neubert, a commercial tomato grower, called the writer's attention to an unusual plant growing in his crop of the Globe variety. The plant was free from leaf mold and was taller and had coarser, heavier leaves than the Globe plants. It bore simple fruit clusters with numerous, small, two-loculed, red fruits. A similar plant was pointed out in 1933 by Mr. Peck, another tomato grower. The foliage and plant type had much in common with that of nearby Globe plants except that the leaves were shorter and broader. The clusters were simple with many red, two-loculed, extremely small and very smooth fruits (Figure 2). When ripe, the color of the inter-locule matrix which surrounds the seed was green and the taste was slightly sweet. Both of these plants occurred in commercial stocks of Globe variety, the seed of which was secured from the Livingston Seed Company, Columbus, Ohio. These are the only individuals of the sort noted by the writer in numerous visits to many tomato greenhouses over a period of 4 years.

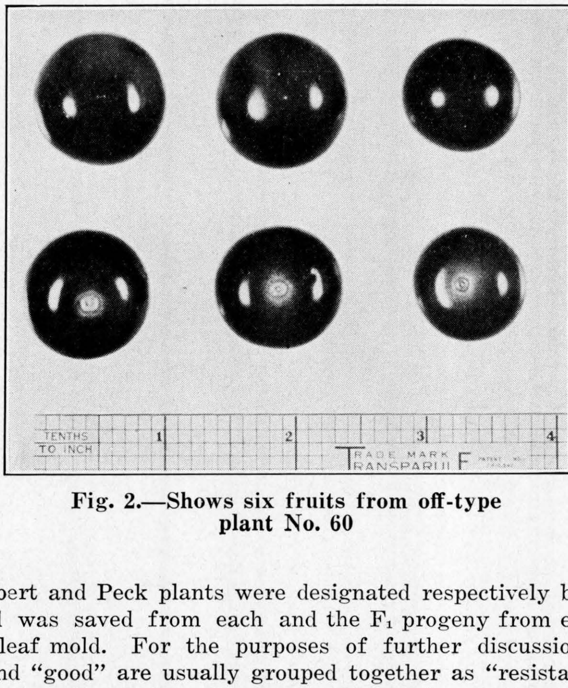

Fig. 2.—Shows six fruits from off-type plant No. 60

The Neubert and Peck plants were designated respectively by numbers 50 and 60. Seed was saved from each and the F_1 progeny from each tested for resistance to leaf mold. For the purposes of further discussion the classes "excellent" and "good" are usually grouped together as "resistant", while the classes "fair", "poor", and "none" are grouped together as "susceptible".

It is seen (Table 3) that the F_1 progeny of Plant 50 was divided into equal numbers of resistant and susceptible individuals; whereas that of Plant 60 contained about twice as many resistant as susceptible plants. Selections from the F_1 progeny of Plant 50 have been continued; time has not permitted this as yet for Plant 60.

In selecting from the F_1 progeny of Plant 50, only resistant individuals were continued. The results with F_2 progenies from 14 F_1 resistant plants are given in Table 3. Three progenies yielded no "susceptible", while 11 progenies segregated into approximately 74 and 26 per cent resistant and susceptible individuals, respectively. Selections of resistant plants were again made from segregating F_2 progenies. Of the 10 F_3 progenies four were all resistant, and the remainder again segregated into about 71 per cent resistant and 29 per cent susceptible plants. Individuals selected from two of the completely resistant F_3 progenies, when tested in the F_4, yielded all resistant progenies.

TABLE 3.—Resistance in Progenies Derived from Two Off-type Tomato Plants (50 and 60)

Parent number	Progeny (number of plants)	
	Resistant	Susceptible
F_1 progenies		
Off-type Plant 50	17	17
Off-type Plant 60	48	22
F_2 progenies		
50–17	9	1
50–18	8	2
50–20	7	3
50–21	10	0
50–24	5	5
50–28	9	1
50–31	7	3
50–35	3	7
50–38	9	1
50–40	10	0
50–41	7	3
50–42	8	2
50–43	9	1
50–46	10	0
F_3 progenies		
50–38–2	5	5
50–38–5	6	4
50–41–5	7	3
50–41–7	8	2
50–41–8	10	0
50–41–9	8	1
50–42–1	10	0
50–42–2	8	2
50–42–3	10	0
50–42–7	10	0
F_4 progenies		
50–41–8–2	10	0
50–41–9–9	10	0
50–42–1–3	10	0
50–42–3–3	10	0
50–42–3–8	10	0

As this series was nearing completion the writer received the paper of Sengbusch and Loschakowa-Hasenbusch (21) which reported complete resistance of *Solanum racemigerum* Lange. This nomenclature, according to Bailey (4), is synonymous with *Lycopersicum pimpinellifolium* Dunal and hybridizes readily with the common tomato (*Lycopersicum esculentum* Mill.). Recent tests with plants of the Red Currant tomato (*L. pimpinellifolium*) showed it to be highly resistant to leaf mold. The plants of the resistant selections developed from Plant 50 have points of similarity to those of Red Currant. Also, it was apparent that pure resistant lines could readily be secured from these plants by selection and that the resistance secured was much higher than that found in occasional varieties of common tomato. Accordingly, this offers the possibility that hybridization of this type with common tomato and further selection may yield a highly resistant and desirable type.

