Genetic Resources and Crop Evolution **43**: 569–574, 1996.

Host-plant resistance to *Pseudomonas solanacearum* in tomato germplasm

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Received 2 January 1996; accepted in revised form 3 April 1996

Key words: bacterial wilt, germplasm evaluation, *Lycopersicon esculentum*, *Pseudomonas solanacearum*, resistance, tomato

Abstract

Seedlings of two hundred and thirty-three accessions of the tomato collection maintained at the Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica (CATIE) and 7 cultivars used as controls were evaluated for host-plant resistance to 4 virulent strains of *Pseudomonas solanacearum* representing race 1 biovars 1 and 3. In general, biovar 3 strains wilted seedlings faster than biovar 1 strains but, after 20 days post-inoculation, no significant differences were noted in susceptible control ratings. Significant differences for disease index were noted, but no line with complete resistance was found. For the USA biovar 1 strain UW-25, only 5 accessions, CATIE 17331, 17334, 17349, 17739, 17740, and 2 of the control cultivars, 'Hawaii 7998' and 'UC-82B' showed some degree of resistance. Conversely, both the frequency and the degree of resistance were high for Costa Rican biovar 1 strain UW-256. For biovar 3, the Costa Rican strain UW-255 was more virulent than the Peruvian strain UW-130. Eight CATIE accessions, 5539, 17331, 17333, 17334, 17345, 17349, 17742, and MIP-CH1, were as resistant as the resistant control 'Hawaii 7998' to 3 strains and accession 17740 was as resistant as 'Hawaii 7998' to all 4 strains.

Introduction

The need to identify new sources of host-plant resistance to pests and pathogens is increasing as the public demands reduced pesticide use. Germplasm accessions of wild and weedy crop relatives and traditional land races or cultivars are potentially rich sources of host-plant resistance, and many elite cultivars have been improved with resistance genes derived from these accessions. In tomato, interest in host-plant resistance to bacterial wilt (BW) incited by *Pseudomonas solanacearum* E. F. Sm. has been heightened by the inability to control the disease through field rotation, soil fumigation, or biological control (Acosta et al., 1964; CATIE, 1990).

Informal groupings using a binary system of races and biovars have been developed to classify BW organisms. Five races and five biovars have been described using the binary system (Aragaki & Quinõn, 1965; Buddenhagen et al., 1962; Buddenhagen & Kelman, 1964; Hayward, 1964; He et al., 1983). Additionally, biovars 1 and 2 are distinct from biovars 3, 4 and 5 on the basis of RFLP genotypes. There are also marked differences in the geographical distribution of the biovars (Cook et al., 1989). In general, biovar 1 is predominant in the Americas, and biovar 3 in the lowland regions of Asia, however, biovars 1 through 4 are present in the Phillipines (Haque & Echandi, 1984; McLaughlin & Sequeira, 1989; Valdez, 1985; Velupillai & Stall, 1985).

Some tomato cultivars have been developed with useful levels of resistance for specific environments. Nevertheless, it is difficult to obtain elite cultivars with stable resistance to BW strains under lowland tropical conditions of high temperature and humidity (Bosch et al., 1990; De Leon, 1987; Henderson & Jenkins,

Journal Paper No. J-16011 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 3123.

1977; Kelman, 1953; Lasso, 1974; Mew & Ho, 1977; Peterson et al., 1983). New sources of BW resistance must be found and incorporated into elite germplasm to ensure the commercial success of tropical tomato production.

