Resistance of Pepper to *Phytophthora* Crown, Root, and Fruit Rot Is Affected by Isolate Virulence

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ABSTRACT

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Greenhouse and laboratory experiments were conducted to determine the virulence of four *Phytophthora capsici* isolates from Michigan to 31 bell and hot pepper cultivars and breeding lines. Resistance to crown and root rot was assessed following the inoculation of soilless media with *P. capsici*-infested millet seed. In a detached fruit assay, fruit rot resistance was evaluated following inoculation with zoospore suspensions of 1.75×10^6 zoospores/ml. The four isolates differed in virulence to pepper lines screened for crown and root rot resistance and were considered to be four different physiological races. The pepper lines CM334, NY07-8001, NY07-8006, and NY07-8007 were resistant to the isolates tested. None of the commercial cultivars were resistant to *P. capsici* isolate 12889, but several cultivars were resistant to the other isolates screened. The isolates varied in their ability to cause infection on the fruits of the different cultivars. Overall, pepper fruit were more susceptible to *P. capsici* than the roots and crowns. Management of *Phytophthora* crown and root rot of pepper can be improved through the use of resistant cultivars. However, since isolate virulence affects resistance, cultivar resistance will need to be utilized on a local scale accordingly.

Phytophthora capsici L. is a soilborne pathogen that was first identified on pepper (*Capsicum annuum* L.) in New Mexico in 1922 (18). Since then, more than 50 plant species, including many Solanaceous and Cucurbitaceous vegetable crops, have been identified as hosts worldwide (7,9,13,22). In 2008, Michigan producers grew over 25,000 ha of vegetables susceptible to *P. capsici*, including 730 ha of peppers (2). *P. capsici* may infect the roots, crown, stem, leaves, and/or fruits of pepper (18,33). The pathogen may enter the roots or base of the stem (25). Eventually, water-soaked lesions develop that rapidly progress to cause girdling of the stem, and plant wilting and death (25). Control of *Phytophthora* crown and root rot requires the use of cultural practices, fungicides, fumigants, and genetically resistant varieties in an integrated program (6,13,25).

Several commercial bell pepper cultivars are tolerant to *P. capsici*, but no cultivar provides resistance to a wide range of isolates (11,19). Peppers are considered tolerant to *P. capsici* if the plant is able to sustain infection without dying or crop loss (1). The cultivars Paladin (Syngenta Seeds Inc., Boise, ID), Aristotle (Seminis Vege-

table Seeds, St. Louis, MO), Declaration (Harris Moran Seed Company, Modesto, CA), Karisma (Harris Moran Seed Company), Intruder (Syngenta Seeds Inc.), and Revolution (Harris Moran Seed Company) are regarded as resistant or tolerant to *P. capsici* by seed distributors. Growers are reluctant to use resistant or tolerant cultivars because of a perceived increase in incidence of silvering (the separation of the fruit cuticle from the epidermis) (37), and because of poor fruit shape (24), both of which result in unmarketable fruit.

The pepper line Criollo de Morales 334 (CM334), a landrace with small Serrano-type fruit, has demonstrated resistance to a variety of *P. capsici* isolates from different hosts and geographic regions (10,11,29,32,35). CM334 is the primary source of root rot resistance currently used in pepper breeding programs (10,32). The inheritance of resistance in CM334 is not completely understood. Guerrero-Moreno and Laborde found two recessive genes that provided resistance (12), and later Gil Ortega et al. proposed a three-gene, multi-allelic system as the source of resistance (10). Initial quantitative trait loci (QTL) analysis proposed that three QTLs were responsible for resistance; other studies confirmed a major QTL, reported to span the entire length of chromosome 5 (16,17,20). In 2003, six regions on chromosomes 4, 5, 6, 11, and 12 were determined to be involved in some part of resistance (32). When using CM334 as the source of *P. capsici* resistance, the resulting pepper lines may only contain some of

the QTLs that provide resistance, and therefore remain susceptible to some isolates. As a result, a bell pepper with levels of resistance comparable to that of CM334 with desired horticultural characteristics has not been developed (31,32).

