ORIGINAL ARTICLE

Population structure of *Phytophthora capsici* in the state of Tennessee

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Abstract

The plant pathogen *Phytophthora capsici* can be found all throughout the USA, and the population genetics of this organism have been studied within many of these states. Until now, no work has been done in the state of Tennessee to investigate the population structure and genetics of *P. capsici* found there. The population structure of *P. capsici* was explored using 296 isolates collected from five counties in Tennessee in 2004, 2007, 2018, and 2019. Samples were genotyped using 39 single nucleotide polymorphism (SNP) genetic markers. Multiple analyses indicate that the population structure of *P. capsici* in Tennessee exists in isolated clusters structured by geography. Geographically separate populations were genetically distinct, suggesting there is limited or no outcrossing among populations, but there is significant sexual reproduction occurring within populations. These findings corroborate previous studies of *P. capsici* throughout the midwestern and northeastern USA, where populations are generally sexually reproducing and structured by geography. This study provides the first characterization of *P. capsici* population structure in Tennessee.

Keywords Oomycetes · SNP · Multi-locus genotyping · Population genetics

Introduction

Phytophthora blight of cucurbits and pepper is caused by the oomycete *Phytophthora capsici* and was first reported on pepper in the state of New Mexico in 1922 (Leonian 1922). The pathogen is now distributed across the USA and throughout the world (Gobena et al. 2012a; Hu et al. 2013). This disease can be devastating to the production of many vegetables such as pumpkin, squash, cucumbers, and peppers (Hausbeck and Lamour 2004; Granke et al. 2012). Symptoms of this disease include plant wilt, crown rot, stem rot, and fruit rot and can lead to complete crop loss. Phytophthora blight is a very challenging disease to manage primarily because of how it reproduces and is spread.

Infestation of a field may start with a very small number of asexual spores known as zoospores. One infected fruit may contain millions of sporangia, each filled with 20 to 40 zoospores which are released in the presence of water.

Once infection of a new host occurs, the asexual cycle is repeated, leading to rapid dispersal of inoculum throughout a site, especially when a rain event or irrigation occurs. This means that a few genotypes may rapidly proliferate to dominate a field (Lamour and Hausbeck 2001b). If these individuals are fit and carry advantages such as fungicide resistance, an entire field of crops could be lost even with an organized plan of cultural and chemical control. In some parts of the world, such as China and Argentina, large portions of farmland are dominated by a few clonal populations (Gobena et al. 2012a; Hu et al. 2013). This is explained by mild or warm fallow seasons where zoospores are not killed by freezing winter temperatures. Contrary to that scenario, there is no evidence that these clonal populations survive from year to year through winter in the midwestern, northeastern, and southeastern USA (Dunn et al. 2010; Granke et al. 2012). In these areas, persistence of *P. capsici* is due to the production of oospores (Lamour and Hausbeck 2001a).

Phytophthora capsici is a heterothallic organism and has two mating types, A1 and A2. When opposite mating types come into contact, sexual reproduction can occur resulting in oospore formation. Oospores are thick-walled sexual spores that serve as overwintering structures, which contribute to reemergence of disease from year to year, and can remain viable in fallow soil for more than 5 years (Lamour

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and Hausbeck 2003). Additionally, there is the potential for formation of asexual survival spores, known as chlamydospores. Although these are uncommon in nature, chlamydospores can enable clonal lines to persist from year to year (Islam et al. 2005). The spread of these three types of propagules from one field to another occurs primarily by two methods: surface waterways and human transmission (Ristaino et al. 1993; Gevens et al. 2007). In large rain events, runoff from infested fields may spread to nearby fields, either across the soil surface or through a connecting watershed, such as an irrigation stream (Gevens et al. 2007). This can lead to the introduction of zoospores into new fields downstream of the primary infection. Humans can move these propagules through transport of infested soil on farm equipment, tools, and boots. Additionally, the spread of infected fruit and potentially seeds can lead to introduction to new locations. These methods occur over relatively short distances and require a significant mechanical force to enable spread and do not allow for even spread across very large areas of land, especially when compared with the wind transmission of other oomycetes such as *Phytophthora infestans* (Fry 2008; Granke et al. 2009). These modes of reproduction and spread of propagules influence the population structure within and among populations in a region (Granke et al. 2009; Campbell and Ristaino 1999).