Accessions with satisfactory levels of host-plant resistance to BW combined with commercially acceptable fruit size, quality and other desirable horticultural characteristics are rare (AVRDC, 1989). Jaworski et al. (1987) evaluated 2064 cultivars and germplasm accessions (PI's) from the National Plant Germplasm System (USA) under Georgia field conditions with natural and artificial inoculation of an indigenous strain of race 1 biovar 1. Only a few partially resistant accessions were found. From these, three selections of *L. esculentum* (GA 1565-2-4 BWT, GA 219-1-2 BWT, and GA 1095-1-4 BWT), and one selection of *L. esculentum* × *L. pimpinellifolium* (GA 1405-1-2 BWT) were shown to be partially resistant. These selections possessed a vigorous indeterminate growth habit which would be considered unacceptable for inclusion in a processing tomato cultivar. In contrast, a preliminary evaluation of the CATIE tomato collection by Stolberg et al. (1986) found that several accessions possessed desirable horticultural characteristics and resistance to a mixture of race 1 biovar 1 BW strains under field conditions at Alajuela, Costa Rica.

The objectives of the present study were to identify CATIE tomato germplasm accessions with resistance to a) two BW strains of biovar 1, b) two BW strains of biovar 3, and c) identify lines which possess combined resistance to both BW biovars.

Materials and methods

Seven control cultivars and 233 tomato plant introductions of CATIE's tomato collection were evaluated for host-plant resistance to *Pseudomonas solanacearum*. Cultivars 'UC-82B' and 'Stevens' served as susceptible controls whereas 'Venus', 'Saturn', 'Rodade', 'Rotam 4', and 'Hawaii 7998' served as resistant controls (Bosch et al., 1985, 1990; González & Summers, 1995; Henderson & Jenkins, 1977; Rouamba et al., 1988; Stevens et al., 1976).

Four experiments were conducted, one per each BW strain, in which plots representing accessions or controls were assigned to a randomized complete block design (Gomez & Gomez, 1984) with 3 replications. Typically 22 plants were evaluated per entry per replicate. In some accessions, both seed availability and viability reduced the number of plants evaluated. Soil media, flat design, and root inoculation technique have been described previously (González & Summers, 1995).

Four strains of *Pseudomonas solanacearum*, two representing race 1 biovar 1 (UW-25 [USA], UW-256 [Costa Rica]), and two representing race 1 biovar 3, (UW-130 [Peru], and UW-255 [Costa Rica]), were used in this study. These strains were obtained from the collection held at the Department of Plant Pathology, University of Wisconsin (UW), Madison. Each strain has been characterized using DNA probes and RFLP analysis, in addition to being identified by race and biovar group (Cook et al., 1989, 1990).

To prepare the inoculum, stock cultures stored in sterile Type 1 water were streaked on Kelman's tetrazolium chloride medium, TZC-agar (Kelman, 1954), and incubated for 48 hours at 30 °C. Fluidal, wild-type colonies were selected and restreaked on the same medium without TZC. After 48 hours at 30 °C, colonies were harvested in sterile 0.1 *M* phosphate buffer, pH 7.2, and washed twice. Bacterial cells were recovered after each cycle by centrifuging at 6000 × *g* for 10 minutes at room temperature. After the last wash, the bacterial cell pellet was resuspended in sterile distilled water and the suspension diluted to 10^8 colony-forming units per milliliter (cfu ml^{-1}), which was determined spectrophotometrically by comparing absorbance at 600 nm with a previously constructed standard curve.

Twenty-one-day-old plants were screened for disease resistance. At this stage of growth, the seedlings possessed two true leaves and were approximately 10 to 15 cm tall. Ratings for bacterial wilt interaction phenotypes (IP) were determined 20 days post-inoculation on a 0 (best) to 9 (worst) scale of increasing disease severity, using a modification of Williams' (1988) scaling for the non-metric quantification of the IP. Disease scores were described as: 0 = no interaction phenotype (immunity), 1 = no wilt symptoms, but foliar yellowing and reduced growth when compared to a non-inoculated control, 3 = one or two leaves partially wilted or dead, 5 = all leaves, except the meristem wilted, 7 = all leaves and the meristem wilted, but at least 50% of the stem erect and turgid, and 9 = dead plant. A disease index (DI) was calculated as the number of plants in an entry with a particular rating, multiplied by that rating. Within an entry, all indices were summed and then divided by the total number of plants in the entry. The DI served as a measure of central tendency or weighted mean (Steel & Torrie, 1980):