Recent studies have indicated that physiological races exist in the pepper-*P. capsici* pathosystem (11,19,29,30), which implies that pepper breeders need to test breeding lines against a wide range of *P. capsici* isolates. Furthermore, research has suggested that different genetic mechanisms may be responsible for resistance to root rot, stem blight, and foliar blight of pepper (3,28).

In Michigan, symptoms on aerial plant parts, including leaf blight and fruit rot, are observed in the field less frequently than root and crown rot symptoms (13). Hence, growers in Michigan would benefit most from a cultivar that is primarily resistant to root and crown rot and stem blight. Furthermore, it may be easier to protect against foliar and fruit disease symptoms with fungicide sprays than against crown and root rot since most fungicides are only registered for foliar applications. To our knowledge, Michigan isolates have not been included in previous screens of pepper lines for root and crown resistance to *P. capsici*. In addition, virulence of *P. capsici* isolates from Michigan on pepper cultivars and breeding lines has not been tested and is relatively unknown. The objectives of this study were to evaluate cultivars and breeding lines of pepper for resistance to *Phytophthora* crown and root rot using isolates of *P. capsici* from three different hosts from Michigan and to measure virulence of three of these isolates on pepper fruit.

MATERIALS AND METHODS

***P. capsici* isolate selection and inoculum preparation.** Isolates of *P. capsici* obtained from infected plants in Michigan were selected from the long-term culture collection of Mary Hausbeck at Michigan State University (MSU). Isolates were classified according to mating type (MT) and sensitivity to mefenoxam, an oomycete-specific fungicide. The isolates OP97 (A1 MT) and SP98 (A2 MT) are sensitive to mefenoxam and were originally isolated from pickling cucumber and pumpkin, respectively. The isolates 12889 (A1 MT) and SFF3 (A2 MT) are insensitive to mefenoxam and were isolated from pepper and pickling cucumber, respectively.

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Isolates were grown on unclarified V8 agar (UCV8, 16 g of agar, 3 g of CaCO₃, 160 ml of V8 juice, and 840 ml of distilled water) under constant fluorescent light at room temperature (21 ± 2°C) for 7 days. Millet seed inoculum was prepared according to the method of Quesada-Ocampo et al. (22). Isolates OP97, SP98, and 12889 were used to screen the harvested fruit for resistance. Zoospore inoculum was prepared by flooding actively sporulating cultures with sterile distilled water and incubating at 4°C for 1 h followed by 30 min at room temperature to initiate zoospore release. The concentration of the zoospore suspension was estimated using a hemacytometer and adjusted to 1.75 × 10⁶ zoospores/ml.

Phytophthora root and crown rot screen. Two experiments were conducted to screen commercial cultivars and breeding lines for resistance to *Phytophthora* root and crown rot. Experiments included 28 or 14 pepper lines, respectively, and nine commercially available cultivars (Alliance, Aristotle, Brigadier, Camelot, Declaration, Paladin, Red Knight, Revolution, and Snapper). Seeds were sown into 72-cell flats filled with potting media (BACCTO Professional Planting Mix, Michigan Peat Company, Houston, TX) and placed into a greenhouse with a 14-h photoperiod. When seedlings developed three or four true leaves, they were transplanted into 1.5-liter pots filled with potting media (described above) that were

arranged in a complete randomized design in a greenhouse with a 14-h photoperiod at MSU's Horticulture Teaching and Research Center, East Lansing, MI. The average air temperature recorded in the greenhouse experiments was 19.4°C (minimum 1.0°C, maximum 39.7°C), and the mean relative humidity was 62.6% (minimum 20.7%, maximum 96.2%).

All isolates and a sterile millet control treatment were replicated eight times for each pepper line that was screened, and one experimental unit consisted of one plant. The potting medium was infested with 1 g of infected millet seed per plant, which was inserted into the media directly adjacent to the pepper seedling's root mass 1 day after transplanting. The plants were watered daily to maintain adequate moisture for plant growth and disease development. In the first 6 weeks of growth, the pots were fertilized weekly with Peter's (Scott's Company, Marysville, OH) 20-20-20 soluble fertilizer at 200 ppm. For the remainder of the experiment, the pots were fertilized three times per week with the same solution. Irrigation water was amended with phosphoric acid at 132 ppm weekly to maintain the media pH at approximately 6.0 to 6.5. The pH was checked monthly by collecting random media samples and using a pH meter (Hanna Instruments, Woonsocket, RI).