CROSSES BETWEEN RESISTANT INDIVIDUALS AND STANDARD VARIETIES

Fortunately, in 1930, 12 F_1 individuals from Plant 50 were grown in the field with Globe and Marhio, the two varieties used most commonly in Ohio greenhouses. One of the 12 F_1 plants (50-12) bore more desirable fruits than the others and it was crossed with individuals of Globe and Marhio. The F_1 self from 50-12 was not tested for resistance. The F_1 progenies from three of the crosses were tested in part by the method already described, and certain of the plants were exposed to infection in commercial greenhouses. All progenies segregated into resistant and susceptible classes (Table 4). All plants were further rated into "good"[2], "fair", "poor", and "none" classes, and representatives of each class were grown to seed and the F_2 progenies tested (Table 5).

TABLE 4.—Resistance Tests of F_1 Hybrid Progenies from Crosses Between Plant 50-12 and Globe and Marhio Individuals

Crosses	Place of infection	Number resistant	Number susceptible
Cross A (Marhio x 50–12)	Wooster (artificial infection)	7	12
	Reitsman (natural greenhouse infection)	2	8
	Martin (natural greenhouse infection)	1	8
Cross B (Globe x 50–12)	Wooster (artificial infection)	4	5
	Martin (natural greenhouse infection)	2	2
Cross C (50–12 x Globe)	Wooster (artificial infection)	3	19
	Total	19	54

TABLE 5.—Resistance and Susceptibility to Leaf Mold in F_2 Progenies from Crosses Between 50-12 and Globe and Marhio Plants

Number of F_1 parent plant	Resistance of F_1 parent	Reaction of F_2 progenies	
		Number resistant	Number susceptible
B-6	None	0	38
A-12	Poor	0	33
A-10	Poor	8	28
A-11	Fair	0	28
A-16	Fair	0	38
A-17	Fair	0	42
A-32	Fair	0	27
A-34	Fair	0	40
A-39	Fair	0	40
B-2	Fair	0	40
B-13	Fair	0	39
C-15	Fair	0	10
C-18	Fair	0	10
A-3	Fair	3	35
B-5	Fair	6	30
A-9	Fair	30	16
A-15	Good	0	35
B-1	Good	4	33
A-8	Good	3	44
A-18	Good	4	20
A-1	Good	12	25
A-19	Good	13	25
A-20	Good	18	26
A-26	Good	21	27
A-35	Good	18	21
B-7	Good	16	22
A-6	Good	29	20
C-3	Excellent	1	9
C-10	Excellent	8	2

[2]At the time of this classification the class ''good'' was used to denote those plants which were later divided into classes ''excellent'' and ''good''.

Most of the progenies from susceptible parents (i. e., those in the "none", "poor", or "fair" classes) were completely susceptible. Four out of the 16 progenies, however, contained resistant individuals, and in one (A-9) a majority was resistant. One resistant parent (A-15) yielded a completely susceptible progeny; whereas the remaining progenies contained various percentages of resistant plants. Resistant individuals were selected from the progenies of the following plants: A-1, A-6, A-9, A-18, A-19, A-20, A-26, A-35, B-5, B-7, C-10, and susceptible individuals were selected from the progeny of A-12. The F_3 progenies were grown and tested in the usual manner (Table 6).

TABLE 6.—Resistance and Susceptibility in F_3 Progenies from Crosses Between Plant 50-12 and Globe and Marhio Plants

Parent plant number	Number resistant	Number susceptible	Parent plant number	Number resistant	Number susceptible	Parent plant number	Number resistant	Number susceptible
A-1-4	7	3	A-9-21	10	0*	A-20-41	7	10
A-1-13	7	2	A-9-24	7	3	A-20-42	23	5*
A-1-17	7	3*	A-9-25	10	0*	A-20-43	10	6
A-1-18	6	4	A-9-26	4	6	A-20-44	15	19
A-1-32	5	5	A-9-27	8	2*	A-20-52	26	2
A-1-37	10	0	A-9-32	9	0*			
A-1-38	5	5	A-9-43	4	3	A-26-2	2	8
			A-9-44	0	25	A-26-6	8	2
A-6-1	5	5	A-9-46	17	6*	A-26-12	4	6
A-6-4	5	5	A-9-47	18	20	A-26-15	7	1
A-6-6	10	0*	A-9-48	20	21*	A-26-24	13	0
A-6-7	10	0*	A-9-50	10	6	A-26-27	6	4
A-6-15	8	2*	A-9-51	4	12	A-26-30	8	2
A-6-20	8	2	A-9-54	11	13	A-26-34	8	2*
A-6-25	8	2*	A-9-55	1	14	A-26-41	17	9
A-6-26	10	0*				A-26-42	18	11*
A-6-27	9	1	A-10-5	10	0*	A-26-46	5	12
A-6-32	9	1*	A-10-12	8	2	A-26-47	25	1*
A-6-34	10	0	A-10-14	7	3	A-26-48	1	28
A-6-43	13	14	A-10-15	10	0	A-26-51	9	15*
A-6-44	25	3*	A-10-18	10	0	A-26-52	0	34
A-6-45	15	7	A-10-31	5	5	A-26-53	7	11
A-6-49	11	1*	A-10-33	8	2	A-26-55	0	2
A-6-51	8	7	A-10-34	4	5			
A-6-52	3	6				A-35-3	6	3
A-6-53	0	15	A-12-17	0	10	A-35-7	8	1*
A-6-54	9	0*	A-12-21	0	10	A-35-8	4	6
						A-35-14	6	4
A-9-1	4	6	A-18-12	4	6	A-35-15	9	0
A-9-3	8	2*	A-18-13	7	3	A-35-18	8	1
A-9-6	3	7	A-18-14	5	4	A-35-31	5	5
A-9-8	5	5				A-35-32	16	4
A-9-9	10	0	A-19-15	6	4	A-35-37	10	10
A-9-10	6	1	A-19-28	8	2			
A-9-11	5	4	A-19-31	6	4*	B-5-5	10	0
A-9-12	4	6	A-19-36	10	0*	B-5-19	10	0
A-9-13	7	2*	A-19-38	9	1	B-5-23	5	5*
A-9-14	6	4						
A-9-16	2	8	A-20-15	8	2*	B-7-30	2	8
A-9-17	8	2	A-20-24	5	5			
A-9-19	15	5*	A-20-29	6	4	C-10-6	9	1
A-9-20	5	5	A-20-36	1	9	C-10-7	30	0*