Table 1. An analysis of variance for disease index (DI) and the percentage of plants with a DI less than or equal to 3 for *Pseudomonas solanacearum* host-plant resistance to strains UW-25, UW-256 (race 1, biovar 1), and UW-130, UW-255 (race 1, biovar 3) in a CATIE'S tomato germplasm collection

		Biovar 1				Biovar 3			
		UW-25		UW-256		UW-130		UW-255	
Source of variance	df	DI	Percent of plants DI ≤ 3	DI	Percent of plants DI ≤ 3	DI	Percent of plants DI ≤ 3	DI	Percent of plants DI ≤ 3
Replication	2	134.00**	29,493.03**	57.06**	10,714.18**	6.43**	4328.06**	20.60**	8233.49**
Accession	239[z]	1.77**	300.67**	4.37**	812.03**	13.20**	2469.69**	5.71**	1051.69**
Error	461	0.70	156.04	1.25	255.63	0.90	196.59	1.06	227.59
CV (%)		10.24		14.46		12.18		12.58	

**Significant at $p = 0.1$.
[z]Missing values.

$$DI = \bar{Y} = \sum f_i Y_i / \sum f_i$$

where f_i = the number of plants possessing a particular disease score. Y_i = disease score.

Within each study, resistant lines were ranked by their mean DI. In order to rank the relative performance of selected resistant lines, their DI's were compared with the resistant cultivar 'Hawaii 7998' by the least significant difference test (LSD; Steel & Torrie, 1980). As an indirect measure of variability, the percentage of plants per accession were classified as highly resistant (DI ≤ 3) were also determined.

Results and discussion

Plant infection occurred in all the greenhouse experiments. Disease symptom expression began 3 or 4 days postinoculation. First the cotyledons, and later the foliage, began to yellow. Seedlings wilted more rapidly when exposed to biovar 3 strains UW-130 and UW-255 than to biovar 1 strains UW-25 and UW-256. But, by 20 days post-inoculation, the initial differences in symptomatology were not evident. The root inoculation technique and using disease index (DI) to measure disease occurrence adequately distinguished differences in bacterial wilt resistance.

Significant differences for DI occurred among accessions for each of the four strains evaluated (Table 1). Only five of the 233 accessions (CATIE 17331, 17334, 17349, 17739, and 17740) and two of the control cultivars, 'Hawaii 7998' and 'UC-82B', had some degree of resistance to strain UW-25 (Table 2). These results agree with Jaworski et al. (1987) who indicated that very few of the 2064 USDA P.I. accessions evaluated in Georgia were resistant to an indigenous race 1 biovar 1 strain.

None of the lines noted above were significantly different when compared to the resistant control 'Hawaii 7998'. CATIE 17334 possessed the lowest mean disease index (DI = 4.0) and the highest percentage of plants with a DI ≤ 3 (63.6%). 'UC-82B' (DI = 5.5) was slightly resistant to strain UW-25. BW resistance in the processing tomato cultivar 'UC-82B' has not been reported before (Stevens et al., 1976).

Resistance to the Costa Rican biovar 1 strain UW-256 was more frequent than for UW-25. Twenty four (10.3%) of the 233 accessions and three control cultivars ('Venus', 'Saturn', and 'Rotam 4') showed some degree of resistance to strain UW-256 when compared to 'Hawaii 7998' (Table 2). A similar frequency of resistance, 10.5%, was found in a preliminary test of 171 accessions of the CATIE tomato collection under field conditions (Stolberg et al., 1986). 'UC-82B', (DI = 7), was ranked as susceptible to this strain. However, 24.1% of the tested plants had a DI ≤ 3. The frequency and degree of resistance to the Peruvian biovar 3 strain UW-130 was higher than expected. Twenty seven of the accessions and one control cultivar ('Rotam 4') were not significantly different from 'Hawaii 7998' producing DI measures of 1.7 to 4.0 (very to moderately resistant). The percentage of plants with a DI ≤ 3 was consistently high (62.9 to 92.6%) for these twenty seven accessions (Table 2).

