Effect of Crop Rotation on the Survival of *Phytophthora capsici* in Michigan

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ABSTRACT

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Phytophthora capsici is a limiting factor for some vegetable producers in Michigan despite crop rotation and fungicide applications. Our objective was to assess the effect of crop rotation on the survival of *P. capsici* at a naturally infested site in Michigan planted to cucumbers in 1998, corn in 1999 and 2000, and tomatoes in 2001. Isolates were characterized for compatibility type (CT), mefenoxam sensitivity, and amplified fragment length polymorphism (AFLP) marker profiles, and compared with isolates recovered from other locations in Michigan during the same time period. The A1:A2 CT ratio was 1:1, and approximately 60% of the isolates recovered in both years were intermediately sensitive or insensitive to mefenoxam. The majority of the isolates (89%) had unique AFLP fingerprints, and no members of the same clonal lineage were recovered among years. Isolates from this location were more similar to each other than to isolates from other locations in Michigan, and it was not possible to distinguish isolates based on the year of isolation. Genetic similarity analyses indicate that isolates from this location are part of a genetically distinct outcrossing population. These data indicate that *P. capsici* persisted as oospores for the 2 years between cucumbers and tomatoes, and that crop rotation and mefenoxam are not likely to provide economic control.

Eleven species of *Phytophthora* are reported to attack tomato (*Lycopersicon esculentum* Mill.) worldwide (3). In the United States, *Phytophthora* root, crown, and fruit rot of tomato is caused primarily by *Phytophthora infestans* (Mont.) de Bary, *P. capsici* Leonian, and *P. parasitica* Dastur (= *P. nicotianae*) (3). In Michigan, *P. infestans* has not been recovered from tomato in recent years, but *P. parasitica* was recovered from a processing tomato field in 1999, and *Phytophthora* blight of vegetable crops, including tomato, caused by *P. capsici* has increased dramatically in the last decade. Some large vegetable producers alternate between cucurbits and tomatoes as part of their crop rotation. While this rotation provides some horticultural benefit, it may be increasing disease caused by *P. capsici*. Growers have been reluctant to recognize *P. capsici* as a threat to commercial tomato production, even though some processing tomato fields could not be harvested because of fruit rot, and in other fields plant stand was significantly reduced by root and crown rot caused by *P. capsici*.

There is no information available concerning *P. capsici* on tomatoes in Michigan. Most of the information on *P. capsici*

and/or *P. parasitica* on tomatoes in the United States was generated by scientists responding to epidemics in Colorado and California during the last 75 years. In Colorado, *P. capsici* caused serious crop losses in cucurbits, peppers, and tomatoes from 1930 to 1945 in the Arkansas River Valley (7-9). In this region, the epiphytotics caused by *P. capsici* in 1938 and 1940 on tomato were estimated by canning companies to be responsible for 50% loss of the total tomato production. Kreutzer and Bryant (9) screened more than 100 commercial tomato varieties for resistance to fruit rot by *P. capsici* but found only one showing slight promise, whereas ridging, staking, and the use of fungicidal dusts containing copper all significantly increased yields in field trials. In 1955, Critopoulos (1) described a crown rot of tomato caused by *P. capsici* in California. Subsequently, Satour and Butler (17) reported losses in tomato fields in the San Joaquin and Sacramento valleys during 1955 to 1965, which were attributed to both *P. capsici* and *P. parasitica*. More recently in California, Ioannou and Grogan (6) reported that *Phytophthora* blight occurred sporadically, causing nearly complete destruction of the crop in some fields. *P. parasitica* was responsible for more than 85% of the root rot on processing tomatoes in the state, and *P. capsici* was recovered infrequently. In field trials, soil treatment with metalaxyl (0.75 to 1.5 kg a.i./ha) was fungistatic to *P. parasitica* and increased total tomato yield (6). Similar to reports for many oomycetous organisms, insensitivity to metalaxyl and mefenoxam has

been reported for isolates of *P. capsici* and *P. parasitica* in natural populations (2,4,10,13,16,19).