*Selections were made from these progenies for F_4 progeny tests (Table 7).

A majority of the F_3 progenies segregated for resistance, but, in the main, there was a larger percentage of resistant than susceptible individuals. A few progenies were completely resistant insofar as this test was concerned, but it was obvious that in most cases the number of plants tested was too small to be a fair index of the whole population of a given progeny. Plants A-12-17 and A-12-19, which were selected for susceptibility, yielded completely susceptible progenies. Plant A-6-34, which yielded 10 resistant and no susceptible plants, was backcrossed to a susceptible plant. The F_1 progeny of 65 plants was completely resistant, and two F_2 progenies with a total of 241 individuals yielded 139 resistant and 102 susceptible individuals. Plants A-9-27 and A-20-29, each of which yielded segregating selfed lines, when backcrossed with a susceptible plant segregated in the F_1 into 60 resistant to 59 susceptible and 40 resistant to 35 susceptible, respectively.

TABLE 7.—Resistance and Susceptibility in F_4 Progenies from Crosses Between Plant 50-12 and Globe and Marhio Plants

Number of F_2 parent	Classification of F_4 progenies	Number of progenies	Resistant	Susceptible
			No.	*No.*
A-1-17	Resistant	0	....	....
	Segregating	3	22	8
A-6-6	Resistant	2	38	0
	Segregating	2	32	5
A-6-7	Resistant	6	120	0
	Segregating	0	....	....
A-6-15	Resistant	0	....	....
	Segregating	5	41	8
A-6-25	Resistant	2	40	0
	Segregating	3	44	6
A-6-26	Resistant	1	10	0
	Segregating	0	....	....
A-6-32	Resistant	0	....	....
	Segregating	5	65	22
A-6-44	Resistant	4	32	0
	Segregating	2	10	4
A-6-49	Resistant	2	16	0
	Segregating	2	13	3
A-6-54	Resistant	2	16	0
	Segregating	0	....	....
A-9-3	Resistant	0	....	....
	Segregating	4	68	12
A-9-13	Resistant	4	40	0
	Segregating	2	12	8
A-9-19	Resistant	2	12	0
	Segregating	2	13	4
A-9-21	Resistant	1	10	0
	Segregating	2	16	4
A-9-25	Resistant	5	110	0
	Segregating	0	....	....
A-9-27	Resistant	1	30	0
	Segregating	5	53	17
A-9-32	Resistant	4	75	0
	Segregating	2	17	3
A-9-46	Resistant	1	8	0
	Segregating	2	11	2
A-9-48	Resistant	0	....	....
	Segregating	7	46	20
A-10-5	Resistant	3	28	0
	Segregating	0	....	....
A-19-31	Resistant	0	....	....
	Segregating	3	38	12
A-19-36	Resistant	1	10	0
	Segregating	0	....	....
A-20-15	Resistant	1	10	0
	Segregating	4	32	7
A-20-42	Resistant	1	10	0
	Segregating	0	....	....
A-26-34	Resistant	1	35	0
	Segregating	1	2	6
A-26-42	Resistant	0	....	....
	Segregating	2	15	5
A-26-47	Resistant	5	47	0
	Segregating	1	9	1
A-26-51	Resistant	0	....	....
	Segregating	3	43	6
A-35-7	Resistant	2	8	0
	Segregating	1	29	1
B-5-23	Resistant	1	5	0
	Segregating	2	17	3
C-10-7	Resistant	1	10	0
	Segregating	0	....	....

In Table 7, the F_4 progenies are classified on the basis of whether or not they segregated or contained only resistant plants. It is to be noted that certain F_4 families consisted of progenies all of which were completely resistant. With the exception of A-20-42, the F_3 parent progeny also had been completely resistant. Selections were made from these F_4 progenies.

The F_4 plants were selfed and backcrossed with plants of susceptible commercial varieties. The results in Table 8 show the resistance of certain F_4 progenies and of the F_5 selfs and F_1 backcross progenies derived from them. This evidence indicates the high degree of resistance had become completely fixed in these F_4 plants, since all plants selected from their progenies yielded self progenies which were completely resistant. It is also apparent that this type of resistance is completely dominant, since all hybrid progenies were completely resistant. Figure 5C shows a comparison of a resistant F_4 individual and a susceptible Globe plant.

