Resistance of *Capsicum* spp. Genotypes to Tobacco Etch Potyvirus Isolates from the Western Hemisphere

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ABSTRACT

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Thirty-six isolates of tobacco etch potyvirus (TEV) from the United States, Mexico, the Caribbean, and Central and South America were mechanically inoculated in the greenhouse to selected pepper genotypes reported to have resistance to one or more TEV isolates. Some resistant genotypes were resistant (symptomless) to most isolates, while other genotypes were resistant to few isolates. Certain TEV isolates infected most of the resistant genotypes, while others infected very few. Other isolates represented gradations between the extremes. Reactions of specific pepper genotypes to specific TEV isolates sometimes varied in the different experiments of the study, possibly due to temperature and light intensity effects on resistance during the different times of the year in which experiments were carried out. Genotypes Agronomico 10C-5, Delray Bell, VR4, Jaloro, and PI 152225 were resistant to many TEV isolates tested and appear to be good sources of resistance for use in breeding programs.

Tobacco etch potyvirus (TEV) is one of the most damaging viruses affecting peppers (*Capsicum* spp.) in the United States (4). TEV has been reported from Florida (30), Georgia (3), Louisiana (19), Texas (23), California (1), and Illinois (29). Other locations in the Western Hemisphere from which TEV has been reported include Canada (13), El Salvador (9), and Puerto Rico (18). High incidences, nearing 100%, have been reported from different locations (1,3). Yield reductions have been reported at up to 70% (16).

Resistance to TEV in peppers has been known since 1952 when the pepper line SC 46252 was described by McKinney (14). Nagai and Smith (15) collected TEV isolates from pepper, tomato, and *Datura* spp. in California and inoculated several pepper genotypes. Genotypes PI 264281, Agronomico 8, Ac. 2120 (PI 342947), PI 152225, and PI 159236 were resistant to the TEV isolates. PI 159236 and PI 152225 are both *Capsicum chinense* accessions; PI 152225 was originally described as TEV-resistant by Greenleaf (10). Smith (21) also tested California isolates of TEV, using genotypes PI 342947, Agronomico 8, Avelar, and Yolo Y, and found five different reaction types among the isolates based on their ability to infect the four genotypes. PI 342947 showed the widest range of resistance of the genotypes.

Zitter (30) inoculated pepper genotypes reported to be resistant to TEV using Florida pepper field isolates. Common isolates of TEV (TEV-C) were able to infect only one genotype (Yolo Y). Three isolates designated as TEV-S (severe) were able to infect 12 genotypes: PI 264281, SC 46252, 23-1-7, Yolo Y, 23-1-7 X Yolo Y, Avelar, Agronomico 8, Ambato Immune, PI 349247, PI 152936, Ac. 2207, and PI 281367. PI 152225 was resistant to the three isolates. Zitter (31) showed that Greenleaf Tabasco, with both PI 152225 and PI 152936 as parents, was resistant to TEV-S. Zitter and Cook (32) determined that the tolerance to pepper mottle potyvirus (PepMoV) exhibited by Avelar was controlled by the same single recessive gene that controlled resistance to TEV and potato potyvirus Y (PVY). Cook et al. (7,8) reported TEV resistance in cultivars Florida VR2 and Delray Bell. Florida VR4, a TEV-resistant cultivar, was derived from Delray Bell (6).

Barrios et al. (2) reported a dominant gene for resistance to TEV in the *Capsicum frutescens* line LP-1. In Georgia, Sowell and Demski (22) tested various *Capsicum* spp. genotypes in the greenhouse and the field against TEV isolates and found that PI 152225, Agronomico 8, PI 342947 (Ac. 2120), and PI 410407 (Avelar) were highly resistant. Another accession of Avelar, PI 342948, was less resistant than previously reported (22). Casca Dura (PI 342949) was reported to be resistant to TEV in the greenhouse, but it was not resistant in the field (22). Kuhn et al. (12) evaluated pepper genotypes in the greenhouse and field in Georgia for their reactions to TEV. One line with PI 264281 in its background, GA-C44-V22, exhibited extreme resistance to TEV, while three others, FL-XVR-3-25, Tambel-2, and Asgrow-XPH-5021, were moderately resistant.

