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A differential series of pepper (*Capsicum annuum*) lines delineates fourteen physiological races of *Phytophthora capsici*

Physiological races of *P. capsici* in pepper

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Abstract The study of the genetics of resistance in pepper to the oomycete pathogen *Phytophthora capsici* has been complicated due to a lack of use of a common set of pathogen isolates and host genotypes. We have developed a differential series for this system using eleven pepper genotypes and thirty-four isolates of the pathogen from California, New Mexico, North Carolina, and Turkey. Through differential patterns of virulence of the isolates on the hosts, we identified fourteen different physiological races of *P. capsici.* There appears to be no restriction of races to particular geographical locations. Isolate mating types were also determined, and both mating types were found in one field in California. The significance of the characterization of physiological races and existence of both mating types in the field to pepper growers and breeders is discussed.

Keywords Pepper root and stem rot · Disease resistance

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Introduction

Phytophthora root rot on pepper (*Capsicum* spp.) is caused by the oomycete *Phytophthora capsici* Leon. (Leonian 1922; Erwin and Ribeiro 1996). Economically, it is one of the most destructive pepper pathogens worldwide, attacks tomatoes and cucurbits as well, and has caused billions of dollars in damage to crops in the United States (Tyler 2002; Oelke et al. 2003). Control is based primarily on the use of mefanoxam, cultural practices such as drip irrigation and black plastic mulch, and the use of genetically resistant varieties.

Several commercial pepper varieties are available that offer some level of resistance to *P. capsici*, but there is no commercially acceptable variety that shows resistance to a majority of the isolates (Oelke et al. 2003). Nor is there consensus about the genetics governing the resistance response. Researchers have reported that resistance may be under the control of one gene with modifiers, two genes, or as many as nine different genes (Barksdale et al. 1984; Ortega et al. 1992; Reifschneider et al. 1992). A number of quantitative trait loci (QTLs) controlling resistance have been mapped (Lefebvre and Palloix 1996; Ogundiwin et al. 2005), and in these studies, the inheritance of resistance is multigenic. Different combinations of pathogen isolates and pepper genotypes were used in these published studies, making cross-study comparisons difficult. In some studies, the isolate used was not even clearly identified.

To enable successful and efficient breeding for resistance to Phytophthora root rot in pepper, the genetic nature of resistance needs to be clarified, and a common set of differentials needs to be developed to delineate physiological races of the pathogen. The screening of *P. capsici* isolates against a bank of differential pepper host plants to reveal different physiological races of the pathogen should prove useful in revealing major resistance genes (Person and Sidhu 1971). A recent study by Oelke et al. (2003) has shown that physiological races exist in *P. capsici.* The current, more extensive study has confirmed the existence of differential virulence of *P. capsici* on different pepper genotypes and expanded the number of identified races.

In this study, a set of thirty-four *P. capsici* isolates collected from various field locations throughout California and from other sources was inoculated in three replicates onto a bank of eleven pepper genotypes in order to delineate those isolates into physiological races. To gain a better understanding of whether virulence may be evolving in the field through sexual recombination, mating type for each isolate was determined as well.

Materials and methods

Collection, isolation, and confirmation of *Phytophthora capsici*

Eighteen *P. capsici* isolates were collected from seven different pepper fields around California in the summers of 2002 and 2003 (Table 1). The pathogen was isolated from the diseased plants by taking small cuttings from lesions at the crown, soaking them in 10% bleach for 10 min, rinsing them with sterile water, and placing them in the center of a 100 × 20 mm sterile polystyrene Petri plate containing the *Phytophthora*-selective medium PARPH (Jeffers and Martin 1986). From each plate showing mycelial growth, a 4-mm plug was aseptically transferred to the center of a new plate containing V-8 juice agar following established protocols (Ribeiro 1978). Plates were sealed with Parafilm (Pechiney Plastic Packaging, Menash, WI.) to prevent contamination and desiccation. Each isolate was subcultured to fresh V-8 juice agar plates once every month in order to retain vigorous growth. In addition to the eighteen isolates collected in California, sixteen other isolates were obtained from outside sources for screening (Table 1). Two control isolates for mating type studies were obtained from the American Type Culture Collection: ATCC 15427 (A1 mating type) and ATCC 15399 (A2 mating type).

