Inheritance of Resistance to Pseudomonas solanacearum in Solanum phureja

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ABSTRACT

Selected clones of *Solanum phureja* had high levels of resistance to *Pseudomonas solanacearum* in greenhouse and growth chamber tests. Eleven hybrid families (50-100 plants each) involving seven parents were tested under growth chamber conditions by inoculation with a race 1 isolate of *P. solanacearum* from tomato (K-60). Each plant was inoculated by stem puncture at the prebud stage and held for 15 days at 28 C, 70 ± 3% relative humidity and 2,000 ft-c on a 14-hr photoperiod. The genetic hypothesis that best fits the observed resistant-susceptible ratios requires that three dominant and independent genes provide resistance. Although the results from all families agreed well with this model, there was evidence of modifying genes. Phytopathology 60:1499-1501.

The low levels of resistance to *Pseudomonas solanacearum* E. F. Sm. that have been reported in *Solanum tuberosum* L. cultivars (2, 4) are not sufficient to withstand infection under the optimal conditions for disease development that occur in tropical areas. Potentially higher levels of resistance have been reported in *Solanum phureja* Juz. & Buk. by Thurston & Lozano (9) and Robinson (5) from greenhouse and field tests, respectively. Further investigation of the resistance in *S. phureja* under greenhouse conditions showed that clones varied in their reaction to 10 diverse isolates of the pathogen (7). Clones with high levels of resistance to all isolates used were detected. The greenhouse tests also led to the hypothesis that relatively few genes were required to confer resistance; however, a precise genetic interpretation was not possible because of erratic results attributed to fluctuations in environmental conditions. To provide the stable environmental conditions needed for a genetic analysis, hybrid progenies were tested under controlled conditions in a growth chamber.

MATERIALS AND METHODS.—The parental *S. phureja* clones were selected from open-pollinated seed provided from the Coleccion Central Colombiana (CCC) by H. David Thurston. The relative resistance of these clones to *P. solanacearum* has been described (7). *Solanum phureja* clones and a 24-chromosome *S. tuberosum* hybrid were intercrossed to produce resistant (R) × susceptible (S), R × R, and S × S combinations. When possible, 100 plants of each cross were grown from true seed. Poor germination or unthrifty growth reduced the number of test plants to less than 100 in some crosses. The seed were germinated in vermiculite in a growth room at a constant temp (21 C) and a 14-hr photoperiod from a combination of Sylvania Gro-Lux and General Electric cool-white fluorescent and tungsten incandescent lights that provided 2,000 ft-c. After 20 days, individual seedlings were transplanted to 3-inch pots, and, 14 days later, to 5-inch clay pots containing sterilized muck soil. Plants were held in the growth room until treated 7 to 8 weeks after planting and were watered daily with Hoagland's nutrient solution. Because of space limitations, only one family could be tested at a time.

A race 1 isolate of *P. solanacearum* from tomato (K-60) was used (3). The stem inoculation procedure and the disease index scale (ranging from 1.0 = no infection, to 5.0 = complete wilting) were as described by Sequeira & Rowe (7). Following inoculation, the plants were transferred to a growth chamber held at 28 C, 70 ± 3% relative humidity and 2,000 ft-c supplied as above on a 14-hr photoperiod. Plants with an index rating of 1.0 to 2.5 at 15 days after inoculation were classified as resistant. This was based on the observation that these plants would grow to maturity in the growth chamber while those rated 3.0 to 4.0 would usually die. Limited numbers of the parental clones were also tested under the same conditions to determine whether their reaction conformed to the results found previously under greenhouse conditions (7).

RESULTS.—The parents had the same reaction to the disease in the growth chamber as in the greenhouse (Table 1). Genotypes were assigned to the parents, based on the observed ratios of resistant to susceptible individuals in each family. The hypothesis that best fits the observed ratios requires that three dominant and independent genes provide resistance. With this model, there was good agreement between observed and expected ratios for the 11 crosses tested (Table 2). This model fits the observed pattern of inheritance of resistance for these parents under the defined growth chamber conditions for one specific isolate (K-60) of the pathogen.

Tests of progenies from crosses among clones rated as resistant and susceptible in these tests should provide additional evidence for the validity of the proposed genetic scheme. This has not been done extensively, but one sequence confirms the scheme suggested above and establishes a correlation between results in the greenhouse and in the growth chamber. When seedlings from the cross CCC 1386.12 × US-W4 were tested in the greenhouse, 14% were resistant to K-60 (7). Twenty-

TABLE 1. The reaction of parental clones of *Solanum phureja* and *S. tuberosum* to *Pseudomonas solanacearum*, and proposed genotype of each

Clone	Greenhouse		Growth chamber		Disease reaction	Proposed genotype
	No. tested	Disease index[a]	No. tested	Disease index[a]		
1339.28	5	4.6 ± 0.1	10	4.3 ± 0.8	Susceptible	rraabb
1386.12	9	1.4 ± 0.1	5	1.0 ± 0	Resistant	RrAABb
1386.13	5	1.8 ± 0.6	20	1.1 ± 0.5	Resistant	RrAABb
1386.26	9	1.2 ± 0.1	5	1.0 ± 0	Resistant	RrAaBB
1388.30	5	1.0 ± 0	3	1.5 ± 0	Resistant	RrAABb
5536.7			10	4.6 ± 0.6	Susceptible	rraabb

[a] Disease index: 1 = no symptoms; 2 = epinasty of inoculated leaf; 3 = wilting of inoculated leaf and epinasty of adjoining leaves; 4 = half of the leaves wilted; 5 = all leaves wilted.