In Texas, Villalon (25–28) used PI 342947, Agronomico 8, PI 264280, or Avelar as a source of potyvirus resistance in the development of cultivars Tam Mild Jalapeño, Tambel-2, Rio Grande Gold, and Jaloro.

Low disease incidence has been observed in TEV-resistant peppers (3,12,17,24). Availability of sources of resistance in the Western Hemisphere is necessary for breeders trying to produce cultivars that are both virus-resistant and horticulturally acceptable. The goal of this research was to evaluate the reactions of *Capsicum* genotypes and cultivars, shown previously to be resistant to one or more TEV isolates, to a range of TEV isolates from different locations in the Western Hemisphere.

MATERIALS AND METHODS

All experiments were conducted in a greenhouse during 1993, 1994, and 1995 at Louisiana State University in Baton Rouge. Greenhouse temperatures ranged from 21 to 35°C during the summer and from 15 to 29°C during the winter. Thirty-six TEV isolates and 36 pepper genotypes were available for testing. In order to obtain maximum information from the isolates and genotypes without inoculating in all possible combinations, three consecutive experiments were carried out.

Experiment 1. Thirty-six field isolates of TEV from different geographic locations that had been identified by serology and host range were used. Ten isolates were from Louisiana, seven from the Dominican Republic, seven from Mexico, five from California, three from Florida, two from Honduras, one from Venezuela, and one from Colombia. Stock cultures of isolates were maintained at 4°C in dehydrated host plant tissues (*Datura stramonium, Nicotiana tabacum,* and *Capsicum annuum)* in sealed containers over anhydrous

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$CaSO_4$ or silica gel. Selected virus isolates were activated by grinding dried tissue in cold 0.025 M potassium phosphate buffer, pH 7.2, with sterilized mortars and pestles, and inoculating 3-week-old datura (*D. stramonium*) planted in methyl bromide–fumigated soil in 10-cm clay pots. Twelve pepper genotypes (Table 1), previously reported to be resistant to one or more isolates of TEV, plus Yolo Wonder as susceptible control, were selected to be evaluated for their responses to inoculation by each of the 36 isolates. The purpose of experiment 1 was to select representative or unusual virus isolates from the 36 total used based on their reactions to the 13 pepper genotypes. Seeds were planted in black plastic, 64-cavity seedling flats (Jiffy Products, Batavia, IL) using Jiffy Mix Plus planting medium (Jiffy) and maintained in a greenhouse.

Two weeks after inoculation, datura leaves showing virus symptoms were used as a source of inoculum. The inoculum was prepared by grinding 1 g of leaf tissue in 5 ml of cold buffer, as described above. The cold inoculum was applied with pestles onto 600 mesh Carborundum-dusted leaves of 3-week-old pepper plants. Sixteen plants were inoculated for each TEV isolate–pepper line or cultivar combination. In separate flats, 16 noninoculated plants of each pepper were maintained as negative controls.

Symptom evaluation. Symptoms were evaluated 3 weeks after inoculation. Disease severity was scored using the following designations: NS = no symptoms, MM = mild mosaic, M = mosaic, SM = severe mosaic, SMD = severe mosaic and leaf distortion, and W = wilting.

Enzyme-linked immunosorbent assay (ELISA). Presence of TEV in selected inoculated pepper genotypes with mild or no symptoms was tested by direct double antibody sandwich ELISA (5), using commercial kits (Agdia 1000, AGDIA Inc., Elkhart, IN). For each isolate–pepper combination tested, 16 leaves were collected (one per plant). Leaves from four different plants were combined to obtain one 0.15-g sample by tearing off portions of the four stacked leaves. Four 0.15-g replicate samples from each isolate–pepper combination were therefore tested. Samples consisted of the youngest fully expanded leaves collected 3 weeks after inoculation. In addition, leaves of noninoculated healthy plants and leaves of a susceptible cultivar inoculated with the same TEV isolate were collected as negative and positive controls, respectively. Plant sap was extracted from each 0.15-g sample in 1.5 ml of extraction buffer (20.0 g of polyvinylpyrrolidone, MW 24 to 40,000, 1.3 g of sodium sulfite, and 20.0 g of Tween 20 dissolved in 1,000 ml of phosphate-buffered saline Tween) using a leaf-roller tissue press. One hundred microliters of extracted sap were placed in each well of the ELISA plate. ELISA plates were read with a Bio-Rad ELISA reader (model 2550) using a 405 nm filter. The threshold criterion used for determining a positive reaction was 2× the average absorbance value of the noninoculated control and greater than 0.100.

