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REVIEW

Phytophthora capsici, 100 Years Later: Research Mile Markers from 1922 to 2022

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Abstract

In 1922, *Phytophthora capsici* was described by Leon Hatching Leonian as a new pathogen infecting pepper (*Capsicum annuum*), with disease symptoms of root rot, stem and fruit blight, seed rot, and plant wilting and death. Extensive research has been conducted on *P. capsici* over the last 100 years. This review succinctly describes the salient mile markers of research on *P. capsici* with current perspectives on the pathogen's distribution, economic importance, epidemiology, genetics and genomics, fungicide resistance, host susceptibility, pathogenicity mechanisms, and management.

Keywords: oospores, Phytophthora blight, *Phytophthora capsici*, sporangia, zoospores

Phytophthora capsici was first observed as a pathogen of chile pepper (*Capsicum annuum* L.) in New Mexico by Leon Hatchig Leonian while working as an assistant biologist at the State Agricultural Experiment Station of the New Mexico College of Agriculture and Mechanic Arts from 1918 to 1919 (Anonymous 1919). The description of *P. capsici* by Leonian (1922) included sporangia, zoospores, tuberous mycelial outgrowths, and oospores; disease symptoms observed on roots, stems, fruit, and seeds; and isolate pathogenicity. Information on management of the new disease was limited to seed selection and fungicide application. Since the 1990s, *P. capsici* has been featured in abstracts, articles, and reviews (Babadoost and Islam 2002; Barchenger et al. 2018; Granke et al. 2012; Hausbeck and Lamour 2004; Ristaino and Johnston 1999; Saltos et al. 2022; Sanogo and Ji 2012, 2013) and book chapters (Erwin and Ribeiro 1996; Lamour 2013; Lamour and Kamoun 2008; Sanogo and Bosland 2013). The salient mile markers (Fig. 1) for 100 years of research on *P. capsici* are reviewed herein with current perspectives on the pathogen's distribution, economic importance, epidemiology, genetics and genomics, fungicide resistance, host susceptibility, pathogenicity mechanisms, and management.

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Global Economic Importance and Distribution

Phytophthora capsici affects the production of numerous annual and perennial crops grown in field and greenhouse systems (Cerkauskas et al. 2015; de Cara et al. 2018) in the Americas, Europe, Asia, Africa, and Australia (Barchenger et al. 2018; Parada-Rojas et al. 2021). Ranking among the most important pathogens of solanaceous and cucurbitaceous crops (Babadoost and Islam 2002; Barchenger et al. 2018; Hausbeck and Lamour 2004; Islam et al. 2004; Ristaino and Johnston 1999; Saltos et al. 2022; Sanogo and Ji 2012), the pathogen can cause total crop loss from root rot, stem and foliage blight, fruit rot, and plant wilting and death (Fig. 2).

Several studies have documented the occurrence and extent of *P. capsici* in various agroecosystems (Erwin and Ribeiro 1996; Lamour 2013). However, there are no data on the cost of yearly losses caused by this pathogen in each region worldwide. In Ontario, Canada, a 1997 disease outbreak caused an estimated yield loss of 40 to 60% and 20% in pepper (*C. annuum*) and butternut squash (*Cucurbita pepo* L.) fields, respectively (Anderson and Garton 2000). In New Mexico, *P. capsici* affected 80% of chile pepper fields surveyed from 2002 to 2004 (Sanogo and Carpenter 2006). *P. capsici* was discovered in North Carolina in 1948. Since 2010, more than 50 *P. capsici* samples across 32 different counties have been received by the Plant Disease and Insect Clinic at North Carolina State University (Parada-Rojas and Quesada-Ocampo 2022). When hot chile pepper fields were surveyed across three provinces in Central Vietnam from 2010 to 2018, disease incidence was estimated to be 5 to 75% (Nguyen and Van Quang Tran 2022). In South Africa, *P. capsici* was identified from solanaceous and cucurbitaceous plants collected from 77 fields in five provinces from 2000 to 2008 (Meitz et al. 2010).