TABLE 8.—Resistance in Certain F_4 Progenies and in the F_5 Selfs and Backcrosses Derived Therefrom

F_4 progenies			F_5 progenies				
Selfed			Selfed			Backcrossed	
F_3 parent number	Resistant	Susceptible	F_4 parent number	Resistant	Susceptible	Resistant	Susceptible
	No.	*No.*		*No.*	*No.*	*No.*	*No.*
A-6-6-4	30	0	A-6-6-4-7	10	0	....	....
			A-6-6-4-10	10	0	20	0
A-6-7-2	30	0	A-6-7-2-1	10	0	....	....
			A-6-7-2-9	10	0	30	0
A-6-7-5	30	0	A-6-7-5-7	10	0	....	....
			A-6-7-5-9	10	0	19	0
A-6-7-6	30	0	A-6-7-6-2	10	0	20	0
			A-6-7-6-10	10	0	20	0
A-6-25-1	30	0	A-6-25-1-4	....	....	40	0
			A-6-25-1-8	10	0	20	0
A-6-25-3	10	0	A-6-25-3-2	10	0	20	0
			A-6-25-3-3	10	0	10	0
			A-6-25-3-8	10	0	20	0
A-9-13-7	10	0	A-9-13-7-9	6	0	16	0
A-9-25-1	30	0	A-9-25-1-5	4	0	10	0
			A-9-25-1-6	8	0	10	0
A-9-25-6	30	0	A-9-25-6-3	4	0	10	0
			A-9-25-6-4	8	0	40	0
			A-9-25-6-6	9	0	....	....
			A-9-25-6-10	7	0	10	0
A-9-27-6	30	0	A-9-27-6-3	10	0	30	0
			A-9-27-6-5	10	0	....	....
A-9-32-1	25	0	A-9-32-1-4	10	0	30	0
A-10-5-4	8	0	A-10-5-4-2	20	0	20	0
A-19-36-10	10	0	A-19-36-10-1	10	0	9	0
A-26-34-1	35	0	A-26-34-1-5	10	0	....	....
			A-26-34-1-12	10	0	....	....
			A-26-34-1-13	10	0	30	0
			A-26-34-1-15	10	0	....	....
			A-26-34-1-23	10	0	....	....
			A-26-34-1-27	10	0	....	....
			A-26-34-1-28	10	0	....	....
			A-26-34-1-31	10	0	....	....

The results so far have shown that the type of resistance which occurred in the progeny of Plant 50-12 is distinct from the relative tolerance in certain of the commercial varieties. It has also been demonstrated that from hybrids with commercial types this high degree of resistance can be recovered by selection within subsequent generations. With this fact well established it becomes a sound procedure to continue backcrossing with the desirable susceptible types and reselecting for lines in which desirable characters and resistance are combined. In the case of the selections from the hybrids just discussed, backcrosses to Globe were made and selection continued. Progress in this direction will now be reported.

Three F_1 plants, A-6, A-9, and A-18, from Cross A (Marhio x 50-12) were crossed with Globe. In the resulting F_1 progenies about one-fourth of the total number of plants was resistant (Table 9). Selections were made within

TABLE 9.—Resistance and Susceptibility in Hybrids Between F_1 Individuals of Cross A (Table 4) and Globe

Parent number	Number resistant	Number susceptible
F_1 progenies		
A-6 x Globe	9	19
A-9 x Globe	8	32
A-18 x Globe	7	13
F_2 progenies		
A-6 x Globe-1	7	3
A-6 x Globe-8	7	3
A-6 x Globe-15	8	2
A-6 x Globe-17	6	4
A-6 x Globe-22	6	4
A-6 x Globe-23	7	3
A-6 x Globe-25	5	5
A-6 x Globe-26	41	14
A-6 x Globe-28	44	10
A-9 x Globe-2	37	18
A-9 x Globe-8	7	3
A-9 x Globe-11	9	1
A-9 x Globe-13	8	2
A-9 x Globe-24	8	2
A-9 x Globe-30	9	1
A-9 x Globe-38	8	2
A-18 x Globe-1	4	6
A-18 x Globe-23	6	4
A-18 x Globe-26	4	6
A-18 x Globe-30	7	3
A-18 x Globe-38	6	4
F_3 progenies		
A-6 x Globe-26-1	24	6
A-6 x Globe-26-7	29	1
A-6 x Globe-28-6	9	1
A-6 x Globe-28-9	20	9
A-9 x Globe-2-6	3	0
F_4 progenies		
A-6 x Globe-26-1-7	7	3
A-6 x Globe-26-7-9	10	0
A-6 x Globe-28-9-3	10	0
A-6 x Globe-28-9-8	10	0

the resistant group of two of the crosses, and, when these plants reached maturity, seed was saved from the most desirable types. This procedure was continued for several generations and in the F_4 generation three out of four of the progenies, in which A-6 was used as the resistant parent, appeared to be homozygous for resistance.

The fruits from these backcross progenies were comparable to fruits from the variety Globe, except for size. In this respect they were larger than those of the resistant parent but smaller than those of Globe.

THE GENETIC NATURE OF RESISTANCE TO LEAF MOLD

The results of Sengbusch and Loschakowa-Hasenbusch (21) show that, when the resistant *Solanum racemigerum* Lange was crossed with susceptible varieties, resistance was controlled by a single dominant Mendelian factor. The F_1 progenies from the three crosses Bonny Best, Danish Export, and Tookswood x *S. racemigerum* were resistant. The F_2 progeny, from the cross Westlandria x *S. racemigerum*, segregated for resistance. Forty-six individuals were tested and yielded 76.1 per cent resistant and 23.9 per cent susceptible, which closely approaches a 3:1 ratio. In the F_3 generation 216 progeny lines—with a total of 6968 individuals from the crosses *S. racemigerum* x susceptible varieties (Lucullus, Danish Export, Allerfruhest Freiland, Golden Queen, Tookswood, and Kondine Red)—were tested for resistance. Of these F_3 progenies 22.86 per cent was susceptible, 11.46 per cent was classified as homozygous resistant, and 65.71 per cent as heterozygous. When the authors crossed the partially resistant Stirling Castle with susceptible varieties, the F_1 progenies were susceptible. On the basis of this, the authors express the opinion that the type of partial resistance which occurs in Stirling Castle is recessive, although sufficient data for a complete genetical analysis were lacking.