The population genetics of *P. capsici* has been a focus of many studies that began with the collection of isolates from specific locations or regions of interest. In these previous studies, isolates were genotyped using various genetic markers such as microsatellites (simple sequence repeats or SSRs), amplified fragment length polymorphisms (AFLPs), or single nucleotide polymorphisms (SNPs) (Dunn et al. 2010; Hu et al. 2013; Gobena et al. 2012a; Castro-Rocha et al. 2017). Information gained in such studies can provide insight into how *P. capsici* is spread throughout a region, what degree of gene flow there may be between locations, and whether populations are primarily reproducing clonally or sexually. From these types of studies, three primary population structures have been observed: widespread clonal populations, isolated sexual populations, and outcrossing sexual populations (Dunn et al. 2010; Hu et al. 2013; Gobena et al. 2012a; Castro-Rocha et al. 2017). These structures are greatly influenced by various factors such as weather, geography, agricultural practices, and regional crop history. Given this, it is important to treat each region differently and to avoid inferring the population structure of one location solely based on the observations of another. Little is known about the population genetics of *P. capsici* in Tennessee. The goals of this study were to (i) identify mating types of *P. capsici* isolates collected in Tennessee to determine A1:A2 mating-type ratios; (ii) identify multi-locus genotypes (MLGs) and compare diversity of these between sampling locations; (iii) determine if significant differences exist among populations; and (iv) document the structure of the populations to

determine if sampling locations are genetically similar or significantly different.

Materials and methods

Sample collections

In 2018 and 2019, samples of pumpkin, squash, zucchini, and pepper showing signs or symptoms of *P. capsici* infection were collected from farms in five counties in middle and eastern Tennessee and taken to the laboratory for processing. In 2018, cuttings of lesions were surface sterilized using a 0.5% sodium hypochlorite solution, rinsed with sterile distilled water, and plated onto PARP-H medium (17 g cornmeal agar, 0.4 ml pimaricin solution (25 mg/ml), 250 mg ampicillin, 1 ml rifampicin solution (10 mg/ml), 5 ml PCNB solution (5 mg/ml), and 2 mg hymexazol per 1 L) (Ferguson and Jeffers 1999). Plated samples were stored at ~24 °C in the dark for 1 to 2 days. From samples with mycelial growth, hyphal tip transfers were plated onto additional PARP-H medium. All cultures were re-isolated as single-zoospore isolates (2018) or hyphal tip transfers (2019) and stored following the methods of Siegenthaler and Hansen (2021). A total of 222 isolates of *P. capsici* were obtained from samples collected in 2018 and 2019. Additionally, data from 74 historical isolates, which were collected from one farm in Grainger County Tennessee in 2004 and 2007, were also included in the study. A total of 296 isolates were genotyped in the study. Ninety-two isolates were from Rhea County, TN, 49 from Bledsoe County, 43 from Putnam County, 38 from Lincoln County, and 74 from Grainger County (Table 1, Fig. 1).

Preparation for DNA extraction

A small amount of hyphal material was collected from each 2018 single-zoospore isolate and used to inoculate PARP-H broth aliquoted into a 24-well plate. Each plate was covered with a breathable sealing film and left to incubate at ~24 °C. Plates were agitated twice daily for 5 to 7 days or until a mycelial mat formed on top of the broth. Mycelia were then transferred into 96-well bead mill plates containing glass beads and stored at –20 °C until further processing. For 2019 isolates, samples of infected plant tissue used for isolation were taken directly from lesions and placed into 96-well bead mill plates. Plates were stored in a –20 °C freezer until further processing.