Two control cultivars ('Rotam 4' and 'Rodade') and 20 PI's showed some degree of resistance to the Costa Rican biovar 3 strain UW-255 and were not different from 'Hawaii 7998'. DI's ranged between 3.2 and 5.7 for the twenty PI's while 40 to 68.4% of the plants

Table 2. CATIE tomato accessions which were not significantly different from 'Hawaii 7998' in resistance to the strains of *Pseudomonas solanacearum* noted.

		Biovar 1[w]				Biovar 3[w]				
		Strain UW-25[v]		Strain UW-256		Strain UW-130		Strain UW-255		
Accession	Origin[v]	Mean DI[x]	Percent of plants DI ≤ 3	Mean DI	Percent of plants DI ≤ 3	Mean DI	Percent of plants DI ≤ 3	Mean DI	Percent of plants DI ≤ 3	Index[u]
Controls										
Rotam 4	SA	7.2**	17.2	3.7	66.7	1.7	93.3	3.2	74.1	15.8
Hawaii 7998	USA	5.2	51.4	4.4	60.6	2.5	88.6	4.0	71.4	16.1
Rodade	SA	7.9**	15.6	7.0**	25.6	5.4**	40.6	4.0	70.0	24.3
Venus	USA	7.0**	24.1	3.9	69.4	8.6**	6.9	9.0**	0.0	28.6
Saturn	USA	6.9*	37.8	4.3	64.3	8.9**	0.0	9.0**	0.0	29.1
UC-82B	USA	5.5	48.7	7.0**	24.1	9.0**	0.0	9.0**	0.0	30.6
Stevens	USA	8.9**	0.0	8.8**	2.7	9.0**	0.0	9.0**	0.0	35.8
PI's										
17334	PA	4.0[y]	63.6[z]	4.0[y]	61.9[z]	4.9**[y]	66.7[z]	5.2[y]	61.9[z]	18.1
CH-1	CR-MIP	7.4**	14.8	3.0	73.9	3.7	77.3	5.4	58.3	19.6
17740	TW	6.1	29.6	5.1	52.5	3.3	68.8	5.6	40.0	20.2
17349	PA	6.1	30.3	6.3*	37.1	2.6	85.3	5.5	42.9	20.5
17333	PA	6.9*	30.6	4.5	60.0	3.8	75.0	5.5	45.7	20.6
17345	PA	7.1**	29.0	5.4	51.5	3.6	71.4	4.8	53.6	20.9
17734	TW	6.7*	35.5	5.9	47.5	2.7	85.3	5.7*	45.5	21.0
17742	TW	7.1**	25.0	6.2	43.2	2.7	86.2	5.3	45.7	21.3
17137	NS	6.9*	22.2	5.3	50.0	3.1	78.8	6.0*	39.4	21.4
17347	PA	6.9*	20.7	7.2**	27.8	2.9	87.5	4.6	60.6	21.6
116-E	CR-MIP	7.3**	23.1	6.5*	40.6	3.9	64.9	4.0	62.1	21.7
5539	PE	6.9*	26.5	6.0	36.7	4.0	62.9	5.1	61.3	21.9
17344	PA	6.8*	30.9	6.8**	29.3	3.9	66.5	4.5	55.9	21.9
14667	GD	8.0**	17.2	7.1**	28.1	2.5	92.6	4.6	57.1	22.2
17348	PA	6.9*	29.4	7.3**	19.4	3.7	68.6	4.4	61.1	22.3
MIP-14667	CR-MIP	7.1**	15.6	7.5**	33.3	4.5*	64.3	3.2[y]	68.4[z]	22.3
116-5	CR-MIP	7.4**	21.2	5.6	47.4	4.3*	62.5	5.1	46.9	22.3
17335	PA	7.4**	22.2	5.7	44.1	3.6	75.8	5.9	37.5	22.6
17331	PA	6.4[y]	33.3[z]	6.8[y]	31.6[z]	3.7[y]	77.8[z]	5.7[y]	52.4[z]	22.6
17352	PA	7.1**	25.8	5.5	46.7	2.8	82.1	7.5**	17.9	22.9
17329	PA	7.2**	17.1	6.4**	33.3	2.4	88.6	6.9**	23.3	22.9
17337	PA	6.6**	25.0	4.7	62.5	4.7**	52.9	7.0**	22.9	22.9
17332	PA	7.4**	27.3	6.8**	28.6	3.6	71.9	5.1	54.8	23.0
117-21	CR-MIP	7.0**	20.7	6.1	35.7	4.1*	70.4	6.0*	31.8	23.1
116-4	CR-MIP	7.4**	28.6	5.9	41.7	4.0	69.0	6.1*	44.8	23.3
Dina-G.	CR-MIP	6.9*	31.4	6.9**	27.5	3.3	71.0	6.3**	35.7	23.3
17343	PA	7.7**	28.9	5.1	54.1	4.5*	59.4	6.1*	37.1	23.4
17338	PA	8.2**	8.8	5.1	61.9[z]	3.9	78.1	6.5**	38.2	23.6
17342	PA	7.2**	29.4	6.3*	31.6	3.9	67.7	6.3**	30.3	23.6
17330	PA	6.7*	31.4	6.1	39.5	5.1**	55.9	5.8*	42.9	23.8
17351	PA	7.2**	18.2	8.1**	11.6	4.1*	68.8	4.4	63.6	23.8
17739	TW	6.3	33.3	7.3**	18.2	3.7	70.0	6.5**	37.1	23.8
17353	PA	6.8*	31.4	5.9	41.2	4.3*	63.6	6.8**	24.2	23.9
17336	PA	7.5**	14.7	6.4*	34.3	4.9**	55.6	5.4	48.6	24.2
17354	PA	8.1**	9.4	7.6**	17.1	2.7	77.8	6.1*	33.3	24.5