Severity of *Phytophthora* crown and root rot was evaluated every 2 days until fruit

were harvested (average 83 days postinoculation). Plants were rated on a 1 to 5 scale (1 = healthy, 2 = minor wilting, 3 = moderate wilting, 4 = severe wilting, 5 = plant death) adapted from Glosier et al. (11). The area under the disease progress curve (AUDPC) was calculated by inserting the disease score into the equation by Shaner and Finney (27) to describe the cumulative plant infection throughout the growing period. Approximately 10% of the symptomatic plants were returned to the laboratory to isolate and verify the pathogen. The root and crown area were rinsed with deionized water and surface-sterilized using a 70% ethanol solution. Three sections of root and crown tissue were excised and plated onto UCV8 plates amended with 25 ppm of benomyl, 100 ppm of ampicillin, 30 ppm of rifampicin, and 100 ppm of pentachloronitrobenzene (BARP). Plates were incubated at room temperature under constant fluorescent lighting for 3 days and observed at ×200 using a compound microscope to confirm *P. capsici* using morphological characteristics according to the *Phytophthora* spp. key by Waterhouse (36). Hyphal-tips of *P. capsici* cultures were transferred onto new BARP-amended UCV8 agar plates. After 7 days, each resulting isolate was screened for mefenoxam sensitivity and mating type to verify the isolate phenotype (15). Each experiment was conducted twice.

Fig. 1. Symptoms produced on cultivars **A to E**, Red Knight and **F to J**, Paladin 6 weeks postinoculation with 1 g of millet seed inoculum prepared with one of four isolates of *Phytophthora capsici*: **B and G**, SP98; **C and H**, SFF3; **D and I**, OP97; and **E and J**, 12889. Controls, **A and F**, were inoculated with sterile millet seed.

Phytophthora fruit rot screen. In the first crown and root rot experiment, the pepper fruits were harvested when the average fruit diameter was between 7 and 10 cm; these were stored for a maximum of 5 days at 2°C. Prior to inoculation, fruits were returned to room temperature, surface-disinfested with a 10% bleach (6.15% NaClO) solution for 10 min, and rinsed with distilled water. Fruits were placed into sterile humidity chambers, and moist paper toweling was placed into each chamber to maintain humidity at ~100%. A 10- μ l drop of the zoospore suspension was placed onto the surface of each fruit. Chambers were sealed with plastic film and maintained at room temperature (21 $\pm$ 2°C). The fruits were incubated in the dark for 60 h, followed by 24 h under constant fluorescent lighting to allow for pathogen sporulation.

The lesion area that developed on the fruits was estimated by measuring the diameter of water-soaked tissue, pathogen sporulation, and/or mycelia growth. To estimate the density of sporulation, a tape mount was prepared from an area of the lesion with pathogen sporulation. The average number of sporangia in five fields of view at $\times 400$ was extrapolated to estimate the number of sporangia per lesion. The experiment was replicated two times.

Statistical analysis. Mean AUDPC values and mean disease severity ratings were subjected to analysis of variance (ANOVA) using the PROC MIXED procedure of SAS v 9.1 (SAS Institute Inc., Cary, NC). Fisher's protected LSD was used for separation of means when effects were found to be statistically significant in ANOVA analysis ($P = 0.05$). AUDPC data from both crown and root rot experiments were log transformed prior to LSD analysis to satisfy assumptions of normality. A pepper line was considered resistant to the isolate if it received an average disease score (DS) < 2, adapted from previously described methods (5,11). To evaluate the lesion area data, all asymptomatic fruits (no lesions) were removed from the analysis. Fruit area measurements were square-root transformed to satisfy normality assumptions of

the test. Satterthwaite's approximation (SAS Institute) was used to account for the differences in number of experimental units in all fruit data analyses. Noninoculated control plants and fruits were removed from the data set prior to statistical analysis.