P. capsici and *P. parasitica* both readily invade young tomato plants (up to the five-leaf stage), causing rotting and disintegration of tissue and plant death (17). In larger plants (six-leaf stage and older), dark brown cankers are produced on infected roots and crowns, and it appears that resistance increases as the plants mature (1,17). In many cases, abundant secondary and adventitious roots are formed above the cankers (17). Green fruit are more susceptible than mature fruit (18), and fruit in contact with the ground have a much higher incidence of infection (9). Detailed studies of the infection process of *P. capsici* on tomato fruit indicate that the stylar ends of green fruit are more susceptible to infection than the stem end (18). Zoospores directly penetrate the cuticle within 1 to 3 h at 25 to 30°C, and abundant sporulation occurs on the surface of fruit at temperatures above 20°C (9). Kreutzer and Bryant (9) reported that excess moisture and soil temperature between 18 and 29°C were key components of an epidemic and cited observations from artificially and naturally infested fields.

In Michigan, common approaches to managing *Phytophthora* blight include crop rotation and fungicide applications. Mefenoxam has been relied on by some producers, and isolates insensitive to mefenoxam have been recovered from cucurbit hosts at multiple locations in the state (10). Although current recommendations advise at least 3 years between susceptible hosts, many Michigan farmers employ shorter rotations due to the relatively low value of field crops traditionally used in crop rotation.

Here we report on naturally occurring epiphytotics of *Phytophthora* during 1998 on cucumber and 2001 on tomato at the same location on a vegetable production farm in Michigan with a history of *P. capsici*. The field was planted to corn in 1999 and 2000. Viable oospores of *P. capsici* were recovered from infected cucumber fruit collected during 1998 (10). Specific objectives of the research were to assess the effect of crop rotation on the survival of *P. capsici* and to determine whether resistance to mefenoxam might be a factor in disease management.

MATERIALS AND METHODS

Isolate recovery. Isolates of *P. capsici* were recovered from a single field in south

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central Michigan that was planted to cucumbers in 1998, corn in 1999 and 2000, and processing tomatoes in 2001. Both the cucumbers and tomatoes were planted on flat ground, and the field was irrigated via a center pivot irrigation system. A field-specific grid that included grid blocks approximately 40 m² was constructed using permanent structures as reference points. From 0 to 4 samples of infected plant material were collected at random within each grid block. In 1998, disease was severe on cucumber fruit, occurring initially as dark, water-soaked lesions and developing into a distinctive white "powdered sugar" layer of spores on the surface of the fruit. Visibly infected fruit were collected. In 2001, stunted tomato plants were collected prior to fruit set.

Infected cucumbers were snapped in half by hand, and a section (1 cm²) of tissue was removed from beneath the cuticle. The root and crown areas of infected tomato plants were rinsed with tap water and blotted with paper towels before a section of tissue at the edge of an expanding lesion was removed. Tissue was not surface sterilized prior to isolation. Isolations were made onto BARP (benomyl 25 ppm, ampicillin 100 ppm, rifampicin 30 ppm, and pentachloronitrobenzene 100 ppm) amended UCV8 (840 ml distilled water, 163 ml unclarified V8 juice, 3 g CaCO₃, and 16 g agar) plates. Plates were incubated at room temperature in the dark for 2 to 3 days before colonies were transferred. Procedures for obtaining single zoospore isolates were as previously described (10). Single zoospore cultures were maintained on RA (rifampicin 30 ppm, ampicillin 100 ppm)-UCV8 plates and transferred bi-monthly. For long-term storage, a 7-mm plug of expanding mycelium from each culture was placed into a 1.5-ml microfuge tube with one sterilized hemp seed and 1 ml of sterile distilled water (SDW). Isolates were then incubated for 2 to 3 weeks at 23 to 25°C before being stored at 15°C.

Compatibility type and mefenoxam sensitivity determination. To determine compatibility type of isolates of *P. capsici*, agar plugs from the edge of an expanding single-zoospore colony were placed at the center of UCV8 plates approximately 2 cm from field isolates OP97 (A1) and SP98 (A2) of *P. capsici* and incubated in the dark at 23 to 25°C for 3 to 6 days. Following incubation, compatibility type was determined by examining the plates under a light microscope to determine if oospores had formed at the interface of the two colonies.