To ensure genetic uniformity of each isolate, cultures growing on V-8 juice media were induced to produce zoospores (procedure described under Inoculations). A sterilized bacterial loop full of zoospore solution was streaked onto PARPH media. Once individual zoospores had begun to produce mycelia, a sterile wire loop was used to obtain a small piece from a single colony. This piece of agar was placed onto V-8 juice media to obtain single-genotype isolates. After one week, an agar plug from this plate was aseptically placed onto a 1 ml cryovial containing 5% DMSO as a cryoprotectant. The vial was placed into a −80°C freezer overnight, and then plunged into liquid nitrogen for long-term storage.

In order to confirm that the *Phytophthora* isolates were indeed *P. capsici*, DNA was extracted according to a procedure used for *Eutypa* DNA extraction (Engel et al. 2000) from mycelial mats of each isolate grown in 40 ml of sterile liquid V-8 medium cultures in the dark for 14 days, and that DNA was used as a template in a PCR with the *P. capsici*-specific primers PCAP and ITS1, according to the method described by Ristaino et al. (1998).

Test plants and experimental design

Eleven pepper lines were selected for disease screening in the greenhouse against each of the *P. capsici* isolates based on their known resistance or susceptibility to Phytophthora root rot. Pepper genotypes Fidel, Jupiter and Paladin were supplied by Craig Sandlin (Novartis Seeds, Gilroy, CA). Criollo de Morelos 334 (=CM334) and Nu Mex Joe E. Parker 003B (=JEP) were supplied by Mark Massoudi (Ag-Biotech, Gilroy, CA.). Cayenne 9852-192 (Cayenne 192), Cayenne 9852-193 (Cayenne 193), Cayenne 9852-194 (Cayenne 194), PI201234, and PSP11 were supplied by Terry Berke (AVRDC, Tainan, Taiwan). Berumasari was supplied by Koji Sakamoto (Takii and Co., Kyoto, Japan).

Seeds were planted in 7.7 × 11 × 5.5 cm plastic potting cells containing a commercial sterile potting

Table 1 *Phytophthora capsici* isolates, host plant, and place of origin

Isolate name	Plant host[a]	Field collection site	Source/date
PPc1	Bell pepper	Gilroy, CA Field 1	J. Prince (CSU Fresno, 2002)
PPc2	Bell pepper	Gilroy, CA Field 1	J. Prince (CSU Fresno, 2002)
PPc3	Bell pepper	Gilroy, CA Field 1	J. Prince (CSU Fresno, 2002)
PPc4	Bell pepper	Gilroy, CA Field 1	J. Prince (CSU Fresno, 2002)
PPc5	Bell pepper	Dos Palos, CA	J. Prince (CSU Fresno, 2003)
PPc6	Bell pepper	San Ardo, CA	J. Prince (CSU Fresno, 2003)
PPc7	Wax pepper	Oxnard, CA Field 1	J. Prince (CSU Fresno, 2003)
PPc8	Wax pepper	Oxnard, CA Field 1	J. Prince (CSU Fresno, 2003)
PPc9	Wax pepper	Oxnard, CA Field 1	J. Prince (CSU Fresno, 2003)
PPc10	Wax pepper	Oxnard, CA Field 1	J. Prince (CSU Fresno, 2003)
PPc11	Wax pepper	Oxnard, CA Field 1	J. Prince (CSU Fresno, 2003)
PPc12	Bell pepper	Gilroy, CA Field 2	J. Prince (CSU Fresno, 2003)
PPc13	Bell pepper	Gilroy, CA Field 2	J. Prince (CSU Fresno, 2003)
PPc14	Bell pepper	Gilroy, CA Field 2	J. Prince (CSU Fresno, 2003)
PPc15	Bell pepper	Gilroy, CA Field 3	J. Prince (CSU Fresno, 2003)
PPc16	Bell pepper	Gilroy, CA Field 4	J. Prince (CSU Fresno, 2003)
PPc17	Bell pepper	Gilroy, CA Field 4	J. Prince (CSU Fresno, 2003)
PPc18	Bell pepper	Gilroy, CA Field 4	J. Prince (CSU Fresno, 2003)
P1314	Bell pepper	California	M. Coffey (UC Riverside)
P1319	Bell pepper	California	M. Coffey (UC Riverside)
P1982	Tomato (*Solanum lycopersicum*)	California	M. Coffey (UC Riverside)
P3490	Tomato (*Solanum lycopersicum*)	California	M. Coffey (UC Riverside)
P6501	Bell pepper	California	M. Coffey (UC Riverside)
P6502	Bell pepper	California	M. Coffey (UC Riverside)
P8074	Watermelon (*Citrullus lanatus*)	California	M. Coffey (UC Riverside)
P8075	Tomato (*Solanum lycopersicum*)	California	M. Coffey (UC Riverside)
P9132	Bell pepper	California	M. Coffey (UC Riverside)
pp87-11-ICA	Pepper	California	T. Day (Sakata Seeds)
pp87-24-ICA	Pepper	California	T. Day (Sakata Seeds)
PpPc3a	Pepper	California	T. Day (Sakata Seeds)
ppGPS1-1	Pepper	California	T. Day (Sakata Seeds)
Sc1b A1	Chile pepper	North Carolina	J. Ristaino (North Carolina State University)
PWB 24	Chile pepper	New Mexico	P. Bosland (New Mexico State University)
PWB 73	Chile pepper	Turkey	P. Bosland (New Mexico State University)

