Resistance to Foliar Blight and Crown Rot of Pepper Caused by *Phytophthora capsici*

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ABSTRACT

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Resistance to foliar blight of pepper (*Capsicum annuum*) caused by *Phytophthora capsici* was found in several plant introduction (PI) lines by using a spore suspension as inoculum in a greenhouse test. PI 201232 and 201234 had the highest level of resistance. These lines had previously been reported resistant to the crown and root rot phase of the disease. For a study of inheritance of resistance, two resistant cultivars, Fyuco and P51, were crossed with the susceptible California Wonder and with each other. In the F_1, F_2, and backcross populations, resistance appeared under the control of a single dominant gene with modifiers and was the same from both sources; however, the F_3 progeny did not fit a single gene hypothesis. Lines selected for resistance to foliar blight in the greenhouse were usually resistant to crown and root rot in the field. Prolonged incubation periods or very high inoculum concentrations of *P. capsici* could occasionally overcome resistance and result in symptoms on some resistant plants.

Phytophthora capsici Leonian causes a root and crown rot of pepper (*Capsicum annuum* L.) in many parts of the world (3,7). In New Jersey, it has become increasingly serious in recent years, and a foliar blight sometimes occurs during prolonged periods of stormy weather. Small farmers do not have enough land to rotate crops as often as needed to reduce the disease pressure to a low level. Partial control in the field can be obtained by growing plants on high soil ridges (1). There are no fungicides registered for control of foliar phase of this disease, although captafol has an emergency permit for use as a foliar spray in New Jersey (S. A. Johnston, *unpublished*). Attempts to find antagonistic microorganisms for biological control have not yet been successful in the field.

Considerable research has been done to develop resistance to the disease in foreign countries (4,5,8), but little recent work has been reported on this method of control in the United States (2,6). A few years ago, the second author obtained seeds of resistant cultivars, Fyuco from H. R. Galmarini (I.N.T.A., 5567 La Consulta, Mendoza, Argentina) and P51 through the courtesy of J. E. van Zanten (Sluis & Groot, P.O. Box 13, Enkhuizen, Netherlands). We began a breeding program to obtain resistance to the disease using these two lines, and the early results of such a breeding program, including a study of the inheritance of resistance, are presented here. In addition, we have reexamined plant introduction (PI) lines previously reported resistant (2) and have screened all entries from Argentina in the PI collection.

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MATERIALS AND METHODS

Screening tests in the greenhouse. Seed of 24 PI lines, Fyuco, P51, and three commercial cultivars (Anaheim, California Wonder, and Red Sweet Cherry) were germinated in sterilized Metro-Mix 300 Potting Soil (W. R. Grace & Co., Fogelsville, PA 18051). For crown rot assessment, seedlings were transplanted in 10-cm plastic pots in soil infested with *P. capsici*. Peppers grown in infested soil were maintained in a greenhouse compartment at 28 C, harvested 1 mo after transplanting, and examined for crown rot symptoms.

For assessment of foliar blight, pepper seedlings were transplanted in sterile Metro-Mix 300 and grown for 6 wk until they were about 15–20 cm tall. For inoculation, the pots were randomized in a mist chamber and sprayed with a sporangial suspension of *P. capsici* containing 2,000 sporangia per milliliter of sterile distilled water. Sporangia were obtained by separately growing isolates S1 (type A^1) and ATCC 15399 (type A^2) on Difco lima bean agar for 10 days, dislodging sporangia with a sterile cotton applicator, counting the sporangia in a hemacytometer, and adjusting the concentration to 1,000 sporangia of each isolate per milliliter in the final inoculum suspension.

After overnight incubation at 100% relative humidity (about 18 hr), seedlings were removed from the mist chamber and placed on a greenhouse bench. Temperature in the mist chamber and greenhouse fluctuated diurnally in the range of 21–30 C. Data on foliar and stem blight were taken 11 or 14 days after inoculation.

Inheritance of resistance. Fyuco and P51 were used as resistant parents. They were crossed with susceptible California Wonder and with each other to obtain F_1 seed. Subsequently, backcross and F_2 populations were obtained for each of the three crosses. In spring 1982, when each set of populations was complete, plants were grown in 10-cm pots as described for foliar screening tests. Plants were randomized in a mist chamber before inoculation. The test was replicated by making inoculations on three different days. A replicate contained about five plants of each parent and F_1, 10 plants of the backcrosses, and 25 plants of F_2 populations. Inoculations were made by spraying plants with a spore suspension containing 2,000 sporangia (1,000 of each of two isolates) per milliliter of suspension.