In 1935, post-harvest Phytophthora rot was observed on watermelon fruit grown in Colorado and shipped to New York (Wiant and Tucker 1940). Today, Phytophthora fruit rot of watermelon is an emerging disease, especially in the Southeast United States (Kousik et al. 2014a, b, 2016). If disease occurs during fruit set, a total loss may occur; fruits are susceptible at all ages (Kousik et al. 2018). Disease outbreaks from 2003 to 2008 and 2013 to 2015 led the National Watermelon Association to rank *P. capsici* as a top research priority (Kousik et al. 2014a, 2016).

Epidemiology and Detection

The unique ability of *P. capsici* to incite economic crop loss is due, in part, to the production of sexual and asexual structures including sporangia, zoospores, and oospores (Fig. 3) enabling the pathogen to persist, disseminate, and infect. Uchida and Agaraki (1985) first documented the formation of chlamydospores by *P. capsici*. The pathogen may be naturally present in some virgin soils prior to the establishment of commercial crops (Erwin and Ribeiro 1996). Use of infested irrigation water from ponds and rivers (Gevens et al. 2007; Hudson et al. 2021) has been identified in some regions as a means of field infestation. When surface irrigation sources in Michigan were monitored over 4 years, Gevens et al. (2007)

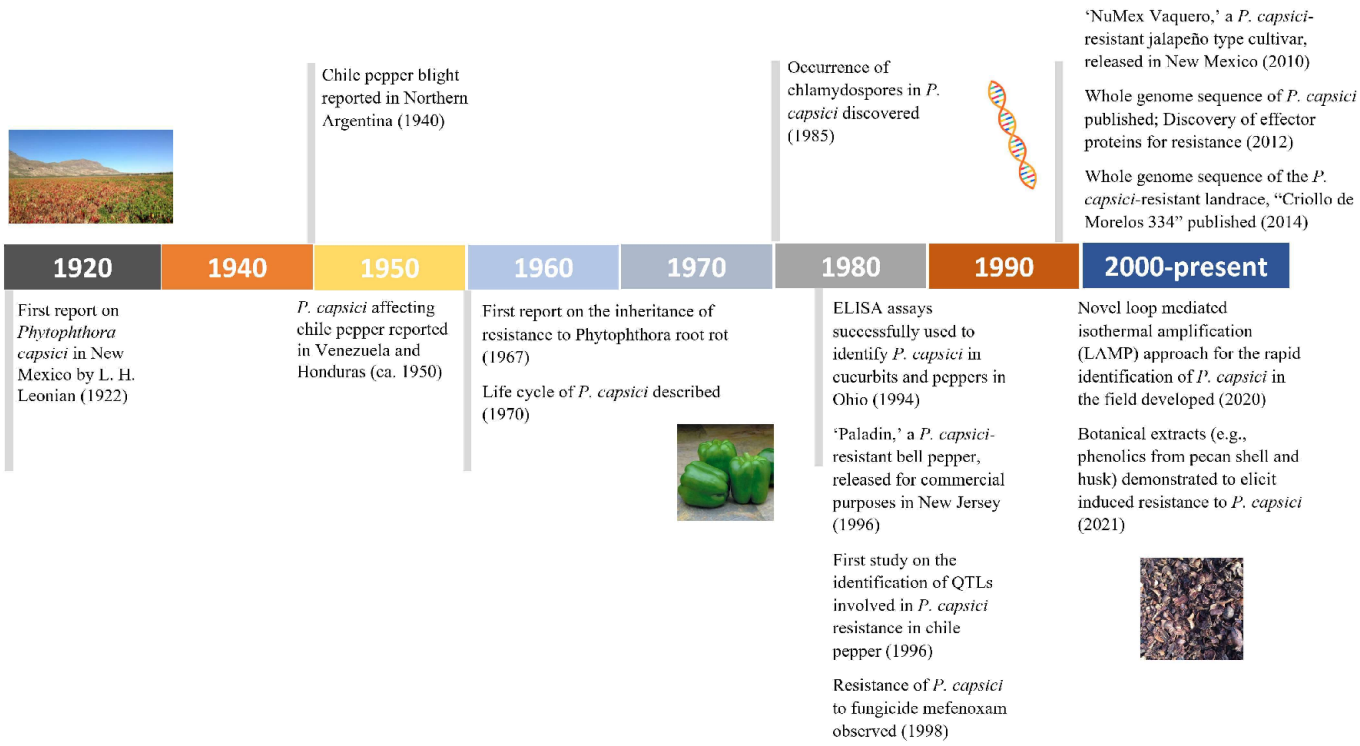

FIGURE 1
Mile markers for 100 years of research on *Phytophthora capsici*. The first report of plant infection by *P. capsici* was in chile pepper in the early 1920s by L. H. Leonian in New Mexico. Over the next couple of decades (1930 to 1950), there were numerous reports of the pathogen occurring across the Americas. Currently, *P. capsici* is a major pathogen affecting production of peppers, cucurbits, and some other vegetable crops in most growing areas of the world. Inheritance of resistance to *P. capsici* root rot and the life cycle of the pathogen were described in the late 1960s and