Experiment 2. Twenty-three pepper (Table 1) genotypes reported to be resistant to some potyvirus isolates were evaluated (along with Yolo Wonder as the susceptible control) for their reactions to 10 isolates of TEV selected from experiment 1. Selected isolates and place of origin were TEV-401 (California), TEV-CAY-90 (Louisiana), TEV-MEX-21 (Mexico), TEV-C1 (Louisiana), TEV-TX-M (Mexico), TEV-VIL (California), TEV-DR93-28 (Dominican Republic), TEV-LMS-M (Mexico), TEV-H93-5 (Honduras), and TEV-V92-4 (Venezuela). Isolates were selected because they represented different levels or patterns of virulence or different geographic origins. Using these 10 isolates permitted comparison of the reactions of the 13 pepper genotypes of experiment 1 with the reactions of the 24 pepper genotypes of experiment 2. Therefore, experiment 2 served to group similar pepper genotypes and identify unusual pepper genotypes from experiments 1 and 2. Sixteen pepper plants from each genotype were mechanically inoculated with each isolate of TEV as described in experiment 1. Test plants were evaluated 3 weeks after inoculation for symptom development, as described previously. As in experiment 1, selected symptomless or

Table 1. Identity and source of pepper genotypes used in experiments 1, 2, and 3

Pepper genotype	*Capsicum* spp.	Seed source	Experiment
Yolo Wonder	*C. annuum*	PetoSeed Co.	1,2,3
Yolo Y	*C. annuum*	PetoSeed Co.	1
VR2	*C. annuum*	PetoSeed Co.	1,3
Agronomico 10C-5	*C. annuum*	PetoSeed Co.	1,3
ELS-2-1	*C. annuum*	PetoSeed Co.	2
Tam Veracruz	*C. annuum*	PetoSeed Co.	2
King Arthur	*C. annuum*	PetoSeed Co.	2
S-20-1	*C. annuum*	PetoSeed Co.	2
VR4	*C. annuum*	PetoSeed Co.	2,3
TSCH-2	*C. annuum*	PetoSeed Co.	2
FLBG-1	*C. annuum*	PetoSeed Co.	2
92LB44409	*C. annuum*	PetoSeed Co.	2
Delray Bell	*C. annuum*	A. A. Cook[a]	1,3
SC 46252	*C. annuum*	A. A. Cook	2
136AACook	*C. annuum*	A. A. Cook	1
Avelar	*C. annuum*	B. Villalon[b]	1
Tam Mild Jalapeno	*C. annuum*	B. Villalon	2
Hidalgo	*C. annuum*	B. Villalon	2
Rio Grande Gold	*C. annuum*	B. Villalon	2
Tambel 2	*C. annuum*	B. Villalon	2
Jaloro	*C. annuum*	B. Villalon	2,3
Casca Dura Ikeda	*C. annuum*	AVRDC[c]	2,3
C01664	*C. annuum*	AVRDC	2
Marquis	*C. annuum*	Rogers NK Seed Co.	2
Elisa	*C. annuum*	Rogers NK Seed Co.	2
Bomby	*C. annuum*	Rogers NK Seed Co.	2
Casca Dura (PI 342949)	*C. annuum*	Rogers NK Seed Co.	1,2
Reinger	*C. annuum*	Rogers NK Seed Co.	2
Magda	*C. annuum*	Rogers NK Seed Co.	2,3
C00943	*C. chinense*	AVRDC	1
PI 159236	*C. chinense*	A. A. Cook	1,3
PI 152225	*C. chinense*	A. A. Cook	1,3
Tabasco	*C. frutescens*	McIlhenny Co.	3
Greenleaf Tabasco	*C. frutescens*	McIlhenny Co.	1,3
Tabasco-Type Mexico 88	*C. frutescens*	McIlhenny Co.	1
LP-1	*C. frutescens*	L. L. Black[d]	2

[a] University of Florida.
[b] Texas A&M University.
[c] Asian Vegetable Research and Development Center.
[d] Louisiana State University.