Mating type

Mating types of all isolates were determined during the same year they were collected using previously described methods (Siegenthaler and Hansen 2021). Briefly, a 5-mm plug of each isolate with an unknown mating type was plated onto clarified

Table 1 Collection information, genotypic diversity statistics, and mating type of *Phytophthora capsici* populations from Tennessee collected in 2004, 2007, 2018, and 2019

Pop ^a	N ^b	MLG ^c	eMLG ^d	λ^e	λC^f	G ^g	Mating type		χ^{2h}	P ⁱ	Collection date
							A1	A2			
R18	20	18	17	0.94	0.98	16.6	14	10	0.67	ns	8/9/2018
R19	72	56	17	0.97	0.90	43.9	30	46	3.37	ns	8/31/2019
B18	19	10	10	0.83	0.87	5.9	7	13	1.8	ns	9/7/2018
B19	30	3	2	0.32	0.33	1.4	32	0	32	0.001	10/11/2018
P18	43	10	6	0.73	0.75	3.7	14	29	5.23	0.05	8/31/2018 and 11/16/2018
L19	38	21	13	0.93	0.96	15.7	14	23	2.19	ns	9/12/2019
G04	23	19	16	0.93	0.97	15.1	17	6	5.26	0.05	2004 ^j
G07	51	50	18	0.98	0.99	49.0	26	25	0.02	ns	2007 ^j
Total	296	187	-	-	-	-	154 ^k	152 ^k	0.01	ns	-

^aPopulations are labeled with a single letter signifying the collection county followed by collection year: R Rhea, B Bledsoe, P Putnam, L Lincoln, and G Grainger

^bNumber of isolates collected from each county and year

^cNumber of multi-locus genotypes (MLGs) per county and year

^dThe number of expected MLGs at the smallest sample size ≥ 10 based on rarefaction

^eSimpson's index (Simpson 1949)

^fSimpson's index (Simpson 1949), adjusted for sampling size

^gStoddart and Taylor's index of MLG diversity (Stoddart and Taylor 1988)

^hChi-square statistic testing whether mating types at each site are 1:1

ⁱSignificance of chi-square test: ns indicating mating-type ratio does not significantly deviate from 1:1

^jExact collection dates are unknown

^kMating type totals include data from isolate which were not genotyped for this study

V8 with another 5-mm plug of an isolate of a known mating type. Plates were incubated for 5 to 7 days, and then viewed under a compound microscope to look for oospores. The presence of oospores indicated that the unknown isolate's mating type was compatible with (i.e., the opposite of) the known isolate's mating type.

DNA extraction

Mycelium or plant tissue was freeze-dried in the 96-well bead plate and processed to a fine powder using a Mixer Mill (Qiagen, Germantown, MD, USA). The powder was processed using a MagMAX DNA Multi-Sample Ultra 2.0

Kit according to the manufacturer's directions (Thermo Fisher, Waltham, MA, USA) and the resulting DNA quantified using a Qubit device according to the manufacturer's directions (Thermo Fisher, Waltham, MA, USA).

PCR and sequencing

Approximately 1000 ng of DNA for each sample was submitted to Floodlight Genomics LLC (Knoxville, TN, USA) for targeted sequencing. Thirty-nine SNP markers were amplified from the nuclear genome using different species-specific primers for each site as described previously (Castro-Rocha et al. 2017). These were processed using an optimized

Fig. 1 Map of Tennessee and the locations isolates were collected from in 2004, 2007, 2018, and 2019

Hi-Plex approach, which includes multiplex PCR amplification of each sample and sequencing of the targets using the Illumina HiSeq X platform. Floodlight Genomics delivered sample-specific raw sequence reads.