Because all plants could not fit in the mist chamber at one time, each replicate was sprayed and incubated separately. Replicates 1, 2, and 3 were incubated in the mist chamber for 18, 22, and 19 hr, respectively, and the plants were examined for symptoms 2 wk after inoculation. Included in a second test were three resistant lines (Phyo 636, Iso-Yolo 8, and Fidelio) obtained from E. Pochard, Station d'Amelioration des Plantes Maraicheres, INRA, Monfavet, France.

Individual resistant plants from each of the three F_2 populations were selected and selfed to produce seed for F_3 generation lines. In autumn 1982, 24 F_3 lines derived from two of the original crosses and 20 F_3 lines from the third cross were grown in flats in the greenhouse. When seedlings were about 6 wk old, they were inoculated by spraying foliage with a sporangial suspension of S1 and ATCC 15399 (2,000 sporangia per milliliter). After 18 hr of incubation in the

mist chamber, flats were returned to the greenhouse. Ten days after inoculation, plants were divided into resistant and susceptible classes.

Field trials. Several populations derived from crossing Fyuco and P51 with California Wonder, selfed survivors of a greenhouse screen of several PI lines, and the two resistant French lines were planted on 3 June 1982 in a field trial at the Rutgers Research and Development Center at Centerton, NJ. This field had severe pepper blight in the three previous years. Each entry plot contained seven plants. The test was replicated four times in a randomized complete block design. Two replicates were located in the midst of a fungicide trial and two in the midst of a biological control trial. A visual estimate of percent blight (crown rot phase) was made on each plot on three dates, 31 August, 15 September, and 18 October. Data were analyzed by analysis of variance and Duncan's multiple range test.

RESULTS

Screening tests in the greenhouse. PI lines 123469, 187331, 201232, and 201234, previously reported resistant to crown rot by Kimble and Grogan (2), were also resistant to foliar blight caused by the two isolates of *P. capsici* in our tests (Table 1). In addition, 12 other PI lines showed some level of resistance to crown rot, foliar blight, or both. Generally, but not always, if a line had some survivors when grown in infested soil, it also had survivors from a foliage inoculation. Several PI lines were not included in Table 1 because all inoculated plants died; the susceptible lines were PI 155349, 260451, 260452, 260456, 281298, 329246, 439207, and 439208. Fyuco and P51 were as resistant as the two best PI lines, 201232 and 201234.

Inheritance of resistance. The pattern of inheritance in F_1 and F_2 and backcross families when either Fyuco or P51 was used as a resistant parent was similar and indicated a single dominant gene for resistance (Table 2). In the populations derived from crossing the two resistant parents, there were a few susceptible individuals and one susceptible Fyuco plant.

For the Fyuco × California Wonder cross, 21 of 24 F_3 lines derived from healthy F_2 plants segregated, whereas 16 (two-thirds) were expected to segregate (Table 3). There were two lines in which all individuals were diseased and one with all healthy plants. Thirteen of 21 lines segregated according to a predicted ratio of three resistant to one susceptible. Similarly, for the P51 × California Wonder cross, 23 of 24 F_3 lines segregated, and one had all resistant plants. Eleven segregated according to a

Table 1. Reaction of pepper seedling to inoculation with *Phytophtora capsici* in greenhouse tests

	Foliar blight[a]			Crown rot[b]	
Line or variety	Total inoculated	No. healthy	Repeat inoculation of healthy seedlings (no. healthy)	Total no.	No. healthy
California Wonder	6	0	...	5	0
Anaheim	6	4	2	5	0
Red Sweet Cherry	6	0	...	5	0
PI 123469	6	3	0	5	4
187331	7	2	1	5	1
201232	7	7	7	5	5
201234	7	4	4	...	...
223551	5	2	0	5	3
260450	7	2	0	...	...
260453	7	3	1	5	0
260454	7	2	0	5	0
260455	7	1	0	5	1
260457	7	0	...	5	1
260537	7	0	...	5	5
267739	7	0	...	5	1
281297	6	0	...	5	1
439209	5	1	...	5	0
439210	7	1	1	5	1
439211	7	1	0	5	0
P51	7	7	7	10	9
P51-1[c]	7	5	5	5	5
P51-2[c]	6	5	5	5	5
Fyuco	7	7	7	5	5
Fyuco-1[c]	7	5	5	5	4
Fyuco-2[c]	7	7	7	5	4

[a] Plants inoculated with a sporangia suspension (2,000 sporangia per milliliter); counts made after 11 or 14 days.
[b] Plants grown in infested soil, counts made 1 mo after transplanting.
[c] Individual plant selections.