Table 2. Continued.

		Biovar 1[w]				Biovar 3[w]				
		Strain UW-25[v]		Strain UW-256		Strain UW-130		Strain UW-255		
Accession	Origin[v]	Mean DI[x]	Percent of plants DI ≤ 3	Mean DI	Percent of plants DI ≤ 3	Mean DI	Percent of plants DI ≤ 3	Mean DI	Percent of plants DI ≤ 3	Index[u]
17350	PA	8.1**	8.8	5.4	52.6	4.1*	67.7	7.0**	22.9	24.6
17340	PA	7.9**	12.8	5.7	51.4	4.5*	69.7	6.7**	30.3	24.8
17341	PA	7.4**	23.7	6.4*	31.4	5.7**	42.9	5.4	51.6	24.9
115-1	CR-MIP	8.0**	15.4	7.9**	15.2	3.4	76.9	5.9*	40.6	25.1
17346	PA	8.3**	5.7	7.8**	16.7	3.1	78.1	6.9**	27.0	26.0
7994	MEX	7.0**y	27.3z	4.2y	36.4z	9.0**y	0.0z	9.0**y	0.0z	29.2
5582	PE	8.2**y	18.2z	6.0y	25.0z	9.0**y	0.0z	9.0**y	0.0z	32.0
17362	USA	8.5**	5.3	5.9	45.7	9.0**	0.0	9.0**	0.0	32.4
Mean		8.1	9.8	7.7	17.0	7.8	16.3	8.2	10.0	
SD		0.8	12.5	1.1	16.0	0.9	14.0	1.0	15.1	
$LSD_{0.05}$		1.3	20.1	1.8	25.7	1.5	22.5	1.7	24.2	