Sequence alignment and variant calling

The sample-specific reads were aligned to their target sequences using CLC Genomics Workbench version 9.5.3 using default settings. Variant sites were assessed using the quality-based variant detection (QVD) workflow with settings to require at least 40X coverage. The QVD settings are as follows: neighborhood radius = 5, maximum gap and mismatch count = 2, minimum neighborhood quality = 15 and minimum central quality = 20 with minimum coverage = 40, minimum variant frequency = 25%, minimum expected alleles = 2, and standard genetic code. Variant Call Format (VCF) sheets were produced for each sample and processed in Excel (Microsoft) to extract the genotypes for further downstream analyses. Loci were considered heterozygous if the alternate allele had a frequency of at least 25%.

Data analyses

Genetic data were analyzed using the excel plugin GENALEX 6.5, R version 3.6.1 (R Core Team 2019) and the R package Poppr version 2.8.6 (Kamvar et al. 2014, 2015). GENALEX 6.5 was used to format the data so it could be read and made an object within R and for calculating pairwise F_{ST} population comparisons. Hardy–Weinberg equilibrium was assessed using the function `hw.test` from the ‘`pegas`’ package (Paradis 2010). Using Poppr, the number of multi-locus genotypes (MLGs) per sampling location and year were identified. Isolates sharing MLGs were considered clones and data were clone corrected to account for these. To further understand the overall diversity of the samples collected in TN, Simpson’s index and Stoddart and Taylor’s index were calculated (Simpson 1949; Stoddart and Taylor 1988). Data were also analyzed by discriminant analysis of principal components (DAPC). In the DAPC, populations were assigned by county and year as predefined inputs. Following the protocol described in the Poppr primer, developed by Kamvar et al., a DAPC cross validation was performed with 1000× replication and an optimal number of principal components to be retained were 20, as well as retaining 500 discriminant components (DC). The results from the DAPC cross validation were then plotted as a scatter plot. A minimum spanning network (MSN) was constructed to compliment the findings from the DAPC. This MSN was developed using the interactive tool provided through Poppr using Provesti’s genetic distance. To detect population differentiation, analysis of molecular variance

(AMOVA) was performed with additional significance testing through randomization tests (Excoffier et al. 1992).

Results

Genetic diversity

A total of 187 unique multi-locus genotypes (MLGs) and 109 repeated MLGs were identified (Table 1). One MLG was shared between two locations, Bledsoe 2018 (B18) and Putnam 2018 (P18). No MLGs that were found in any 2018 population were detected in 2019. Populations from Rhea 2018 (R18), Rhea 2019 (R19), Lincoln 2019 (L19), Grainger 2004 (G04), and Grainger 2007 (G07) contained the majority of these unique MLGs and were more diverse than Bledsoe 2018 (B18), Bledsoe 2019 (B19), and Putnam 2018 (P18). The disparity in genotypic diversity is reflected in the Stoddart and Taylor’s index and Simpson index values calculated for each population, where R18, R19, L19, G04, and G07 all have indices that are much greater than that of B18, B19, and P18 (Table 1).

Mating types and Hardy–Weinberg equilibrium

In all populations excluding B19, P19, and G04, the A1:A2 ratios did not differ significantly from 1:1. B19 was the only population that did not have isolates of both mating types. In a population-wise comparison of Hardy–Weinberg equilibrium (HWE) statistics for all 39 loci and the eight populations, approximately 30% of loci significantly departed from the expectations HWE (Fig. 2).

Population structure

Discriminant analysis of principal components (DAPC) grouped most isolates from the same county and the same year together. Isolates collected from the same county, but different year, were genetically similar as shown by the R19 and R18 or the G04 and G07 clusters (Fig. 3). DAPC indicated that isolates that were geographically different are also genetically different. Similarly, geographically similar isolates have more genetic similarities. This suggests that the general population is structured by geographic location and that each sampling location is distinct from one another. The minimum spanning network (MSN) supports this result by illustrating that, in general, isolates from different counties are genetically distant from one another (Fig. 4). In a pairwise comparison of F_{ST} statistics, all populations were statistically different at P value < 0.05, including isolates collected within the same field but in different years. Isolates collected within the same field in different years did have lower F_{ST} values