To determine the sensitivity of isolates to the fungicide mefenoxam, agar plugs from the edge of actively expanding single-zoospore colonies were placed at the center of 100 × 15 mm UCV8 plates amended with 0 or 100 ppm mefenoxam (Ridomil Gold EC, Novartis, Greensboro, NC; 48% AI, suspended in SDW; added to UCV8

cooled to 49°C). Inoculated plates were incubated at 23 to 25°C for 3 days, and colony diameters were measured. Percent growth of an isolate on amended media was calculated by subtracting the inoculation plug diameter (7 mm) from the diameter of each colony and dividing the average diameter of the colony on amended plates by the average diameter of the colony on unamended control plates. All tests were conducted at least twice to determine if isolates consistently fell into the same mefenoxam sensitivity category and had the same compatibility type. An isolate was scored as sensitive (S) if growth at 100 ppm was <30% of the control, intermediately sensitive (IS) if growth was between 30 and 90% of the control, and insensitive (I) if growth was >90% of the control (10).

DNA extraction and amplified fragment length polymorphism (AFLP) fingerprinting. Bacterial contamination was avoided by using a modified Van Teigham cell (3). The uppermost portion of a 7-mm plug of mycelium was placed onto the surface of RA-WA plates (rifampicin 30 ppm, ampicillin 100 ppm, 1,000 ml distilled water, and 16 g agar), and an autoclaved cap from a 1.5-ml microfuge tube was placed over the plug, which forced the isolate to grow through the amended medium. Isolates were incubated in the dark for 2 to 3 days before two 7-mm plugs were transferred to approximately 15 ml of RA-UCV8 broth in 100 × 15 mm petri dishes and incubated in the dark for 3 days at 23 to 25°C. Mycelial mats were washed with distilled water and dried briefly under vacuum before being frozen to -20°C and lyophilized.

Lyophilized mats were ground with a sterile mortar and pestle. Whole genomic DNA from approximately 50 mg of ground mycelium was extracted using a QIAGEN DNeasy Plant Mini Kit (QIAGEN Inc., Valencia, CA) according to the manufacturer's directions. DNA was quantified using Nucleic Acid QuickSticks (CLONTECH, Palo Alto, CA) according to the manufacturer's directions or on 1.5% agarose gels. Approximately 100 ng of DNA was then subjected to a restriction/ligation reaction, preselective amplification, and selective amplifications using the polymerase chain reaction (PCR) core mix, adaptor sequences, core primer sequences, and fluorescence labeled primers provided in the AFLP Microbial Fingerprinting Kit (Perkin-Elmer Corp., Foster City, CA) and performed exactly as described in the PE/ABI AFLP Microbial Fingerprinting protocol part no. 402977 Rev A (20). All PCR reactions were performed using an MJ Research Minicycler (MJ Research Inc., Waltham, MA) in 0.2-ml tubes according to the cycling parameters outlined in the microbial fingerprinting protocol.

An initial optimization set of reactions was performed using preselective products from isolate OP97 of *P. capsici*, which was

isolated from a cucumber fruit in 1997 (10). Amplifications with the selective primers *EcoRI*-AA, AC, AG, and AT were performed in all 16 combinations with the *MseI*-CA, CC, CG, and CT selective primers. *EcoRI* selective primers were labeled at the 5' end with either carboxyfluorescein (FAM), carboxytetramethylrhodamine (TAMRA), or carboxy-4',5'-dichloro-2',7'-dimethoxyfluorescein (JOE) fluorescent dyes. The fluorescent dyes were excited by laser radiation and visualized by their characteristic absorption-emission frequencies. Only the fragments containing an *EcoRI* restriction site were resolved.

Selective amplification AFLP products and a carboxy-X-rhodamine (ROX) size standard were loaded into each lane on a denaturing polyacrylamide gel and the fragments resolved in an ABI Prism 377 DNA Sequencer. Results were prepared for analysis in the form of electropherograms using GeneScan Analysis software (PE/ABI). AFLP fragments were scored manually as present = 1 or absent = 0 using Genotyper (PE/ABI). Only DNA bands that consistently exhibited unambiguous presence/absence profiles were scored.

In order to assess the reproducibility of AFLP profiles, isolate OP97 was subjected to the aforementioned protocol using three optimal primer pair combinations on three separate occasions approximately 3 months apart.