early 1970s, respectively. Occurrence of a "resting spore" for *P. capsici* was discovered in the 1980s. The following decade marked the development of novel proteomic tools including ELISA, which was successfully used to identify *P. capsici* and the release of a resistant bell pepper. Genomic revolution between the 1990s and 2000s allowed the identification of quantitative trait loci (QTLs) and the sequencing of the whole genome of *P. capsici* and 'Criollo de Morelos 334', a resistant landrace from Mexico. Novel PCR tools such as loop-mediated isothermal amplification (LAMP) resulted in rapid determination of *P. capsici* in the field in the 2020s. Pecan husks and shells were recently demonstrated to induce disease resistance, leading the way for more efficient management practices.

detected *P. capsici* at several sites along a river system. Lewis Ivey and Miller (2013) combined species-specific PCR (Silvar et al. 2005) with cucumber baiting to detect *P. capsici* in ponds and ditches used as sources of irrigation water for vegetable production in northwestern Ohio. *P. capsici* was detected between late June and late September in water samples, representing a high risk of contamination of vegetable crops during the growing season.

Once introduced in a production field, *P. capsici* may persist in debris of susceptible host plants, including seeds (Leonian 1922) and weeds (French-Monar et al. 2006; Ploetz and Haynes 2000; Tian and Babadoost 2004). Leonian (1922) emphasized the importance of clean seed based on his observation of chile pepper infection by *P. capsici*. However, research has not focused on the survival and reproduction of *P. capsici* in weed host tissue. It is possible that in today's modern seed production systems, *P. capsici* does not pose the threat that it did in Leonian's time.

Phytophthora capsici and its interactions with host plants are influenced by environmental aerial and edaphic variables including