RESULTS

Phytophthora root and crown rot screen. Susceptible pepper plants exhibited crown rot and stem lesions followed by wilting and death when inoculated with *P. capsici*-infested millet seed containing one of the Michigan isolates (Fig. 1). All isolates of *P. capsici* obtained from inoculated plants were confirmed to have the same phenotype as the isolate used for inoculum (*data not shown*). None of the noninoculated control plants showed disease symptoms. Significant differences ($P \leq 0.05$) were found among AUDPC values calculated for the isolates and pepper lines, but the interaction was not significant.

In both experiments, the mean AUDPC values were statistically different for *P. capsici* isolates; isolate 12889 was more virulent than OP97, and both were more virulent than SP98 and SFF3 (Fig. 1, Table 1). All of the pepper lines tested except for CM334, NY07-8001, NY07-8006, and NY07-8007 were susceptible to isolate 12889 (Table 2). In the first experiment investigating root and crown rot, 19 of the 26 pepper lines tested were susceptible to the pickling cucumber isolate OP97 (DS ≥ 2), and 6 of the 14 pepper lines tested in the second experiment were susceptible to this isolate. No pepper lines were susceptible to SP98 in the first experiment (DS < 2), and only one was susceptible in the second experiment (DS = 2.0). One pepper line was susceptible to SFF3 in the first experiment (DS = 2.1), and all were asymptomatic in the second experiment (DS < 2).

Four of the nine cultivars showed different disease responses to the *P. capsici* isolates in the two experiments (Table 2). In the first experiment, Aristotle, Declaration, and Red Knight were susceptible to isolates 12889 (DS = 5.0) and OP97 (DS = 2.1 to 4.8), but resistant to SP98 (DS = 1.1

to 1.9) and SFF3 (DS = 1.1 to 1.8). In the same experiment, Snapper was susceptible to isolates 12889 (DS = 5.0), OP97 (DS = 5.0), and SFF3 (DS = 2.1), but resistant to SP98 (DS = 1.9). In the second experiment, Aristotle and Declaration were susceptible to only 12889 (DS ≤ 4.3) and resistant to OP97 (DS ≤ 1.5), SP98 (DS ≤ 1.3), and SFF3 (DS = 1.0). Red Knight was resistant only to SFF3 (DS = 1.8), and Snapper was resistant to SP98 (DS = 1.3) and SFF3 (DS = 1.3).

When data from the nine cultivars were combined from both experiments, Aristotle and Declaration were only susceptible to 12889 (DS ≤ 4.6), and Red Knight and Snapper were susceptible to 12889 (DS ≤ 4.9) and OP97 (DS = 4.3). Plant death (%) caused by isolates 12889 and OP97 progressed rapidly over time compared to SP98 and SFF3 on Red Knight (Fig. 2). Isolate 12889 caused more plant death than OP97, SP98, and SFF3 on Paladin.

Phytophthora fruit rot screen. Harvested pepper fruits did not have any apparent disease symptoms (rot, water-soaking) or pathogen signs (mycelial growth or pathogen sporulation). None of the fruit inoculated with sterile distilled water developed disease symptoms. Lesions on inoculated fruits expanded from the point of inoculation and were elliptical, with elongation from the stem end to blossom end of the fruit (Fig. 3). While some lesions displayed water-soaking only, other lesions exhibited pathogen mycelial growth and/or sporulation at the time of evaluation (84 h postinoculation, Fig. 4). Fruit infection incidence (%) was least for fruit inoculated with isolate SP98 and greatest for isolate 12889, the latter of which caused the greatest percentage of fruit with water-soaked lesions, pathogen mycelial growth, and pathogen sporulation. Inoculations with isolate SP98 resulted in the lowest incidence of fruit with water-soaked lesions and pathogen mycelial growth, and fruit inoculated with isolate OP97 resulted in the smallest percentage of fruit with pathogen sporulation. When isolates 12889 and OP97 were used, more pepper lines supported pathogen sporulation on fruits than when isolate SP98 was used as inoculum (*data not shown*).