Table 2. Number of tobacco etch potyvirus (TEV) isolates that did not induce symptoms in 13 pepper genotypes after mechanical inoculations in experiment 1

Pepper genotype	TEV isolates/ total isolates
Yolo Wonder	0/36[a]
Casca Dura	0/36
Yolo Y	1/36
Avelar	8/36
136 A A Cook	10/36
C00943 (selection)	11/36
VR2	11/36
PI 159236	11/36
Tabasco-Type Mexico 88	21/36
Agronomico 10C-5	21/36
Greenleaf Tabasco	22/36
Delray Bell	23/36
PI 152225	24/36

[a] Sixteen plants were inoculated for each virus isolate–pepper genotype combination. Symptoms were read 3 weeks after inoculation.

mild-symptomed inoculated pepper genotypes were tested by ELISA.

Experiment 3. Ten pepper genotypes (Table 1) that showed potential as sources of resistance to TEV isolates were selected from experiments 1 and 2. These genotypes all had resistance to a relatively large number of isolates in experiment 1 or 2. Twelve pepper genotypes were inoculated 3 weeks after planting with the 10 TEV isolates used in experiment 2. Tabasco and Yolo Wonder were used as susceptible controls. Test plants were evaluated for symptom expression 3 weeks after inoculation.

ELISA. ELISAs were performed similarly to experiment 1. However, all isolate–pepper genotype combinations except those involving Tabasco were tested. Negative controls (leaf tissue from uninoculated plants) were included in the same ELISA plate for each pepper genotype. A separate ELISA plate was used for each of the 10 virus isolates, with 11 pepper genotypes × 4 wells = 44 wells used for infected samples and 11 peppers × 4 wells = 44 wells, used for uninoculated control plants of the same pepper genotypes.

RESULTS AND DISCUSSION

Experiment 1. The reactions of 13 pepper genotypes to 36 TEV isolates are shown in Table 2. Pepper genotypes Yolo Wonder (susceptible control) and Casca Dura were susceptible to all 36 TEV isolates. Yolo Y, a PVY-resistant genotype, was resistant (symptomless) to only one isolate. ELISAs of Yolo Y plants inoculated with that isolate revealed the presence of TEV (data not shown). The Avelar genotype used was symptomless when inoculated with only eight of 36 isolates. It is possible that this particular accession of Avelar, obtained in 1975, is less resistant than other accessions. Differences among Avelar accessions with respect to TEV resistance were reported by Sowell and Demski (22). In experiment 1, pepper genotypes PI 152225, Delray Bell, Greenleaf Tabasco, Agronomico 10C-5, and Tabasco-Type Mexico 88 were resistant to more than half of the TEV isolates tested.

Experiment 2. Reactions of 24 pepper genotypes to 10 TEV isolates are shown in Table 3. Peppers VR4 and Jaloro were resistant to nine of 10 TEV isolates. Pepper genotype LP-1 was resistant to eight of 10 isolates of TEV. Six of 24 tested pepper genotypes (Yolo Wonder [susceptible control], Casca Dura, ELS-2-1, S-20-1, Tam Veracruz, and Tam Mild Jalapeño) were susceptible to all 10 TEV isolates.

Experiment 3. Table 4 shows the symptom and ELISA results of 12 pepper genotypes inoculated with 10 TEV isolates. ELISA was not performed with Tabasco pepper due to the death of most plants. Tabasco and Yolo Wonder (susceptible controls) were susceptible to all TEV isolates tested. In contrast, Jaloro, VR4, Delray Bell, and Agronomico 10C-5 were resistant to many TEV isolates tested. Most plants with symptoms were ELISA-positive and most symptomless plants were ELISA-negative. But some symptomless plants were ELISA-positive and some plants with symptoms were ELISA-negative, as can be seen in the differing totals for some pepper genotypes of symptomless and ELISA-negative isolates (Table 4).