[a] All peppers in this work belong to the species *Capsicum annuum*

soil (Supersoil Potting Soil, Rod McLellan Co., San Mateo, CA) and thinned to 2–3 plants/cell. A split-plot design was used. Sets of six plants of each pepper genotype at the 4-true-leaf stage were randomized into 23 × 46 × 5.5 cm plastic potting flats without drainage holes so that each flat contained one set of each of the eleven pepper genotypes. Three replicates were done at separate times for each pepper genotype-*P. capsici* isolate combination, for a total of eighteen plants per combination. Once the plants had begun to produce their first pair of true leaves, they were fertilized with 1 g of controlled-release fertilizer beads per cell (Osmocote 14-14-14 NPK, Grace Sierra Horticulture Products, Milpitas, CA). Greenhouse temperatures ranged from 28 to 32°C throughout the experiment.

Inoculations

The plants were inoculated with *P. capsici* zoospores six weeks after germination at the four-true-leaf stage. For each isolate, fifteen V-8 agar plugs were placed in a sterile Petri plate, submerged in sterile water and incubated at 25°C for 48–72 h, after which the water was decanted out of the plates, replaced with a sterile soil suspension (R. Heisey, personal communication), and allowed to incubate for another 48–72 h. Plates were incubated at 10°C for 90 min, then at 25°C for 30 min. The zoospore-containing soil suspension was decanted into a flask, counted by using a hemacytometer, adjusted to a concentration of 2,000 zoospores per ml with 4°C water, and then 5 ml of the suspension (10,000 zoospores) was inoculated onto each cell in the flat. This number of zoospores has previously been shown to prevent susceptible escapes and has given consistent reaction types on genetically resistant and susceptible plants (Bosland and Lindsey 1991). Flats were flooded with water, and the plants remained flooded for 48 h to ensure root contact with zoospores before being transferred into flats with holes for proper drainage.

Disease scoring

Once susceptible check genotypes Jupiter and NuMex Joe E Parker began to exhibit severe disease symptoms, all lines were scored for disease severity. This was typically 30–40 days post-inoculation. Each plant of the batch of six was scored on a scale of 0–5 based on the following criteria: 0 = no symptoms/healthy plant; 1 = leaf yellowing and no stem necrosis; 2 = minor stem necrosis; 3 = moderate stem necrosis and some wilting; 4 = severe stem necrosis and severe wilting, but not yet dead; 5 = dead plant. For each pepper line, the resistance scores were averaged over all replicates. ANOVA was performed using SAS (SAS Institute Inc., Raleigh NC). Plants that received an average score of 0 or 1 were classified as resistant, while those that received an average score of 2, 3, 4 or 5 were classified as susceptible (R vs. S). Patterns of these two contrasting reaction types over all eleven differentials were used to assign *P. capsici* isolates to physiological races.

Mating type

P. capsici has two different mating types: A1 and A2. All isolates tested were crossed to isolates of both mating types. We tested all of the isolates that we had collected from the field in California (all isolates with the PPc designation) and the 4 isolates obtained from Sakata Seeds (GPS1-1, Pc3a, 87-11-ICA, 87-24-ICA). The other isolates had already had their mating type previously determined by their collectors. As controls, crosses between known A1 and A1, A2 and A2, and A1 and A2 isolates were made. Crosses were done by placing agar plugs from rapidly growing cultures on the same Petri plate. Mycelia grew out from each plug. The production of oospores along the boundary between mycelia derived from each plug indicated that the isolates were of opposite mating types.