[u]Summation index. Summation of DI ratings across the four BW strains.
[v]CR = Costa Rica, GD = Guadeloupe, NS = Not Stated, MEX = Mexico, MIP = Integrated Pest Management Program, CATIE, PA = Panama, PE = Peru, SA = South Africa, TW = Taiwan, USA = United States. UW = University of Wisconsin bacterial wilt strain numbers.
[w]Different statistical analyses were used for each BW strain. Direct comparisons among mean DI or percentage of plants with a DI ≤ 3 for different strains are not possible.
[x]Disease index (DI). Resistant classes based on DI: very resistant = DI of 0 to 3, moderately resistant = DI of 3.1 to 5, slightly resistant = DI of 5.1 to 6, susceptible = DI of 6.1 to 7, and very susceptible = DI of 7.1 to 9. Data are means of 3 replications, except where indicated.
[y]Mean of 2 replications. $LSD_{0.05}$ for comparisons of means from 3 vs. 2 replications: 1.5 for strain UW-25, 2.0 for strain UW-256, 1.7 for strain UW-130, and 1.9 for strain UW-255.
[z]Mean of 2 replications. $LSD_{0.05}$ for comparisons of means from 3 vs. 2 replications: 22.4 for strain UW-25, 28.7 for strain UW-256, 25.2 for strain UW-130, and 27.1 for strain UW-255.
*,**Significant at $p = 0.05$, or 0.01, respectively when compared to 'Hawaii 7998' within each BW strain.

produced DI rating of 3 or better (Table 2). These data suggest that strain UW-255 was more virulent than strain UW-130.

The results reported here demonstrate that several accessions of the tomato collection maintained at CATIE, Costa Rica, possess partial resistance to *Pseudomonas solanacearum* strains UW-25, UW-256 (biovar 1), UW-130, and UW-255 (biovar 3). Differences in the degree of resistance to BW strains were observed for all the accessions tested. No complete BW resistance (DI = 0) was detected for any of the 233 accessions or control cultivars evaluated. This finding is in agreement with Grimault and Prior (1993) who reported that, regardless of the degree of resistance, all tomato germplasm in their research program was capable of being infected with *Pseudomonas solanacearum*.

Resistance to the four BW strains was prevalent in accessions derived from Panamanian breeding lines. Many of these accessions expressed a mean DI resembling 'Hawaii 7998'. The response of 'Hawaii 7998' was of particular interest because it was consistently resistant to all strains. Most of the resistant accessions possess some degree of resistance to more than one BW strain. The most important accessions are CATIE 5539, 17331, 17333, 17334, 17345, 17349, 17742, and MIP-CH1, which were as resistant as 'Hawaii 7998' to three BW strains, and accession CATIE 17740 which was as resistant as 'Hawaii 7998' to all 4 strains. Some accessions were resistant to two BW strains while others were only resistant to one strain. 'Venus' and 'Saturn' which were selected for resistance to biovar 1 in North Carolina, were found moderately resistant to the Costa Rican biovar 1 strain UW-256 (DI's 3.9 and 4.3 respectively), but susceptible to the USA biovar 1 strain UW-25 and very susceptible to both strains of biovar 3 (Table 2). These tests confirm that resistance to one strain or biovar of BW does not necessarily confer resistance to other strains or biovars of BW. These findings suggest that before these or other sources of host-plant resistance are incorporated into a plant breeding program, the germplasm should be carefully screened for resistance to the specific strains prevalent in the region of interest. Finally, it is important to note that the degree of resistance assigned to each accession by this study is based on disease indices estimated from tomato seedling tests conducted in greenhouses. Further research is needed to determine the correlation between resistance in greenhouse seedling tests and field resistance in mature fruit-producing plants.

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