Table 5 shows the symptoms of five of the 10 TEV isolates inoculated to 12 pepper genotypes. These five isolates were chosen for Table 5 to illustrate the contrasts among some of the isolates used in experiment 3. All five isolates of TEV induced wilting in Tabasco. Isolate 401 induced symptoms on all the pepper genotypes, while V92-4 did not induce symptoms on eight of 12 pepper genotypes. Isolates LMS-M and H93-5 gave nearly opposite reactions in the resistant pepper genotypes of experiment 3. LMS-M induced symptoms, generally severe, in all genotypes except Greenleaf Tabasco, PI 159236, and PI 152225. Isolate H93-5 induced symptoms in Greenleaf Tabasco, PI 159236, and PI 152225 but not in the other resistant genotypes. Isolate LMS-M was unable to overcome the *C. chinense* resistance of PI 152225 and PI 159236, but it caused symptoms, often severe, on the resistant *C. annuum* genotypes. Isolate H93-5 was unable to induce symptoms on the resistant *C. annuum* genotypes, but it caused severe symptoms on *C. chinense* resistant genotypes. This isolate not only shows an interesting contrast with LMS-M, but also contradicts Greenleaf's model of resistance alleles to potyviruses. According to Greenleaf (11), PI 152225 has a higher level of resistance to TEV than did VR2.

Diversity of symptom severity was evident among the TEV isolates used. Examples representing extremes were isolates LMS-M and V92-4. Symptoms induced by LMS-M in most susceptible pepper genotypes included severe mosaic and leaf distortion. Isolate V92-4 induced mild symptoms on most of the pepper genotypes it infected.

In these experiments, some isolates from different geographic areas induced similar reactions. At the same time, some isolates from the same area had similar host ranges, while others had dissimilar ones. It seems that the best approach for choosing germ plasm sources that could be utilized for breeding for resistance to TEV isolates from different geographic areas is to use pepper genotypes resistant to the maximum number of isolates.

Some genotypes showed changes in apparent resistance between experiment 1 (November 1993 to May 1994), experiment 2 (July and August 1994), and/or experiment 3 (November 1994 to April 1995). Possible explanations for these inconsistencies include seasonal temperature changes or seasonal light intensity–quality changes. Mechanical inoculations using

Table 3. Number of tobacco etch potyvirus (TEV) isolates that did not induce symptoms in 24 pepper genotypes after mechanical inoculations in experiment 2

Pepper genotype	TEV isolates/ total isolates
Yolo Wonder	0/10[a]
Casca Dura	0/10
ELS-2-1	0/10
Tam Veracruz	0/10
S-20-1	0/10
Tam Mild Jalapeno	0/10
C01664	1/10
SC 46252	3/10
92LB4449	3/10
TSCH-2	3/10
FLBG-1	3/10
Marquis	3/10
Elisa	3/10
King Arthur	3/10
Hidalgo	4/10
Bomby	4/10
Reinger	4/10
Rio Grande Gold	5/10
Magda	5/10
Tambel-2	5/10
Casca Dura Ikeda	6/10
LP-1	8/10
Jaloro	9/10
VR4	9/10

[a] Sixteen plants were inoculated for each virus isolate–pepper genotype combination. Symptoms were read 3 weeks after inoculation.

Table 4. Number of tobacco etch potyvirus (TEV) isolates that did not induce symptoms in 12 pepper genotypes after mechanical inoculations and number of isolates that gave ELISA-negative reactions in experiment 3

Pepper genotypes	TEV isolates: Symptomless	TEV isolates: ELISA-negative
Tabasco	0/10[a]	NT[b]
Yolo Wonder	0/10	0/10[c]
PI 159236	1/10	2/10
Greenleaf Tabasco	2/10	2/10
Magda	3/10	2/10
Casca Dura Ikeda	3/10	2/10
VR2	3/10	2/10
PI 152225	3/10	3/10
Jaloro	5/10	4/10
VR4	6/10	4/10
Agronomico 10C-5	6/10	5/10
Delray Bell	6/10	7/10

[a] Isolates that did not induce symptoms/total isolates tested. Sixteen plants were inoculated for each virus isolate–pepper genotype combination. Symptoms were read 3 weeks after inoculation.

[b] Not tested.