The project of breeding a new tomato variety resistant to leaf mold started in the spring of 1930 with the finding of the first resistant off-type plant and was conducted, until recently, without knowledge of the German findings. The project has been developed with the primary purpose of breeding a new variety resistant to the disease, and only minor attention has been given to genetical studies.

The data at hand concerning the inheritance of resistance to leaf mold are not sufficient to warrant final deductions. However, they show that the resistance which occurred in Plant 50 is dominant. This was first suggested by the fact that certain F_1 individuals of the three original crosses, A, B, and C, were resistant. It was substantiated when the F_1 hybrid progeny, which resulted from crossing the homozygous resistant individual A-6-34 with an individual of the susceptible Ponderosa variety, proved to be resistant. Further proof was obtained when a large number of homozygous resistant F_4 individuals was crossed with individuals of the susceptible varieties Marhio, Globe, Ponderosa, and Bonny Best. In all cases the F_1 progenies were resistant.

It appears that relatively few factors are involved, possibly only one, as suggested by Sengbusch and Loschakowa-Hasenbusch (21). When heterozygous individuals were crossed with individuals of susceptible varieties, the F_1 progenies segregated into approximately a ratio of 1 resistant to 1 susceptible, and the selfed progenies of Plant 50 in the F_2 and F_3 generations segregated for resistance into ratios which approximate 3 resistant to 1 susceptible.

However, some ratios are obtained which may indicate that resistance is governed by more than one factor. This was especially so in the F_2 progeny from the cross A-6-34 x Ponderosa, which segregated into a ratio of approximately 9 resistant to 7 susceptible. A project to study the inheritance of the resistance to leaf mold found in Plant 50 has been initiated.

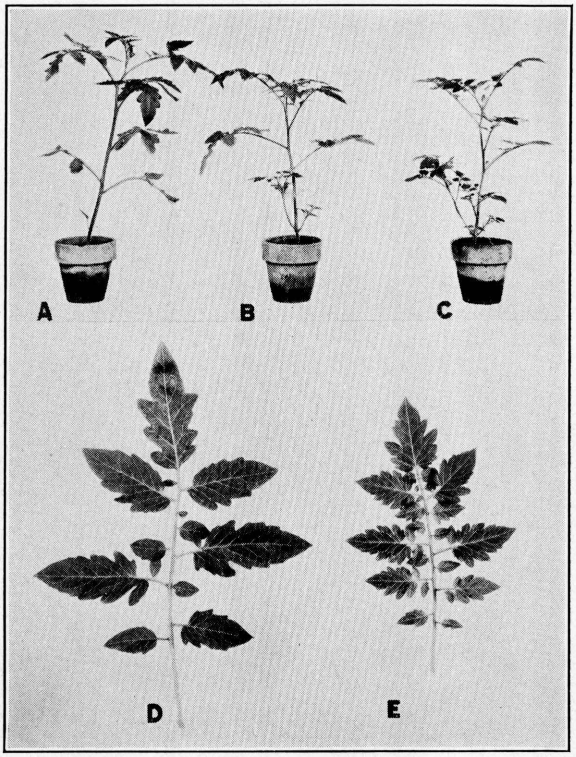

Fig. 3.—A. Globe plant.
B and C. Typical off-type plants derived from Plant 50. Note tendency to produce excessive number of "suckers".
D. Leaf of Globe plant.
E. Leaf of off-type plant. Note relative size compared with Globe.

In a breeding project for resistance to plant diseases, it is necessary to consider the possibilities of biological specialization of the parasite. Sengbusch and Loschakowa-Hasenbusch (21) in their report discuss the possibility of the existence of biological strains of *Cladosporium fulvum* Cooke and state that they saw no evidence of their existence. In this work pure cultures of the fungus have not been used. Spores for inoculation purposes were washed from the under surface of diseased leaves, which were gathered from numerous greenhouses in the vicinity of Cleveland, Ohio. Thus far, there are no indications that more than one strain of the fungus exists in this area. However, final conclusions can not be drawn until a large number of collections of the parasite from a wide range of sources has been made and their ability to infect the homozygous resistant lines tested.