Isolate 12889 produced water-soaked lesions that were larger than those caused by OP97, but similar to SP98 (LSD, $P = 0.05$) (Fig. 5). No statistical differences in area with pathogen mycelial growth or sporulation were noted among the three isolates when subjected to Fisher's protected LSD analyses. The density of sporangia in lesions with the sporulating pathogen was greater for isolates OP97 and SP98 than for isolate 12889 (LSD, $P = 0.05$). Statistical differences among cultivars were not noted for lesion area and sporangial density on infected fruit (*data not shown*).

Table 1. Mean area under the disease progress curve (AUDPC) values for *Phytophthora capsici* isolates causing crown and root rot symptoms in 27 pepper lines (experiment 1) and 14 pepper lines (experiment 2)

Isolate	Host	MT ^y	MS ^y	AUDPC ^x	
				Experiment 1 ^z	Experiment 2
SFF3	Pickling cucumber	A2	I	94 a	97 a
SP98	Pumpkin	A2	S	95 a	100 a
OP97	Pickling cucumber	A1	S	186 b	135 b
12889	Bell pepper	A1	I	308 c	276 c

^x AUDPC was calculated by using the disease score determined every 2 days using a 1 to 5 rating scale (1 = healthy, 2 = minor wilting, 3 = moderate wilting, 4 = severe wilting, 5 = plant death).

^y Isolate phenotypes are indicated by mating type (MT) and mefenoxam sensitivity (MS, I = insensitive, S = sensitive).

^z Column means with a letter in common are not statistically different according to Fisher's LSD ($P = 0.05$).

DISCUSSION

Pepper producers in Michigan would benefit from a cultivar that is resistant to *Phytophthora* crown and root rot. In our study, the susceptibility of pepper lines to *Phytophthora* root and crown rot differed significantly when four Michigan isolates of *P. capsici* were used. None of the com-

mercial cultivars included in our screen had resistance to the highly virulent isolate 12889, but several cultivars were resistant to the three other isolates. In our study, the breeding lines CM334, NY07-8001, NY07-8006, and NY07-8007 were resistant to all four isolates, and are the most promising sources of resistance for

future breeding efforts and commercial use.

Several methods have been developed to screen pepper seedlings for resistance to *Phytophthora* root and crown rot (5,11,19,29). The chi-squared method has been used to make comparisons with a standard resistant pepper, such as CM334,

Table 2. Pepper lines screened for crown and root rot resistance to four Michigan *Phytophthora capsici* isolates obtained from pepper (12889), pickling cucumber (OP97, SFF3), and pumpkin (SP98)