Fig. 2 Heatmap of population-wise P value comparisons of Hardy-Weinberg statistics between Tennessee *P. capsici* populations and SNP markers. Rows (y-axis) represent *P. capsici* populations in TN and columns (x-axis) represent the 39 SNP markers used in the study. All loci marked with pink are suspected of not being in HWE

with $P \leq 0.05$. Population abbreviations are written as the county where isolates were collected followed by the year of collection, where G=Greene County, B=Bledsoe County, P=Putnam County, R=Rhea County, and L=Lincoln County

such a 0.03 for R18 and R19, compared to 0.46 for B19 and L19 (Table 2). The analysis of molecular variance (AMOVA) also supports these results, where a significant amount of variation was detected between populations (17%, $P=0.001$) and within populations (83%, $P=0.001$) (Table 3).

Discussion

Our analysis indicates that populations of *P. capsici* in Tennessee are genetically isolated. This is similar to a study by Dunn et al., 2012, where populations of *P. capsici* throughout New York were genetically diverse and clustered by geographic location. Quesada-Ocampo et al.

(2011) and Lamour and Hausbeck (2001b) also found that *P. capsici* populations were structured by geographic location and were clearly distinct from one another. This trend has also been observed in Mexico, where Castro-Rocha et al. (2016) reported a high proportion of unique MLGs and little gene flow between locations. This contrasts with other studies where there was evidence of out-crossing populations with significant numbers of shared clonal genotypes across farms in Massachusetts and Long Island, New York (Gobena et al., 2012b; Castro-Rocha et al., 2017). Like these studies, we identified isolates of both mating types A1 and A2, providing evidence of sexual reproduction within most Tennessee populations of *P. capsici*. *Phytophthora capsici* is not dispersed long distances by air (Granke et al. 2009). Therefore, genotypes

Fig. 3 Discriminant analysis of principal components (DAPC) of all *P. capsici* isolates collected in 2004, 2007, 2018, and 2019. Rhea 2019 (R19), Lincoln 2019 (L19), Bledsoe 2019 (B19), Rhea 2018 (R18), Putnam 2018 (P18), Bledsoe 2018 (B18), Grainger 2007 (G07), and Grainger 2004 (G04)

Fig. 4 Minimum spanning network of Tennessee *P. capsici* populations constructed using the Provesti's distance

POPULATION

- R19
- L19
- B19
- R18
- P18
- B18
- G07
- G04

generally have a limited geographic distribution in the absence of another dispersal mechanism, like surface water. The distance separating populations in our study explains why the populations were genetically distinct. Our collection sites were separated by approximately 180 to 275 km, except for Bledsoe and Rhea Counties which are adjacent. The distance separating collection sites reduces the likelihood of genotypes being shared across sampling locations. Although Bledsoe and Rhea Counties are adjacent, the sampling sites were not adjacent farms and were not directly connected by surface waterways.

This is in contrast to the study by Gobena et al. (2012b), where clonal genotypes were readily detected at multiple sampling sites, but all sampling sites were either adjacent farms or within 25 km of each other. The authors suggest that there is likely significant local spread via surface water in the eastern end of Long Island, New York.

Populations P18 and B19 had significantly lower MLG diversity than other regions and contained large numbers of clonal genotypes. This was reflected by the mating-type ratios of these populations, which were highly skewed to A1 or A2, rather than the expected 1:1 ratio for a sexually

Table 2 Pairwise comparison of F_{ST} values of *Phytophthora capsici* populations sampled from eight counties in Tennessee from 2004, 2007, 2018, and 2019