PROGRESS IN COMBINING RESISTANCE WITH DESIRABLE TYPE

The success of a breeding project for disease resistance in plants hinges upon the ability to combine resistance with desirable quality and type. In this instance the desirable type parents are completely susceptible and the resistant parent is an extremely undesirable type which segregated for fruit and vegetative characters in the F_1 generation. The undesirable characters which appeared in certain hybrids resulting from crosses between resistant and susceptible plants are: Leaves, small; vines, weak with tendency to excessive branching; fruit, small, red, 2 to 3-loculed, unpleasant to taste, and when ripe

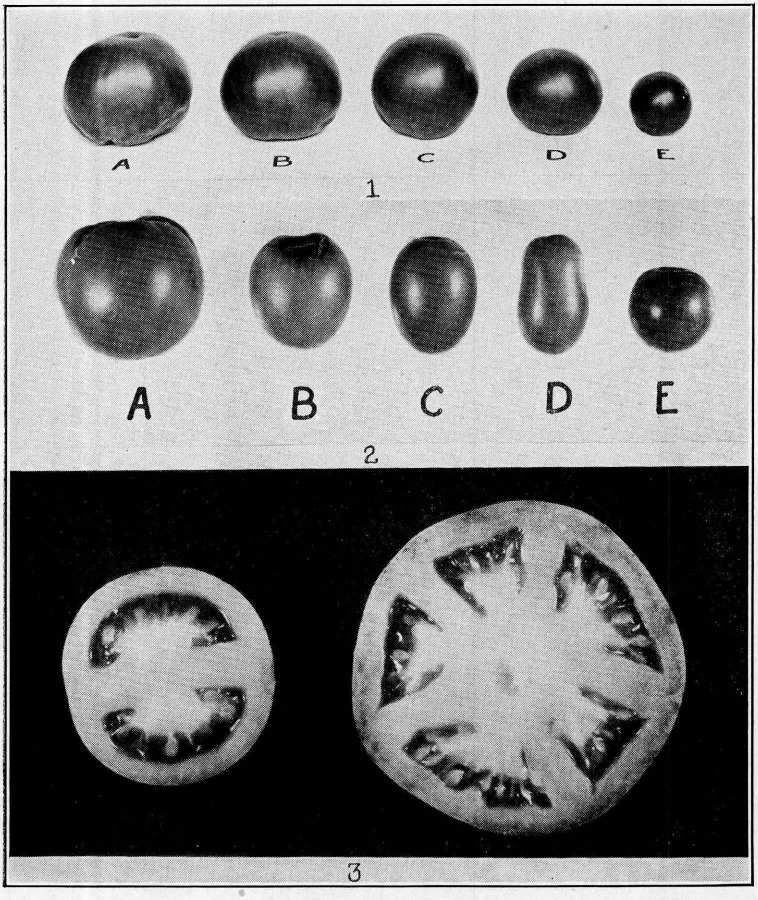

Fig. 4.—1. Comparison of fruit sizes. A. Globe fruit. B. Fruit from an F_1 plant of the cross (A-6-34 x Ponderosa). C, D, and E. Representative fruits from three homozygous resistant hybrid lines.

2. Comparison of fruit shapes. A. Fruit from Globe. B, C, D, and E. Representative fruits from four hybrid lines.

3. Representative fruits from two hybrid lines illustrating a meaty fruit, left, and a non-meaty fruit, right.

the inter-locule matrix which surrounds the seed is green colored. The two plants B and C in Figure 3 illustrate the excessive tendency toward branching of progeny derived from Plant 50 in comparison with a normal Globe plant, A. The small size of the leaves of these plants is illustrated by the Leaf E in contrast with the Leaf D (Figure 3) from a Globe plant of the same age.

It has been shown earlier in this paper that certain of the F_1 hybrid progeny, resulting from crosses between the desirable susceptible varieties, Marhio and Globe, and an F_1 individual from the resistant Plant 50, inherited

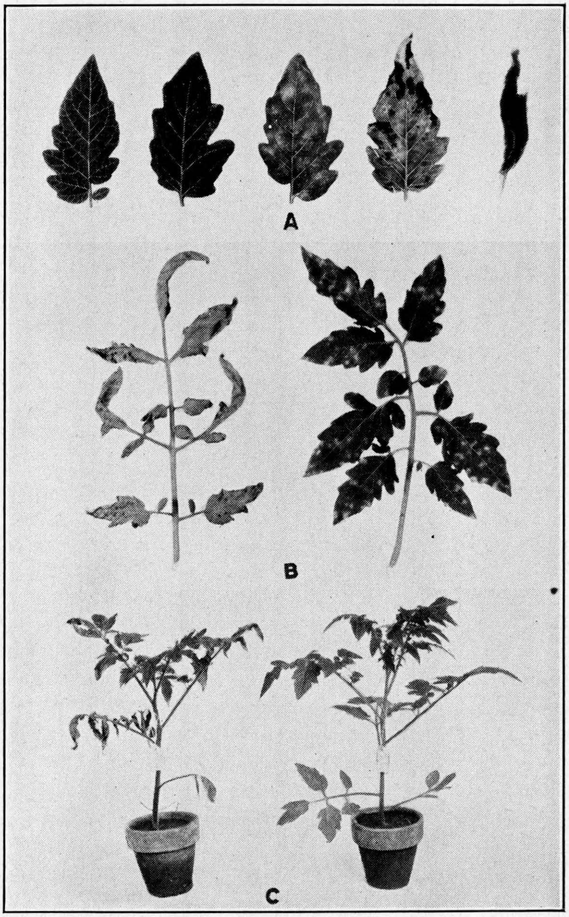

Fig. 5.—A. Representative leaflets of the five classes of resistance 16 days after artificial inoculation. From left to right the classes are "excellent", "good", "fair", "poor", and "none".

B. Artificially infected leaves. Left, leaf of a susceptible Globe; right, leaf of a partially resistant English variety.

C. A comparison of susceptible Globe plant, left, with a resistant F_4 hybrid plant, right. Both plants inoculated artificially.

resistance and that by selection this resistance could be recovered in a homozygous condition. The vine and fruit characters of these F_1 hybrid progenies also segregated. Some plants had a vine type closely resembling that of Globe or Marhio (the two are similar in this respect); others resembled certain of the F_1 progeny from Plant 50; and still others were intermediate. Likewise, the fruits were variable; none, however, was as large as those of the desirable parents.