Table 2. Number of pepper plants resistant to foliar blight/total number inoculated with *Phytophthora capsici* in populations derived from three crosses

Entry	Generations	Rep. 1	Rep. 2	Rep. 3	Totals	χ^{2}[a]
Fyuco	P1	4/4[b]	3/3	3/3	10/10	
California Wonder (CW)	P2	0/6	0/6	0/6	0/18	
CW × Fyuco	F_1	6/6	3/6	4/4	13/16	
Fyuco × F_1	BC1	10/10	8/9	10/10	28/29	
CW × F_1	BC2	5/10	0/10	7/10	12/30	(1:1) 1.200 NS
F_2	F_2	17/25	16/24	20/26	53/75	(3:1) 0.751 NS
P51	P1	2/2	2/2	1/1	5/5	
CW	P2	0/5	0/4	0/5	0/14	
CW × P51	F_1	3/6	6/6	5/6	14/18	
P51 × F_1	BC1	10/10	10/10	10/10	30/30	
CW × F_1	BC2	4/10	2/10	7/10	13/30	(1:1) 0.533 NS
F_2	F_2	18/22	16/21	24/25	58/68	(3:1) 3.843*
Fyuco	P1	4/5	7/7	5/5	16/17	
P51	P2	5/5	6/6	6/6	17/17	
P51 × Fyuco	F_1	6/6	5/6	6/6	17/18	
Fyuco × F_1	BC1	11/11	10/10	11/11	32/32	
P51 × F_1	BC2	9/9	10/10	10/10	29/29	
F_2	F_2	26/16	22/24	26/26	74/76	

[a] NS = not significant, * = χ^2 significant at 0.05.
[b] Results of greenhouse inoculation of 6-wk-old pepper seedlings with 2,000 sporangia per milliliter of *P. capsici*. Data taken 2 wk after inoculation.

Table 3. Number of pepper plants resistant or susceptible to *Phytophthora capsici* in F_3 populations derived from individual resistant F_2 plants in greenhouse tests

F_3 population	Fyuco × California Wonder			P51 × California Wonder			P51 × Fyuco	
	R[a]	S[a]	χ^2 (3:1)[b]	R	S	χ^2 (3:1)	R	S
A	15	3	0.667	16	2	1.852	18	0
B	8	10	8.963**	17	1	3.630	11	1
C	19	1	4.266*	20	4	0.889	24	0
D	0	24	...	24	0	...	24	0
E	0	21	...	21	1	4.909*	24	0
F	19	5	0.222	9	15	18.000**	24	0
G	13	5	0.074	1	17	46.296**	18	0
H	11	7	1.852	14	4	0.074	16	0
I	24	0	...	17	7	0.222	23	0
J	13	11	5.556*	5	17	32.061**	24	0
K	23	1	5.556*	4	19	40.710**	23	1
L	11	13	10.889**	10	14	14.222**	20	4
M	4	14	26.741**	16	2	1.852	18	0
N	14	4	0.074	9	9	6.000*	18	0
O	18	6	...	...	...	...	24	0
P	21	3	2.000	9	15	18.000**	24	0
Q	20	4	0.889	16	8	0.889	22	0
R	21	3	2.000	18	6	...	24	0
S	9	9	6.000*	13	11	5.556*	24	0
T	15	3	0.667	8	10	8.963**	24	0
U	18	6	...	13	5	0.074	...	...
V	11	13	10.889**	23	1	5.556*	...	...
W	20	4	0.889	...	...	...	...	...
X	17	7	0.222	17	7	0.222	...	...
Y	...	...	...	16	8	0.889	...	...
Z	...	...	...	17	7	0.222	...	...

[a] R = resistant, S = susceptible. Plants were counted resistant if they were healthy, showed only superficial blemishes on the stem, or showed only bud blight at the growing tip. Susceptible plants were killed.
[b] Chi-square values that are not significant indicate that the data fits the hypothesis that segregation occurs in the predicted ratio of 3 resistant:1 susceptible. * = χ^2 Significant at the 0.05 level,** = χ^2 significant at the 0.01 level.