TABLE 2. Reaction of hybrid potato progenies to *Pseudomonas solanacearum* and chi-square values for goodness-of-fit to expected ratios

Cross	No. plants tested	R:S[a] Ratio		Chi-square	P value
		Expected	Observed		
1339.28 (S) × 5536.7 (S)	100	0:100	2:98	0.04	0.85
1386.12 (R) × 1339.28 (S)	80	20:60	20:60		0.99
× 5536.7 (S)	50	12:38	12:38		0.99
× 1386.26 (R)	100	75:25	73:27	0.21	0.65
× 1388.30 (R)	100	56:44	57:43	0.04	0.85
1386.13 (R) × 1339.28 (S)	100	25:75	26:74	0.05	0.82
× 5536.7 (S)	100	25:75	22:78	0.48	0.50
1386.26 (R) × 1339.28 (S)	100	25:75	27:73	0.21	0.65
1388.30 (R) × 1339.28 (S)	100	25:75	21:79	0.85	0.40
× 1386.26 (R)	79	59:20	56:23	0.50	0.50
413.6 (R) × SELF	95	40:55	41:54	0.04	0.85

[a] R = resistant; S = susceptible.

five per cent resistant plants would have been expected if the genotype proposed for 1386.12 (RrAABb) is used, and US-W4 (a *S. tuberosum* haploid) is assumed to be recessive at the three loci. All resistant plants would be RrAaBb. One of the resistant plants in this family (413.6) was then selfed, and the progeny was tested under growth chamber conditions. The observed R:S ratio was very close to that expected if the genotype was as designated above (Table 2).

The numbers of plants in each disease index class 15 days after inoculation do not provide evidence for an additive system, although the gene designated as B seems to provide more resistance than A. A portion of the data is given in Table 3 to illustrate the variation in degree of wilting which is not explained by the three-gene hypothesis. Most of the families tested had many plants in the 3.0-4.5 range (wilting of inoculated leaf and epinasty of adjacent leaves to wilting of one-half the leaves). Although these plants were rated as susceptible, they usually wilted much more slowly than the check plants. The two R × R crosses in Table 3 satisfied the expected 3:1 ratio, but there was no advanced wilting (index 4.0-5.0) in the 1388.30 × 1386.26 family. Progeny from 413.6 × self gave the best results in terms of clear separation of highly resistant and highly susceptible plants. These data suggest either that there are modifying genes which could not be defined by the present analysis, or that there is still some uncontrolled variation from plant to plant. This could be due to minor environmental fluctuations or, since these are heterogeneous families grown from true seed, to differences in vigor. When several plants of an individual clone were grown from tubers and tested under the growth chamber conditions, there was very little plant-to-plant variation (Table 1).

The designation of genes R, A, and B is only tentative. Additional information concerning the inheritance of resistance must be obtained before genetic symbols can be assigned.

DISCUSSION.—Useful levels of resistance to *P. sola-*

TABLE 3. Number of plants in each disease index class in hybrid potato progenies 15 days after inoculation with *Pseudomonas solanacearum*

Cross	Disease index[a]					Total
	1.0-1.5	2.0-2.5	3.0-3.5	4.0-4.5	5.0	
1386.12 (R) × 1386.26 (R)	64	9	11	3	13	100
1388.30 (R) × 1339.28 (S)	5	20	54	17	4	100
1388.30 (R) × 1386.26 (R)	20	36	23	0	0	79
413.6 (R) × SELF	35	6	9	11	34	95

[a] Disease index as in Table 1.

nacearum have been found in tobacco, eggplant, pepper, tomato, and peanut (2). Although resistant varieties have been selected, relatively little is known about the inheritance of resistance. Several genes with partial dominance provide resistance in tomato (1). Conflicting results have been reported in the case of tobacco, however. Smith & Clayton (8) found that multiple recessive genes conferred resistance, whereas Schweppenhauser (6) found resistance to be multigenic but dominant. These studies were conducted under field conditions, and population means were used to determine possible mechanisms of inheritance. Since the host-pathogen interaction is extremely sensitive to environmental conditions, at least in the potato-*P. solanacearum* interaction, field studies might yield confusing results. When potato hybrids similar to those used in this study were analyzed under fluctuating environmental conditions, variable results were obtained (7). This indicates that constant environmental conditions must be established before genetic interpretations are attempted.

The data obtained in this study provide an explanation of the inheritance of resistance to only one isolate of the pathogen. Since resistance appears to be influenced greatly by environmental factors, tests with different temp or light conditions may require changes in the genetic interpretations. Also, more tests are needed to determine whether additional genes are required to provide resistance to more highly pathogenic isolates of *P. solanacearum*. These and other studies now in progress may determine if modifying genes are indeed responsible for some of the noted variation.

It appears, however, that few genes are involved, and that high levels of resistance can be transferred to potato types suitable for cultivation. Simple inheritance will be very helpful in breeding because of the necessity to combine *Pseudomonas* resistance with many other traits, such as general resistance to *Phytophthora infestans* (Mont.) d By., to produce a potential variety for subtropical areas.

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