In selecting for resistance in succeeding generations, in some cases, care was used to select resistant individuals which most closely approached the desirable type. By this method lines in the fifth generation have been secured which are homozygous for resistance and, at the same time, have quite uniform fruit and vegetative characters. Thus, they are a decided improvement over the original resistant plant. In other instances, resistant individuals were selected without regard to fruit or vine characters. Generally, these lines, although homozygous for resistance, show very little improvement except that their characters are uniform.

In Figure 4, the top section illustrates the variable fruit size of certain of the hybrids. Fruit A is from a desirable Globe plant. Fruit B is from an F_1 plant from the cross (A-6-34 x Ponderosa) and is only slightly smaller than the Globe fruit. C, D, and E are representative fruits from four selfed lines four generations removed from the original crosses. The fruit shapes obtained when selections were made for resistance without regard for type are illustrated in the middle section of Figure 4. The bottom section of Figure 4 shows a cross section of fruits from two hybrid lines. The one at the left has two locules and is undesirable because of a lack of meatiness. All fruits in Figure 4 were picked from tomato plants grown in the field.

Selections in Families A-6, A-9, and A-26 are homozygous for resistance and are the most desirable for vegetative and fruit characters. Selections in Family A-6 are desirable for vegetative characters and yield a large number of fruits but lack desired fruit size and shape and a uniformly pleasant taste. Selections in Family A-9 have a tendency to produce 2 to 3-loculed, medium-sized fruits, with a tendency for the inter-locule matrix which surrounds the seed to be green. Family A-26 is desirable, but the yields are poor, the taste is uniformly slightly acid, and the fruits are too flat. In the last two families there is a tendency for the pistils to be exceptionally long, but Burke and Roberts (6) state that in crossing short- and long-pistil types the former tends to be dominant. Consequently, it should be possible to select away from this character in further crosses.

It is planned to use selections from these three families for a series of three backcrosses in which the resistant individuals from each backcross will be selected and used as resistant parents for further backcrosses. It is hoped that by this procedure it will be possible to select a resistant line of desirable type. That such a procedure should be successful is indicated by the results which were secured when three F_1 individuals from Cross A were backcrossed with Globe. After self-pollination through four generations the lines resemble Globe in many respects but lack desirable fruit size.

DISCUSSION

This paper is a report of progress on the development of a new tomato variety resistant to the leaf mold disease, caused by the fungus *Cladosporium fulvum* Cooke. It purports to show that the resistance which exists in certain commercial varieties is not suitable for hybridization with desirable-type susceptible varieties. However, a higher type of resistance exists which can be recovered in a homozygous condition in hybrids resulting from crosses between resistant and desirable susceptible individuals.

The F_1 progenies of the reciprocal crosses (Stirling Castle x susceptible varieties) were completely susceptible, and only a small percentage of the F_2 individuals was as resistant as Stirling Castle. These results are in agreement with those of Sengbusch and Loschakowa-Hasenbusch (21), who concluded that the resistance of Stirling Castle is recessive. The F_1 progenies of the reciprocal crosses (Satisfaction x susceptible varieties) and about 50 per cent of the F_2 progenies was as resistant as Satisfaction. These results are in contrast to those of Newhall (18), who reported the resistance of Satisfaction to be recessive.

Two off-type plants resistant to leaf mold were found in commercial crops in greenhouse. What appear to be pure lines for resistance were secured from the first plant, designated by the number 50, as shown in Table 3. In the fourth generation all individuals in the five progenies tested were resistant. The parent individuals of four of these progenies were selected from completely resistant F_3 progenies. It is realized that if the selections in the F_3 generation had been backcrossed to susceptible individuals, as well as selfed, more evidence that these F_4 progenies were homozygous for resistance would be at hand.

These studies show that the high resistance of Plant 50 can be recovered in hybrids resulting from crosses between the F_1 progeny of it and susceptible varieties. The F_1, F_2, and F_3 progenies from these crosses largely segregated for resistance when resistant individuals were used as parents. However, certain of these F_3 progenies were completely resistant. The progenies resulting when susceptible individuals were used as parents were largely susceptible.

The exceptions, where susceptible individuals yielded segregating progenies and resistant individuals susceptible progenies, are undoubtedly due to improper classification of the parent plants. Since the classes used to designate the various degrees of resistance are purely arbitrary, it is next to impossible to classify every plant correctly. However, the results in Table 5 show the method of distinguishing between resistant and susceptible individuals to be fairly accurate.

The fact that pure lines for resistance were secured in these hybrids is shown in Table 8, which shows that certain F_4 progenies, as well as the selfs and backcrosses derived therefrom, were resistant.

Three of the F_1 hybrid individuals from the cross (50-12 x Marhio) were backcrossed with susceptible individuals. The resulting progenies in the F_1 generation segregated for resistance, but, after selfing for four generations, three out of four progenies appeared to be homozygous for resistance. When F_2 individuals from the cross (50-12 x Marhio) were again backcrossed with susceptible individuals, two of the F_1 backcross progenies segregated for resistance into a ratio which closely approached 1 resistant to 1 susceptible.

The third produced only resistant individuals, thus showing that, after two generations of selfing from the original crosses, pure lines for resistance were secured.