Results

Isolate confirmation and Phytophthora root rot screening

All thirty-four isolates tested with the *P. capsici*-specific PCR showed the same 172 bp product expected, supporting the isolates' identity as *P. capsici* (data not shown).

Eleven pepper genotypes were inoculated with zoospores from each of the 34 *P. capsici* isolates. Significant differences ($P < 0.0001$) were found between isolates, between pepper genotypes, and in the pepper genotype-by-isolate interaction (Table 2).

Pepper lines that received a root rot disease score (or "index") of 2 or greater when averaged over all replicates were classified as susceptible, whereas lines that received average disease indices below 2 were classified as resistant. *P. capsici* isolates that caused the same set of susceptible or resistant reaction types across all 11 pepper lines were placed in the same physiological race.

Based on the observed disease reaction patterns, a total of 14 putative physiological races (A through N) were found (Table 3). Seven California isolates, ppPc3a, P6502, pp87-11-ICA, P1314, P3490, PPc15, and PPc12, showed unique reaction patterns and were placed into seven physiological races B, D, E, F, I, K, and N, respectively. Four races each containing two California isolates: P1982 and pp87-24-ICA, P1319 and P8075, PPc2 and PPc3, and P8074 and PpGPS1-1 were classified as A, G, M, and C, respectively. Race C also contained one isolate from North Carolina

Table 2 Analysis of variance for *P. capsici* root rot inoculation experiments

	Degrees of freedom	Sum of squares	Mean squares	F value	$P > F$
Replicate	2	0.03	0.02	0.02	0.9818
Isolate	33	893.19	27.07	32.45	<0.0001
Replicate × Isolate	40	58.65	1.47	1.76	0.004
Pepper genotype	10	2074.31	207.43	248.68	<0.0001
Pepper genotype × Isolate	329	1294.78	3.94	4.72	<0.0001

(Sc1B A1). Isolates PPc1, PPc4, PPc5, each from California, and PWB 24 from New Mexico, were classified as Race H. Isolates PPc6, PPc9, PPc11, and PPc16, each from California, were designated Race J. Finally, race L designation was assigned to the largest group of isolates, PWB 73 from Turkey, and P6501, P9132, PPc7, PPc8, PPc10, PPc13, PPc14, PPc17, and PPc18, all from California.

Mating type

A list of mating types for the *P. capsici* isolates used in the study is given (Table 4). Isolates of both mating types were found, even among collections from the same field. For example, isolate PPc16, with an A1 mating type, was found in the same field as PPc17 and PPpc18, both with A2 mating types. Due to a lack of oospore formation in crosses with either A1 or A2, it was not possible to determine the mating type of the following isolates: PPc7, PPc8, PPc10, PpPc3a, 87-11-ICA, and 82-24-ICA.

Discussion

In this work, we delineated fourteen physiological races of *Phytophthora capsici* (Leon.) based on the inoculation of thirty-four individual isolates onto a differential series of eleven pepper genotypes. The pepper lines ranged in their spectrum of resistance from CM334 (resistant to all races) to Cayenne 192 and JEP (susceptible to all but two races). The *P. capsici* races ranged from being virulent on nine genotypes of pepper to being virulent on none. Both mating types A1 and A2 were found in our collection, and isolates of different mating types were discovered in the same field, indicating the real possibility of sexual reproduction and pathogen evolution in the field in California.

As in the study by Oelke et al. (2003), significant isolate, host genotype, and isolate x host genotype effects indicated differential disease interactions (Table 2). Based on the disease reactions across the differential series of peppers, this study placed thirty-four *P. capsici* isolates into fourteen physiological races, denoted A through N (Table 3). Races are not restricted to any specific geographical area. Isolates from New Mexico, North Carolina, and Turkey fell into races that also contained isolates from California. Races are not restricted to certain areas within California either, since some isolates from different races were collected from the same fields. For example, isolates PPc12, PPc13, PPc14 were all collected from the same field, but PPc12 belongs to race N, while PPc13 and PPC 14 belong to race L.