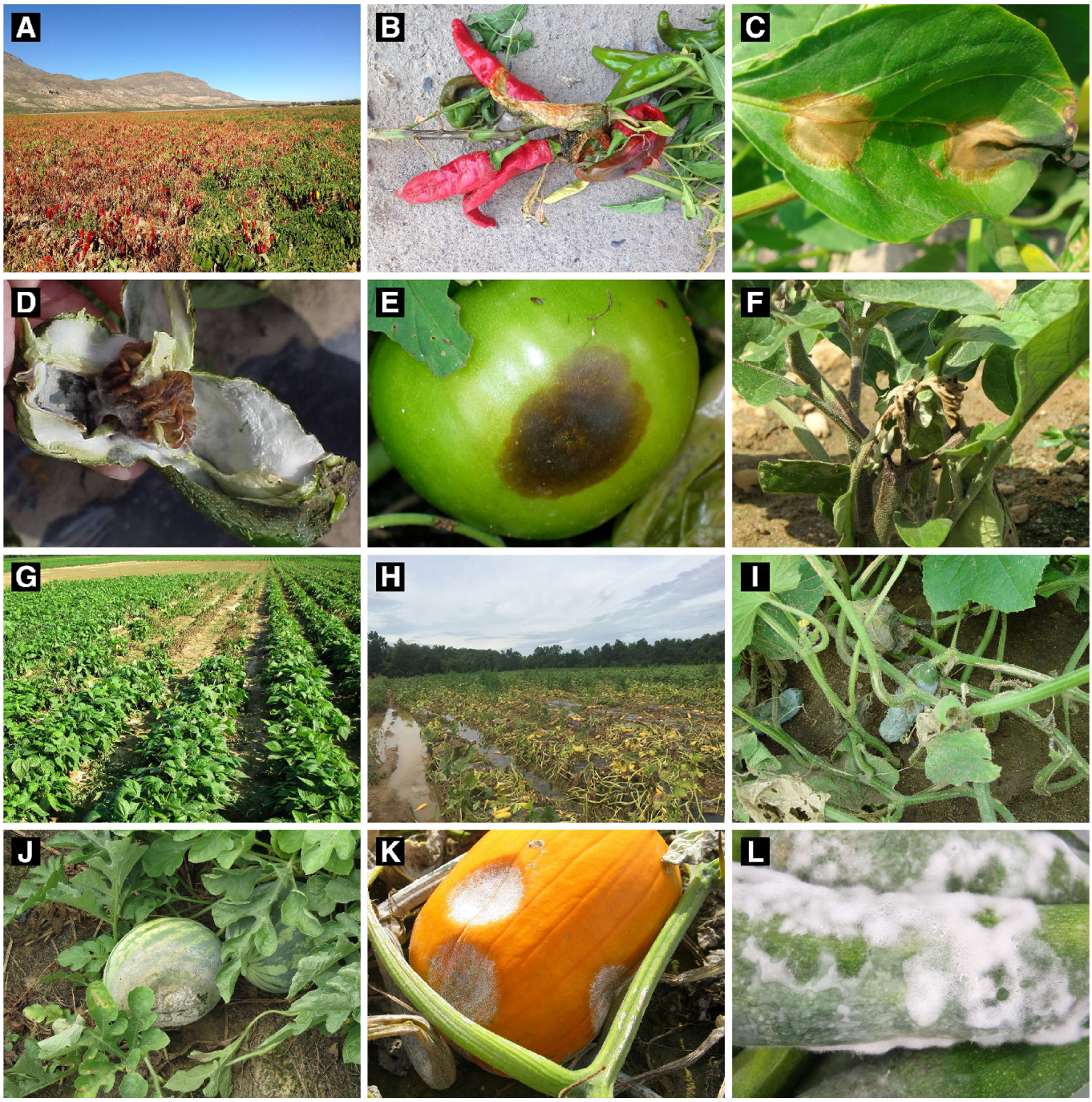

FIGURE 2
Symptoms and signs of Phytophthora blight on **A and B,** plants and fruit of chile pepper, **C,** bell pepper leaf, **D,** fruit and seeds of bell pepper, **E,** tomato fruit, **F,** eggplant, **G,** snap bean, **H,** squash, **I,** cucumber fruit, **J,** watermelon fruit, **K,** pumpkin fruit, and **L,** squash fruit. Note the abundant production of mycelium growth on fruits infected by *Phytophthora capsici* in I to L. Photo credits: A and B, S. Sanogo; C, D, and I, S. Miller; E, F, G, and K, M. McGrath; and H, J, and L, C. Parada-Rojas and L. Quesada-Ocampo.