The genetical nature of the resistance to leaf mold found by Sengbusch and Loschakowa-Hasenbusch (21) was reported by them to be controlled by a single, dominant, Mendelian factor. Since the primary purpose of this investigation was not a genetical study, data are not at hand to make a genetical analysis of the inheritance of this resistance to leaf mold. However, it is conclusively shown in Table 8 that this resistance is dominant, because all individuals of the F_1 progenies resulting from crosses between homozygous resistant lines and susceptible commercial varieties are resistant. The data reported in this paper also further suggest that relatively few factors are involved. Resistance may also be affected by biological strains of the parasite. However, no indications of such strains have been observed either in this work or that of Sengbusch and Loschakowa-Hasenbusch (21) and in both instances all inoculations were made with spores collected from infected plants. Although this does not preclude the possibility that there is more than one strain of the fungus, it does suggest that only one strain of the fungus exists in the northern half of Ohio.

The origin of the two off-type resistant plants is problematic and may always be open to question. However, it is possible that the resistance which existed in them is the same as that reported by Sengbusch and Loschakowa-Hasenbusch (21). If that is the case, it is necessary to assume that they originated from chance crosses between individuals of the common Globe variety of tomato, *Lycopersicum esculentum* Mill., and Red Currant, *L. pimpinellifolium* Dunal. Bailey (4) lists *Solanum racemigerum* Lange as a synonym for the latter. Circumstantial evidence which supports this assumption is provided by the facts that the two species readily hybridize and that in both cases the Globe seed used in the plantings in which the off-type plants occurred was secured from the Livingston Seed Company, which also lists Red Currant as one of its small tomatoes. It is unnecessary to know the origin of the two off-type plants in order to breed a new tomato variety resistant to leaf mold. However, their origin has considerable scientific interest and value.

The homozygous, resistant hybrid lines are distinctly superior to the original source of resistance for resistant parents for further breeding work. By hybridization and selection, fruit size and shape have been improved, pink fruit color has been developed, the number of sections in the fruits has been increased, and the tendency for the color of the inter-locule matrix surrounding the seed to be green has been reduced and in some lines practically eliminated; also a sturdy vine has been developed. As a consequence, there should be fewer undesirable characters to contend with in subsequent crosses.

To date, no undesirable linkage groups have been encountered which would interfere with the development of a desirable variety. Lindstrom (12, 13) has shown that size of fruit is controlled by more than one factor. MacArthur (14) has listed the 15 factors studied, exclusive of fruit size, in six linkage groups, but no difficulty is anticipated from this grouping.

No studies to ascertain the nature of this resistance have been conducted by the author. However, Schmidt (25), using spores from artificial cultures of the fungus, studied the nature of the resistance to leaf mold which occurs in *Solanum racemigerum* and found it to be of a chemical nature. He temporarily named the substance "prohibitin". It is water soluble, and its toxic effect is destroyed by boiling for 20 to 30 minutes and by precipitation of the leaf decoction with tannic acid. In a more recent paper by Agerberg, Schmidt, and Sengbusch (1) it was shown that the spores of *Cladosporium fulvum* produced in artificial culture differ morphologically and physiologically from those produced on tomato leaves. Spores secured from leaves were able to germinate normally in leaf decoctions made from *Solanum racemigerum* and it was concluded as unproven that resistance was due to "prohibitin".

SUMMARY

This report is concerned with the progress thus far made in the development of a new tomato variety resistant to leaf mold, a disease caused by the fungus *Cladosporium fulvum* Cooke. The majority of the plants were tested for resistance artificially in a humidity chamber, although a few were grown during each crop period in one or more commercial greenhouses.

Five out of 180 varieties of the common tomato, *Lycopersicum esculentum* Mill., were found to possess a partial resistance to leaf mold. One other species, *L. pimpinellifolium* Dunal, commonly known as Red Currant tomato, was resistant to the disease.

Stirling Castle and Satisfaction had the highest degree of resistance of the commercial varieties, and this partial resistance was recovered in some of the F_2 hybrid individuals. The partial resistance of Stirling Castle appeared to be recessive in contrast to that of Satisfaction which appeared to be dominant.

Individuals of both varieties, Satisfaction and Stirling Castle, growing in commercial greenhouses became seriously diseased following a prolonged infection period. As a result, it was concluded that the type of resistance to leaf mold which these varieties showed made them unsuitable for further breeding work.

Two off-type plants resistant to leaf mold were found in crops of the variety Globe in two commercial greenhouses. The F_1 progenies of both these plants segregated for resistance and fruit and vegetative characters. After selfing the first plant (Plant 50 in this study) for four generations, four F_4 progenies appeared to be homozygous for resistance.

The degree of resistance which existed in segregating progenies formed a gradation from complete susceptibility to high resistance and has been grouped in five arbitrary classes. The two most resistant classes were later thrown together as resistant and the three most susceptible classes as susceptible.

When crosses were made between an F_1 individual from Plant 50 and Marhio and between the same individual and Globe, the F_1, F_2, and F_3 progenies largely segregated for resistance. One selfed F_2 and a large number of selfed F_4 individuals were shown to be homozygous for resistance by the fact that the selfs and backcrosses derived from them were all resistant.

Resistance is shown to be dominant, and, thus far, there is no evidence that biological strains of the parasite exist which would interfere with a genetical study.

Definite progress in combining resistance with desirable type has been made. Several of the homozygous resistant selections possess desirable vegetative characteristics, and the fruit characters have been greatly improved over those of the original off-type Plant 50.

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