Race A was avirulent on all pepper lines included in the differential series. The possibility thus existed that the isolates in race A may not be *P. capsici*, but all isolates in this study were determined to be *P. capsici* based on PCR amplification using Ristaino's *P. capsici*-specific ITS primers. It is also possible that a larger array of differentials would include a pepper genotype that would be susceptible to race A.

Since no differential disease responses were found with CM334 in this study or that of Oelke et al. (2003), it is not possible to determine whether race-specific resistance exists in this pepper line. Indeed, CM334 has been found to be "universally resistant" by many investigators, and it has been used as a primary source of root rot resistance in breeding programs for many years (Oelke et al. 2003). It may be possible to examine the susceptible responses of the other pepper genotypes and estimate the number of resistance factors operating in the differential series. For example, susceptibility to race N may be due to a resistance gene that is not present in any of the pepper genotypes except CM334 and Cayenne 193, which were the only lines resistant to that race (Table 3). With fourteen putative races, thirteen of which gave differential responses across the pepper lines, there could be as many as thirteen individual resistance genes or alleles

Table 3 Physiological races arranged according to root rot disease reaction patterns (resistant vs. susceptible) of pepper lines to various *P. capsici* isolates

Race	Isolate	Pepper line										
		CM334	PI	193	Fid	Pal	Ber	Jup	194	Psp	192	JEP
A	P1982	R[a]	R	R	R	R	R	R	R	R	R	R
	pp87-24 ICA											
B	ppPc3a	R	R	R	R	R	R	R	R	R	S	R
C	Sc1b A1	R	R	R	R	R	R	S	R	S	S	S
	P8074											
	PpGPS1-1											
D	P6502	R	R	R	R	R	S	S	R	S	R	S
E	pp87-11-ICA	R	R	R	R	R	N	S	S	R	S	S
F	P1314	R	R	R	R	R	R	N	S	S	S	S
G	P1319	R	R	R	R	R	R	S	S	S	S	S
	P8075											
H[b]	PPc1	R	R	R	R	S	R	S	S	S	S	S
	PPc4											
	PPc5											
	PWB 24											
I	P3490	R	R	S	R	R	S	R	S	S	S	S
J	PPc6	R	R	R	R	S	S	S	S	S	S	S
	PPc9											
	PPc11											
	PPc16											
K	PPc15	R	R	S	R	S	S	R	S	S	S	S
L[c]	P6501	R	R	R	S	S	S	S	S	S	S	S
	P9132											
	PWB 73											
	PPc7											
	PPc8											
	PPc10											
	PPc13											
	PPc14											
	PPc17											
	PPc18											
M	PPc2	R	R	S	S	S	S	S	S	S	S	S
	PPc3											
N	PPc12	R	S	R	S	S	S	S	S	S	S	S

[a] R = resistant; S = susceptible; See text for details; N = not tested

[b] May correspond to Race 1 of Oelke et al. (2003)

[c] May correspond to Race 2 of Oelke et al. (2003)

CM334 = Criolo de Morelos 334; PI = PI201234; Fid = Fidel; Pal = Paladin; Ber = Berumasari; Jup = Jupiter; 194 = Cayenne 194; Psp = Psp-11; 192 = Cayenne 192; JEP = NuMex Joe E Parker

that account for the race-specific reactions. If more pepper genotypes were added to this study, some of the races may separate out into additional races, each with a unique disease reaction pattern. Inoculation onto a single host plant genotype can identify two races based on two alternative reactions, resistant vs.

Table 4 Mating types of *Phytophthora capsici* isolates

Mating type	Isolate	Collection Site
A1	PPc15, PPc16	Gilroy, CA
	ppPc31, ppGPS1-1, P1314, P3490, P6501, P9132	CA, specific locations unknown
	Sc1b A1	North Carolina
	PWB 73	Turkey
A2	PPc1, PPc2, PPc3, PPc4, PPc12, PPc13, PPc14, PPc17, PPc18	Gilroy, CA
	PPc9, PPc11	Oxnard, CA
	PPc5	Dos Palos, CA
	PPc6	San Ardo, CA

Mating types of isolates in boldface were determined as part of this study. Mating types of other isolates shown were provided to us by their sources. The mating type of six isolates was not able to be determined (see text)

susceptible. Eleven genotypes could potentially identify $(2)^{11}$ races, so any estimate that we make of the number of physiological races must be taken as a minimum. Nevertheless, our races can serve as scaffolding upon which further studies can be built.