AFLP fragments for each field isolate were scored for presence or absence, and the binary data matrix was converted to a similarity matrix with the program NTSYSpc version 2.02k (Applied Biostatistics Inc., Exeter Software, Setauket, NY). Unweighted pair group method with arithmetic averages (UPGMA) cluster analysis was performed on the similarity matrix, and a tree was generated. Isolates with identical profiles were considered to be clones and, except for a single representative isolate, were excluded from population genetic analysis (14).

Genetic analysis. Sample sets collected from single fields during a single year were considered a population. Populations were assumed to be in Hardy-Weinberg equilibrium, and each AFLP locus was assumed to be di-allelic and selectively neutral. As reported previously, analysis of segregation patterns supports these assumptions (12). The program "Tools for population genetic analysis" (TFPGA) (M. P. Miller, Northern Arizona University, Flagstaff) was used to assess genetic diversity within each population on the basis of estimated average heterozygosity (15) and the proportion of polymorphic loci at the 95% level (5), and to calculate pairwise and overall fixation indices (*F* statistics) according to the methods of Weir and Cockerham (21). Confidence intervals for *F* statistics at the 95% confidence level were generated by bootstrapping using 1,000 iterations. Estimates of the percentage of polymorphic loci and estimated average heterozygosity

were calculated based on the 68 AFLP markers resolved.

Using the program NTSYSpc, the combined 0/1 data matrix for isolates from the isolates presented here, as well as >500 isolates from Michigan described previously (12), was used to construct a genetic similarity matrix of all possible pairwise comparisons of individuals within and among populations using Jaccard's similarity coefficient: $GS(ij) = a/(a + b + c)$. $GS(ij)$ is the measure of genetic similarity between individuals i and j , where a is the number of polymorphic bands shared by i and j , b is the number of bands present in i and absent in j , and c is the number of bands present in j but absent in i . A tree was constructed using UPGMA cluster analysis to provide a graphic representation of the relationships among isolates.

Genetic structure was also examined by analysis of molecular variance (AMOVA) using the ARLEQUIN software package (L. Excoffier, University of Geneva, Geneva, Switzerland). The AMOVA analysis was used to partition the variance in banding patterns within and among the populations. Significance values were assigned to variance components on the basis of a set of null distributions generated by a permutation process which randomly assigned individuals to populations and drew 1,000 independent samples.

RESULTS

Disease symptoms and isolate recovery. In 1998, 141 isolates of *P. capsici* were recovered from infected cucumber fruit. Phenotypic characterization of all 141 isolates and genetic characterization of 57 isolates has been reported previously (10,12). Here we report only on the 57 isolates characterized genetically. At the time of harvest in 1998, the majority of the cucumber fruit present in this field had obvious signs and symptoms of disease ranging from discrete water-soaked lesions to being entirely covered with a white, powdery layer of sporangia. Plants appeared to be healthy with no symptoms of disease on the foliage, vines, or stems. Close inspection indicated that less than 5% of the plants scattered throughout the field were stunted.

In 2001, 47 isolates of *P. capsici* were recovered from infected tomato plants. The

most frequent aboveground symptom on tomatoes infected with *P. capsici* was stunting with crown or root rot lesions present. A small number of the infected plants showed wilt symptoms. Foliar lesions were not observed. Plants were sampled prior to fruit set, and the incidence of fruit infection was not determined. Infected plants often had a brown, crumbly epidermis from the soil line to the taproot and a significant reduction in feeder roots. Often, there was a black lesion beneath the epidermis from the soil line to the taproot. In some cases, plants with infected taproots had numerous adventitious roots above the point of infection.

Sensitivity to mefenoxam, compatibility type, and AFLP diversity. The percentages of isolates falling into the three mefenoxam sensitivity categories were 40 and 44% sensitive, 56 and 38% intermediately sensitive, and 4 and 18% insensitive for 1998 and 2001, respectively (Table 1). The ratio of A1:A2 isolates was 29:21 in 1998 and 21:22 in 2001 (Table 1). These numbers approximate the 1:1 ratio expected for a randomly outcrossing diploid organism. Repeated tests of the isolates gave identical results, with isolates unambiguously reacting as A1 or A2 compatibility types and assigned to the same mefenoxam sensitivity categories.