Table 4. Percent pepper blight caused by *Phytophthora capsici* in the field on dates indicated[a]

Entry	31 August	15 September	18 October
Phyo 636	7.2 a	17.9 ab	17.9 ab
Fidelio	0.0 a	3.6 a	3.6 a
P51	0.0 a	0.0 a	0.0 a
P51-1[b]	0.0 a	0.0 a	0.0 a
P51-2[b]	0.0 a	0.0 a	0.0 a
California Wonder × P51 (F_1)	3.6 a	12.2 ab	12.2 ab
P51 × (California Wonder × P51)	0.0 a	3.6 a	10.7 ab
California Wonder × (California Wonder × P51)	32.2 c	39.3 c	39.3 c
P51[c]	3.6 a	3.6 a	3.6 a
P51 × Fyuco (F_1)	0.0 a	0.0 a	0.0 a
P51 × (P51 × Fyuco)	7.2 a	3.6 a	3.6 a
PI 123469-1[b]	10.7 ab	10.7 ab	14.3 ab
PI 187331[c]	25.0 bc	25.0 bc	28.6 bc
PI 201232-1[b]	0.0 a	3.6 a	3.6 a
PI 201232-2[b]	0.0 a	0.0 a	0.0 a
Yolo Wonder[d]	...	...	27.9

[a] Means are for four replicates and means in each column followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[b] Individual plant selection.
[c] Bulk selection.
[d] Yolo Wonder, a susceptible cultivar, was not included in this test. Mean was obtained from untreated check plots of Yolo Wonder in adjacent fungicide trials and is included for comparison.

predicted 3:1 ratio, and eight segregated 50% or more susceptible. For the P51 × Fyuco cross, 17 of 20 F_3 lines contained all healthy plants, and there were a few susceptible individuals in the other three.

Susceptible plants had blighted foliage, crown rot, or rapidly growing stem lesions. Resistant plants were usually symptomless, but there were two general exceptions. In the second replicate (Table 2), many plants classed as resistant had patches of a superficial brownish purple speckling on the stems. Even the resistant French lines included in this replicate and the Fyuco and P51 parents showed this symptom. In the screening of F_3 lines, many plants classed as resistant had a terminal bud blast that was often difficult to see. Neither the superficial speckling in the stems nor the blasting of a minute portion of the growing tip of the plant developed further to engulf other portions of the plant.

Field trials. All lines entered in the field trial were expected to have resistance, based on experience with greenhouse tests. Yet, most lines had a few diseased plants, and six of them had a foliar blight as high as or higher than that of the Yolo Wonder susceptible check (Table 4). P51 and the F_1 of P51 × Fyuco were the most resistant entries. Most of the incidence of disease occurred in the first part of the growing season. Disease did not increase much between late August and mid-October.

DISCUSSION

Greenhouse tests confirmed the existence of sources of resistance in the PI collection that had been previously reported by others (2) and indicated that several additional lines had resistance. Screening of lines or segregating populations by using the foliar inoculation method gave similar results to planting in infested soil in the greenhouse or field, and the foliar inoculation method was simpler to manage.

Data from the F_1, F_2, and backcross populations indicated that resistance is due to a single dominant gene. However, a few susceptible individuals appeared in populations (F_1 or backcrosses to the resistant parent) that should not have segregated if the explanation of a single dominant gene were correct (Table 2). Furthermore, F_3 data did not conform to this simple hypothesis. It may be necessary to postulate additional modifier genes or irregular dominance under certain environmental conditions. Smith et al (6) reported data indicating single and duplicate dominant genes acting

independently. Pochard and Daubeze (4) reported a case of polygenic resistance. From the standpoint of seed companies' current interest in hybrid varieties, a parental line developed with the kind of resistance we studied could be used to produce F_1 hybrids that would give good control in the field, regardless of a genetic interpretation of our data.

Occurrence of an occasional blighted plant in populations of resistant parents, F_1s, or backcrosses to the resistant parent is difficult to explain. Incomplete penetrance of the genes has been suggested. Populations derived from crossing two resistant parents had infrequent instances of segregation, and this indicates we are dealing with essentially the same genetic system in both Fyuco and P51.

Resistance may be overcome by prolonged incubation periods or by massive doses of inoculum. In the second replicate of the inheritance study, the incubation period was longer than in the other ones and many other plants showed superficial stem lesions. In the tests with F_3 populations, terminal bud blast occurred on less than 1 mm of tissue. The configuration of very young leaf axils at the growing tip could have permitted inoculum to collect at the growing point, and it could also have prevented rapid drying when plants were removed from the mist chamber. In the field, blighted plants in resistant populations could also be the result of locally high inoculum potential or of very favorable conditions for infection over a long time period. Smith et al (6) found that resistance to the crown and root rot phase of the disease could be overcome by prolonged exposure to the fungus. The possible effect of inoculum concentration or long incubation periods on resistance should be studied further.

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