Previous work at New Mexico State University identified nine physiological races in *P. capsici* (Oelke et al. 2003). However, only ten isolates were tested in that study. It should be noted, however, that some of the races characterized in the current study may correspond to some of the races in the New Mexico study. For example, isolates PWB 24 and PWB 73 were tested in both studies. The New Mexico study placed these isolates into different races, 1 and 2, respectively. In our study, they were also placed into two different races, races H and L, respectively. Therefore, our races H and L may correspond to races 1 and 2 of Oelke et al. (2003). Other identified races may also correspond, but additional work with a common set of pepper genotypes and oomycete isolates between both laboratories needs to be undertaken to confirm this.

Considerably different patterns of virulence are seen among the 14 physiological races of *P. capsici* in this study. Race A is avirulent on all pepper genotypes tested. It is important to note that all of the most virulent isolates except two (PWB 24 and PWB 73) were collected recently from California. It is also important to note that, within California, the most highly virulent isolates were those collected from fields in Gilroy (PPc2, PPc3, PPc12, PPc13, PPc14, PPc17, and PPc18) and Oxnard (PPc7, PPc8, PPc10). Isolates with the lowest levels of virulence were those obtained from the collections at UC Riverside and Sakata Seeds. The isolates P1982 and pp87-24-ICA within race A, which did not cause disease on any of the pepper lines, were also among the oldest isolates. Having been collected in the early 1980s and kept in liquid nitrogen for long-term storage, they may have lost some virulence potential as suggested by Erwin (1983). The New Mexico and Turkey isolates acquired from a collection at New Mexico State University had been passed through living plants several times a year. This would likely help those isolates maintain virulence.

Information from this study will be useful in future studies of the genetics of resistance in the host plant and the genetics of virulence in the pathogen. Further study of the genetics of the pepper—*P. capsici* system may help to reveal the number of resistance genes in the pepper host and virulence genes in the *P. capsici* pathogen, leading to a better understanding of potential strategies for disease management. In related work, we have identified QTLs conferring resistance to *P. capsici* from the two most resistant genotypes used in our differential series: CM334 and PI201234 (Ogundiwin et al. 2005). It may soon be possible through marker-assisted selection to create pepper genotypes of different horticultural types that possess universal resistance to Phytophthora blight. However, while this might be an ideal long-term approach for combating the disease in pepper, for now it may be more practical to pyramid combinations of race-specific R-genes against *P. capsici* isolates from certain geographic regions into pepper varieties that are commonly grown in those same regions. Unfortunately, since both mating types can be present in the field in California, it may be difficult to maintain the durability of resistant varieties due to sexual recombination in the pathogen.

Additional isolates obtained in the future could be assigned to one of the fourteen physiological races by inoculating them onto our set of differential pepper genotypes. Patterns of resistance and susceptibility that match one of those seen in Table 3 would mean that an isolate would be assigned to that race. Patterns that do not match any of those seen would indicate that a new isolate is in a race other than those reported here. Addition of more differential pepper genotypes in the future may also provide a higher level of dissection of isolates into additional races other than the fourteen discussed here.

Testing of all of the California isolates for mating type revealed eight isolates with A1 mating types and thirteen having A2 mating types (Table 4). Isolate PPc16, determined to be A1, was collected from the same field as isolates PPc17 and PPc18, both determined to be A2. While both mating types have been found together frequently in the US (Lamour and Hausbeck 2000, 2001), this is the first report of finding both mating types in the same field in California.

In summary, it is evident that at least fourteen physiological races exist among isolates of the pepper pathogen *Phytophthora capsici*, and that these races are not restricted to any particular geographical region within or outside of California. There also appeared to be a wide range of virulence among the isolates and of resistance in the pepper varieties. The presence of both A1 and A2 mating types in California may lead to increased virulence through sexual recombination. Information from this study will help facilitate the selection of individual *P. capsici* isolates and pepper genotypes that can be crossed for the study of respective segregating populations and the genetics of resistance and virulence. This could aid in the search for the genetic and physical locations and identification of R-genes in pepper and of avirulence genes in the pathogen. This information may also help pepper growers in California to manage root rot disease in the field more effectively and facilitate the development of durably resistant commercial pepper varieties.

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