The *EcoRI* + *AC/MseI* + *CA* primer combination described previously was used

to amplify genomic DNA from all isolates in both the 1998 and 2001 sample sets (11,12). This primer combination resulted in 68 clearly resolved fragments, of which 42 were polymorphic in 1998 and 45 were polymorphic in 2001 (Table 2). All 68 fragments were present in both 1998 and 2001, and no novel fragments were detected among years.

In 1998, there were five clonal lineages detected, with three lineages comprised of two members and two lineages with three isolates each. In 2001, there were four clonal lineages detected with two members each. Clonal lineages detected in 1998 were not detected in 2001.

Temporal changes in AFLP diversity. The fixation index (Φ_{ST}) among the populations of *P. capsici* recovered in 1998 and 2001 was 0.05 with a standard deviation of 0.01. This indicates very little genetic differentiation, or loss of heterozygosity, occurred between years at this location. The number and identity of bands that were polymorphic at the 95% level and the estimated average heterozygosity (0.17 for both years) remained similar over time (Table 2). AMOVA analysis partitioned 3% of the total variability between years, indicating that 97% of the variation found in 1998 was also found in 2001 (Table 3). UPGMA analysis showed that unique genotypes were between 76 and 96% similar and that isolates from 1998 and 2001

Table 2. Estimates of genetic diversity within populations of *Phytophthora capsici* recovered from cucumbers (1998) and tomatoes (2001) planted at the same location in south central Michigan

Year	No. isolates	No. unique isolates ^a	No. AFLP bands	No. polymorphic bands (%)	Est. avg. heterozygosity
1998	57	50	68	42 (62)	0.17
2001	47	43	68	45 (66)	0.17

^a Isolates with unique multilocus amplified fragment length polymorphism (AFLP) profiles.

Table 3. Results of nested analysis of molecular variance (AMOVA) for isolates of *Phytophthora capsici* based on 68 amplified fragment length polymorphism (AFLP) markers^a

Source of variation	df	Sum of squares	Variance component	Percentage of variation	<i>P</i> ^b
Among populations	1	17.676	0.232	3.40	<0.0001
Within populations	67	618.386	6.578	96.60	

^a Variance is partitioned between isolates recovered in 1998 (N = 50) from cucumbers and in 2001 (N = 43) from tomatoes at the same location in south central Michigan.

^b *P* = the probability of obtaining a more extreme component estimate by chance alone based on 1,000 sampling realizations.

Table 1. Phenotypic diversity of isolates of *Phytophthora capsici* recovered from cucumbers (1998) and tomatoes (2001) planted at the same location in south central Michigan

Year	No. isolates ^a	Compatibility type/mefenoxam sensitivity ^{b,c}					
		A1/S	A1/IS	A1/I	A2/S	A2/IS	A2/I
1998	50	10 (0.20)	17 (0.34)	2 (0.04)	10 (0.20)	11 (0.22)	—
2001	43	7 (0.16)	10 (0.24)	4 (0.09)	12 (0.28)	6 (0.14)	4 (0.09)
Total	93	17 (0.18)	27 (0.30)	6 (0.06)	22 (0.24)	17 (0.18)	4 (0.04)

^a Total number of isolates with unique multilocus amplified fragment length polymorphism (AFLP) profiles.

^b Sensitivity determined by in vitro screening on amended media with 100 ppm AI mefenoxam where S = <30% growth of control (GC), IS = between 30 and 90% GC, and I = >90% GC.

^c Observed numbers are followed by proportion of total sample size in parentheses.

were dispersed randomly throughout the tree (Fig. 1). When the isolates from this location were similarly analyzed with more than 500 isolates of *P. capsici* from six other locations in Michigan, the isolates clustered discretely based on location (data not shown). Although it was clear that the isolates from the south central Michigan location presented here were more similar to each other than to isolates from other locations in Michigan, there was no grouping of isolates based on year when comparing isolates recovered in 2001 to those recovered in 1998 (Fig. 1).