[c] Four bulked samples representing four plants each were tested for each virus isolate–pepper genotype combination by DAS-ELISA. Averages of the four absorbances were compared with those of uninoculated control plants of the same pepper genotypes. Absorbances 2× those of uninoculated controls and greater than 0.100 were considered positive.

sap extracts were highly successful in all experiments. Plants of susceptible control genotypes that escaped infection were rare. Therefore, differences among experiments in inoculation effectiveness are not a likely explanation for different results. Environmental effects on PVY resistance in pepper were reported by Shifriss and Cohen (20). Pepper genotypes resistant to PVY in summer greenhouse tests were susceptible to PVY in an unheated greenhouse and in the field during the winter in Israel.

ELISAs of pepper genotypes inoculated with the various isolates revealed some complex relationships between symptoms and apparent virus concentration, as estimated by ELISA absorbance. As would be expected, plants with symptoms were usually ELISA-positive, and most plants without symptoms were ELISA-negative. However, in some virus isolate–pepper genotype combinations, symptomless plants were ELISA-positive. In other cases, some plants with symptoms were ELISA-negative. Apparently, despite having visible symptoms, the concentration of the virus present in the plants was below the threshold of ELISA detection. All TEV isolates used in these experiments were detectable by the commercial ELISA system utilized. All isolates were passed through differential hosts for TEV, including *D. stramonium,* which is resistant to PepMoV, PVY, and tobamoviruses. Therefore, contamination with another strain of TEV or with another virus is unlikely. A similar phenomenon was encountered by Kuhn et al. (12), who observed that 18% of plants in a field test of the TEV-resistant line GA-C44-V22 had mild mottle symptoms, but all were ELISA-negative. In addition, 85% of TEV-resistant line FL-XVR-3-25 had mild virus symptoms in the field, but only 8% were ELISA-positive.

Pepper genotypes GA-C44-V22 and FL-XVR-3-25 were symptomless after mechanical inoculation with TEV in greenhouse tests conducted by Kuhn et al. (12), but they exhibited symptoms after natural infection in the field. The three most susceptible genotypes used in their study showed symptoms both in the greenhouse and in field tests. Sowell and Demski (22) tested six TEV-resistant or moderately resistant pepper genotypes in the greenhouse and in the field. Five of the six gave similar reactions in greenhouse mechanical inoculation and in field natural infection tests, but one line was intermediate in greenhouse tests and susceptible in the field. These examples demonstrate that greenhouse testing may not always correlate perfectly with field results for TEV resistance screening in pepper. However, field testing of virus resistance is usually confined to local virus strains due to concerns over the effect of releasing exotic isolates.

Cultivar Casca Dura Ikeda had reactions to the isolates that were similar to Magda's. Likewise, Agronomico 10C-5 reacted similarly to Delray Bell. There were generally consistent trends with respect to resistance of pepper genotypes in the different experiments. Delray Bell, Agronomico 10C-5, VR4, Jaloro, and PI 152225 were among the pepper genotypes showing symptomless reactions to many of the isolates against which they were tested. These genotypes would appear to be good TEV resistance sources for pepper breeders looking for resistance useful in broad geographic areas.

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Table 5. Reactions of 12 pepper genotypes inoculated with five tobacco etch potyvirus (TEV) isolates tested in experiment 3[a]

	TEV isolates				
Genotypes	401	TX-M	LMS-M	H93-5	V92-4
Tabasco	W[b]	W	W	W	W
Yolo Wonder	SMD	SM	SMD	SMD	M
PI 159236	SM	M	NS	SMD	MM
Greenleaf Tabasco	M	M	NS	SMD	M
Magda	M	M	SMD	NS	NS
Casca Dura Ikeda	M	MM	SMD	NS	NS
VR2	SM	M	SMD	NS	NS
Jaloro	MM	MM	SM	NS	NS
PI 152225	M	M	NS	SM	NS
VR4	M	NS	SMD	NS	NS
Agronomico 10C-5	M	NS	M	NS	NS
Delray Bell	M	NS	M	NS	NS

[a] Sixteen plants were inoculated for each virus isolate–pepper genotype combination. Symptoms were read 3 weeks after inoculation.
[b] W = wilt, SMD = severe mosaic and leaf distortion, SM = severe mosaic, M = mosaic, MM = mild mosaic, NS = no symptoms.

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