Pepper line ^{a,r}	Disease response ^o				AUDPC ^p				Death (%)			
	12889	OP97	SP98	SFF3	12889	OP97	SP98	SFF3	12889	OP97	SP98	SFF3
Experiment 1												
9925776 ^s	S	S	R	R	339	202	100	91	100	63	13	6
9931126 ^s	S	R	R	R	239	111	87	93	81	25	0	13
9941819 ^s	S	S	R	R	335	201	86	86	100	69	0	0
9943084 ^s	S	S	R	R	330	171	107	86	100	44	13	0
9943095 ^s	S	S	R	R	358	306	125	87	100	94	19	0
Alliance ^t	S	S	R	R	363	283	101	94	100	94	19	6
Aristotle (nonpelleted) ^s	S	S	R	R	332	174	98	100	100	44	6	6
Aristotle (pelleted) ^s	S	S	R	R	354	148	89	96	100	31	0	13
Brigadier ^u	S	S	R	R	362	301	118	99	100	94	25	13
Camelot ^s	S	S	R	R	361	259	94	108	100	94	13	19
Declaration ^t	S	S	R	R	305	119	101	86	100	25	19	0
Paladin ^u	S	R	R	R	200	105	87	87	63	6	0	0
Plato ^s	S	S	R	R	347	252	95	104	100	81	13	6
PRO3-13×14R-4 ^v	S	R	R	R	227	90	88	90	63	0	6	6
PRO3-15×16R-5 ^v	S	R	R	R	136	93	87	95	38	6	0	13
PRO4T-11×12 ^v	S	S	R	R	315	130	91	90	100	25	6	6
PRO5-C71×72 ^v	S	S	R	R	321	159	86	86	100	31	0	0
PRO5-C81×82 ^v	S	R	R	R	225	92	86	88	81	13	0	6
PRO5-C85×86 ^v	S	S	R	R	329	143	96	88	100	56	6	6
PRO5-C87×88 ^v	S	S	R	R	342	184	86	100	100	63	0	13
Prophet ^s	S	S	R	R	335	204	86	94	94	50	0	6
PX9942595 ^s	S	S	R	R	329	213	86	86	100	63	0	0
Red Knight ^s	S	S	R	R	353	283	113	112	100	94	13	25
Revelation ^s	S	S	R	R	351	283	95	86	100	88	13	0
Revolution ^t	S	R	R	R	326	98	89	101	100	25	0	13
Snapper ^w	S	S	R	S	368	299	112	106	100	100	19	25
XPP2548 (poblano type) ^x	S	R	R	R	124	113	89	88	25	13	13	0
LSD ($P = 0.05$) ^y					44	62	NS	NS				
Experiment 2												
Alliance ^t	S	S	R	R	371	165	105	104	94	44	6	6
Aristotle (pelleted) ^s	S	R	R	R	389	117	109	90	100	13	6	0
Brigadier ^u	S	S	R	R	405	195	125	106	100	44	25	13
Camelot ^s	S	S	R	R	391	173	103	90	100	38	6	0
CM334 (serrano type) ^z	R	R	R	R	90	90	90	90	0	0	0	0
Declaration ^t	S	R	R	R	255	90	91	90	88	0	0	0
Karisma ^t	S	S	R	R	369	144	91	107	94	25	0	6
NY07-8001 ^z	R	R	R	R	126	90	90	90	13	0	0	0
NY07-8006 ^z	R	R	R	R	90	90	90	90	0	0	0	0
NY07-8007 ^z	R	R	R	R	90	90	90	90	0	0	0	0
Paladin ^u	S	R	R	R	208	90	90	90	44	0	0	0
Red Knight ^s	S	S	S	R	368	252	128	128	94	69	25	19
Revolution ^t	S	R	R	R	313	90	90	90	88	0	0	0
Snapper ^w	S	S	R	R	392	216	110	104	100	63	6	6
LSD ($P = 0.05$) ^y					49	55	NS	NS				

^o Disease response was determined based on average plant disease score (1 to 5 rating scale, 1 = healthy, 2 = minor wilting, 3 = moderate wilting, 4 = severe wilting, 5 = plant death) at the end of the experiment. If the score was <2, the pepper line was considered resistant (R); if the score was ≥2, the pepper line was considered susceptible (S).

^p Area under the disease progress curve (AUDPC) was calculated by using the plant disease score evaluated every 2 days.

^q Potting media was inoculated with 1 g of prepared millet seed inoculum per plant.

^r Bell pepper line unless otherwise indicated.

^s Seminis Vegetable Seeds, St. Louis, MO.

^t Harris Moran Seed Company, Modesto, CA.

^u Syngenta Seeds Inc., Golden Valley, MN.

^v Pepper Research Inc., Belle Glade, FL.

^w Enza Zaden, Enkhuizen, Netherlands.

^x Sakata Seeds, Morgan Hill, CA.

^y Least significant difference.

^z Provided by Cornell University, Ithaca, NY.

to determine relative resistance of pepper lines (29). However, this method could not be used in our study because the resistant standard CM334 was not included in our first experiment. We used a method adapted from Glosier et al., who used a 0 to 5 disease rating scale (0 = no symptoms, 1 = leaf yellowing, 2 = minor stem necrosis, 3 = moderate stem necrosis and some leaf wilt, 4 = severe stem necrosis and severe wilt, 5 = plant death) and considered plants with an average disease score of <2 as resistant (11). Both Sy et al. (29) and Glosier et al. (11) determined physiological races by the patterns in resistant and susceptible pepper lines to specific *P. capsici* isolates. The methods of Sy et al. (29) and Glosier et al. (11) are helpful, but determining if the physiological races are the same among geographic regions is difficult because the statistical methods

and cultivars used differed between the two experiments. Also, using the currently acceptable methods, it appears that a high number of physiological races can be determined from a relatively low number of isolates (11,19,29), which would imply that cultivars need to be resistant to several different races. However, this has not been tested under field conditions.