DISCUSSION

This is the first report of *P. capsici* on tomato in Michigan and the first study investigating the survival of *P. capsici* in the field following a typical 2-year crop rotation (2 years of production with crops not susceptible to *P. capsici*) using molecu-

lar tools. Our objectives were to investigate the potential for dormant inoculum to survive a 30-month nonhost period and to determine whether insensitivity to mefenoxam in this population could be a factor in tomato disease management. In Michigan, land suitable for vegetable production without a history of *P. capsici* infestation is becoming increasingly scarce, and determining how long *P. capsici* can survive dormant is important to the future profitability of many vegetable production farms. Research in California suggests that mefenoxam should be helpful in combating Phytophthora blight of tomatoes (6), but cucurbit crops in Michigan have been lost despite mefenoxam applications (11), and the usefulness of mefenoxam on tomatoes in Michigan may be compromised at some locations due to the increase of insensitive isolates.

The population of *P. capsici* recovered from processing tomatoes in 2001 was very similar to the population recovered from cucumber in 1998. Both populations had a similar ratio of A1 and A2 compatibility types, similar proportions of isolates insensitive to mefenoxam, and very similar pools of genetic diversity based on AFLP analysis. If the isolates of *P. capsici* recovered from tomato in 2001 survived in the soil as oospores generated during the epidemic on cucumber in 1998, then we would expect to see (i) both the A1 and A2 compatibility types in a 1:1 ratio, (ii) similar or increased proportion of isolates insensitive to mefenoxam, (iii) a similar pool of polymorphic AFLP markers, (iv) multiple unique genotypic combinations, and (v) no members of the same clonal lineage persisting over time.

All five of the above expectations were achieved. Within each population there

Fig. 1. Unweighted pair group method with arithmetic averages (UPGMA) cluster analysis of isolates of *Phytophthora capsici* recovered from cucumbers (1998, $N = 50$) and tomatoes (2001, $N = 43$) at the same location in south central Michigan based on the Jaccard similarity coefficient using 68 amplified fragment length polymorphism (AFLP) markers. The ratio of isolates recovered in 1998 (cucumber) to the number recovered in 2001 (tomato) within subclusters is indicated at major branch points.

was a 1:1 ratio of the A1:A2 compatibility types, which has been found in the majority of populations of *P. capsici* examined in Michigan (12). The number of isolates falling into the six possible mefenoxam sensitivity/compatibility type categories was similar between the 2 years, with an increase in the proportion of fully insensitive isolates from 4% in 1998 to 18% in 2001, which is expected for a population under mefenoxam selection pressure (11). Pools of AFLP fragments resolved in each population were identical, and frequencies of the polymorphic AFLP markers recovered in 1998 were very similar to those recovered in the 2001 populations. This overall similarity is reflected by the low fixation index, similar estimated average heterozygosities, and the random clustering of isolates in the genetic similarity tree. The majority of the isolates (89%) had unique genotypes, and clones recovered in 1998 were not recovered in 2001. These results support the hypothesis that the isolates of *P. capsici* recovered at this location are part of the same outcrossing population. Long-distance dispersal of *P. capsici* within Michigan does not appear to be a significant factor.

Mefenoxam sensitivity and AFLP data from >500 isolates of *P. capsici* recovered between 8 and 265 km away during the same time period indicate that the population residing at this location is reproductively isolated (12). The isolates presented here had only 68 of the 94 possible AFLP markers reported for Michigan isolates of *P. capsici*. Proportions of isolates insensitive to mefenoxam were also distinctive because isolates of *P. capsici* from six other locations were either predominantly sensitive or insensitive to mefenoxam, whereas the isolates at this location were mostly intermediately sensitive to mefenoxam (12). The low level of differentiation ($\Phi_{ST} = 0.05$) between the isolates recovered from cucumber in 1998 and tomato in 2001 is consistent with the high similarity of populations of *P. capsici* re-

covered from other sites in Michigan sampled over more than 1 year and not associated with a rotation to nonsusceptible hosts (12).

In this study, *P. capsici* survived as oospores for a 30-month nonhost period, and 58% of the genotypically unique isolates were either intermediately sensitive or insensitive to mefenoxam. These results indicate that management strategies that rely wholly on crop rotation and mefenoxam may not provide economic control of *P. capsici* on tomatoes in Michigan.

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