F_{ST} values							
Populations ^a	R19	L19	B19	R18	P18	B18	G04
R19	0						
L19	0.24	0					
B19	0.17	0.46	0				
R18	0.03 ^b	0.27	0.23	0			
P18	0.16	0.34	0.37	0.19	0		
B18	0.13	0.20	0.30	0.11	0.22	0	
G04	0.14	0.24	0.33	0.17	0.23	0.13	0
G07	0.20	0.23	0.37	0.21	0.27	0.16	0.07

^aPopulations are labeled with a single letter signifying the collection county followed by collection year: R Rhea, B Bledsoe, P Putnam, L Lincoln, and G Grainger

^b F_{ST} values were calculated in GenAlex 6.5 with distances between populations based on AMOVA of each population. All values were significantly different from zero at $P < 0.001$, using 999 permutations, unless indicated otherwise

Table 3 Analysis of molecular variance (AMOVA) for clone-corrected samples of *Phytophthora capsici* from Tennessee collected in years 2004, 2007, 2018, and 2019

Source of variation	df	Sum of squares	Variance components	Percentage of variation	<i>P</i> value ^a
Between populations	7	905	2.71	17	0.001
Within populations	187	2490	13.31	83	0.001

^a*P* values based on randomized significance testing performed to test the significance of the variance components

reproducing population. This is likely explained by the seasonal cycle of *P. capsici* reproduction and spread. In Tennessee, where winter temperatures reach freezing, *P. capsici*'s asexual spores do not survive from one growing season to another, except when chlamydospores are produced, which is uncommon (Islam et al. 2005). Therefore, oospores are the primary inoculum and, following infection, asexual sporangia and zoospores are responsible for secondary disease spread. Similar patterns were found by Gobena et al. (2012b). As the season progresses, fit genotypes dominate a field, and the observable genetic diversity decreases. This is reflected in the populations P18 and B19, where isolates were collected later in the growing season, after harvest, when only culls and late-ripening fruit were left in the field. This is the most likely explanation for the lack of diversity given there was no evidence of clonal genotypes persisting from 2018 to 2019. These results contrast those found in places such as China and Argentina, where large clonal populations persist from year to year (Hu et al. 2013; Gobena et al. 2012a). These locations have mild or warm fallow seasons, allowing for the persistence of clonal genotypes, in contrast to the freezing temperatures of Tennessee winters.

One unexpected result was that one MLG was shared between two counties that were geographically distant. This MLG was found five times across the state, with four from P18 and one from B18. Even if the two populations are descended from a single founder population, the possibility of finding the same genotype at both locations could only be explained through the movement of plant material, soil, or water. This seems unlikely given the large amount of geographic distance between locations, but this cannot be ruled out. Most likely, this event is explained by a labeling error somewhere in the workflow, which placed the one isolate from B18 into the P18 population.

Ultimately, this study supports and is consistent with current knowledge about *P. capsici* populations in the USA. Like Dunn et al. (2010), our results suggest that spread is limited between locations and that populations are genetically distinct. Our findings support pathogen dispersal mitigation as the most important strategy for disease management. It is imperative to limit behavior that may aide in the spread of this pathogen. Cleaning and washing equipment, tools, and boots worn by workers is important.

It is also crucial to ensure that clean seed, transplants, and irrigation water are used when growing susceptible vegetable crops (Granke et al. 2012; Jones et al. 2014). Dispersal mitigation also is important in reducing the spread of fungicide resistance, which was recently documented in Tennessee (Siegenthaler and Hansen 2021). Overall, this study provides a characterization of *P. capsici* population structure in Tennessee, and provides useful information for agricultural professionals and researchers to better understand and further explore the persistence, dispersal, and evolution of *P. capsici* in Tennessee and the southeastern USA.

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Author contribution TBS—collected isolates, conducted experiments and analyses, primary manuscript author. KL—performed isolate genotyping, organized raw genotype data, assisted with manuscript preparation. ZRH—conceived the study, assisted with data analysis and interpretation, assisted with manuscript preparation.

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Code availability Not applicable.

Declarations

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Consent for publication Not applicable.

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