There appeared to be differences in virulence between the *P. capsici* isolates tested and the susceptibility of pepper lines in our study. The pepper isolate used in our study was highly virulent on the crown, roots, and fruits of pepper; however, this does not necessarily indicate that pepper isolates are more virulent than cucurbit isolates. Ristaino found cucurbit isolates were, in some cases, just as virulent on pepper as pepper isolates (24). Polach and Webster (21) observed different levels of virulence

among *P. capsici* isolates, and others have made similar observations in previous studies with pepper (11,19). However, *P. capsici* isolates 12889, OP97, SP98, and SFF3 did not differ in virulence when inoculated onto Fraser fir seedlings (22), and OP97, SP98, and SFF3 did not differ in virulence on cucumber fruit (8). A recent study with tomato found significant differences in virulence among the *P. capsici* isolates 12889, OP97, SP98, and SFF3 (23) in agreement with the results of this study. Tomato is part of the *Solanaceae* family and therefore more likely to have resistance mechanisms similar to those of pepper (32,34) than to those of cucurbits or Fraser fir. Differences in incidence of *P. capsici* infection in our study were observed in the fruit screen with isolate 12889 (from pepper) causing more disease than isolate OP97 (from pickling cucumber), which caused more disease than isolate SP98 (from pumpkin). Although significant differences in virulence were observed among the isolates, they cannot be considered different *Phytophthora* fruit rot races because they caused infection on the fruits of all pepper lines.

Our results indicate that pepper fruits are more susceptible to *P. capsici* than are roots and crowns. Other reports have indicated different levels of resistance exist to foliar blight, stem blight, and root rot of pepper (14,19,28). Also, different mechanisms are responsible for resistance to these three diseases in pepper (3,19). Similarly, potato breeders found plants exhibiting tuber resistance to *P. infestans* did not necessarily have resistance to foliar or vine infection by the same *P. infestans* races (4,26). These results, along with differing physiological races of *P. capsici*, have great implications for pepper breeders. Instead of breeding for resistance to one disease in pepper, breeders must now potentially breed for resistance to four: root rot, fruit rot, stem blight, and foliar blight (3,19,28).

Fig. 2. Plant death (%) recorded weekly of **A**, pepper cultivar Red Knight, and **B**, pepper cultivar Paladin, caused by *Phytophthora capsici* isolated from pickling cucumber (OP97, SFF3), pumpkin (SP98), and pepper (12889).

Fig. 3. Pepper fruit 84 h postinoculation with a 10- μ l drop of *Phytophthora capsici* zoospore suspension (1.75×10^6 zoospores/ml).

Once a small standard set of cultivars and pepper lines is established, a greater number of isolates can be screened to determine those groups of cultivars that may provide the highest level of resistance in a particular geographic region. This information could be pooled across regions, which would help pepper producers manage *Phytophthora* crown and root rot more effectively and further facilitate the development of resistant pepper cultivars. Also, producers could consider growing several cultivars in their fields to determine which has the highest level of resistance to local *P. capsici* isolates. This study demonstrates that information from one region may not accurately predict the response of a resis-

tant cultivar used in another region, including diverse geographic regions within a single state.

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Fig. 4. Pepper fruit (%) with or without disease symptoms averaged across all pepper lines when inoculated with 10- μ l drops (1.75×10^6 zoospores/ml) of *Phytophthora capsici* isolates obtained from pepper (12889), pickling cucumber (OP97), and pumpkin (SP98). NL = no lesion, WS = water-soaking only, MY = mycelial growth and water-soaking, and SP = sporulation, mycelial growth, and water-soaking.

Fig. 5. Area of A, water-soaking, B, mycelial growth, and C, pathogen sporulation on pepper fruit inoculated with 10- μ l drops (1.75×10^6 zoospores/ml) of *Phytophthora capsici* isolates 12889, OP97, and SP98. Areas were calculated by measuring two diameters perpendicular to each other across the fruit lesion.

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