moisture and temperature (Babadoost and Pavon 2013; Barchenger et al. 2018; Bowers et al. 1990; Erwin and Ribeiro 1996; Hausbeck and Lamour 2004; Lamour 2013; Ristaino and Johnston 1999; Sanogo and Ji 2012). Sanogo (2004, 2006, 2007b) examined the relationship of salinity, soil water saturation, and soil chemical composition with pathogen reproduction and infection of pepper. Sporangium and zoospore production was observed to decrease with increasing salinity levels, but disease severity increases with salinity levels. Furthermore, soil salinity increases salt injury and disease severity in *P. capsici*-susceptible plants but not in *P. capsici*-resistant plants. Additionally, soil water saturation does not predispose pepper plants to infection by *P. capsici*, and nonagricultural soils are more conducive to asexual reproduction than agricultural soils. Several studies have examined the interaction of *P. capsici* with other pathogenic microorganisms such as *Verticillium dahliae* (Sanogo 2007a; Sanogo and Carpenter 2006) and beneficial soil microbiome (Li et al. 2019).

Epidemiological and etiological studies are dependent on efficient detection and identification of isolates of *P. capsici* recovered from soil, water, and plant tissues. Beginning in the late 1980s, several commercial serological assays for *Phytophthora* became available. The laboratory assays were based on double antibody sandwich enzyme-linked immunoassay (DAS ELISA) in a 96-well plate format with a polyclonal capture antibody and a monoclonal detection antibody. These were followed later by rapid (less than 10 min) field-usable assays in flow-through and lateral flow formats. The assays are genus specific, detecting a wide array of *Phytophthora* species, including *P. capsici*, but cross-react with a few other oomycetes. Flow-through and ELISA assays were used successfully to detect *P. capsici* in pepper and cucurbit tissues in Ohio (Miller et al. 1994). ELISA was also used to detect and quantify *P. capsici* in soil (Miller et al. 1997); four pepper fields were intensively sampled, and *P. capsici* was detected at low to moderately high levels but was highly heterogeneous, limiting the ability to predict *P. capsici* levels in soil or ascertain treatment thresholds without intensive, cost-prohibitive sampling prior to planting. Commercial lateral flow assays are now widely used for routine diagnosis in the field and diagnostic lab of Phytophthora blight and diseases caused by other *Phytophthora* spp. when sporangia are not present on the sample, whereas PCR and isothermal nucleic acid amplification assays provide species-specific *P. capsici* detection (Parada-Rojas et al. 2021).

Hudson et al. (2020) developed a novel loop-mediated isothermal amplification (LAMP) primer set that could rapidly identify *P. capsici* in the field. This assay detects *P. capsici* at inoculum concentrations as low as 1.2×10^2 zoospores/ml, making it 40 times more sensitive than conventional PCR methods, and the results can be easily visualized with colorimetric LAMP dye in the field. When tested against closely related oomycete relatives of *P. capsici*, including *P. sansomeana*, *P. sojae*, *P. cinnamomi*, *P. palmivora*, *Pythium ultimum* var. *ultimum*, and several others, it was still able to differentiate between the different pathogens and only showed positive results for *P. capsici*. This LAMP assay was then used to test 42 irrigation ponds in nine counties in southern Georgia, and 10 ponds in five different counties were found to contain *P. capsici* (Hudson et al. 2021). A summary of the morphological and molecular features used in the identification of *P. capsici* has been provided by Parada-Rojas et al. (2021).

Genetics and Genomics

The increase in the epidemiological understanding of *P. capsici* has been achieved through breakthroughs in many research areas, including the genetics and genomics of *P. capsici*. Some of these breakthroughs came from studies focused on the rise of populations of *P. capsici* resistant to the fungicides metalaxyl and mefenoxam (Parra and Ristaino 1998, 2001). These fungicides were quickly overcome by co-dominantly controlled resistance (Lamour and Hausbeck 2000). *P. capsici* is a diploid organism with dormant sexual spores (oospores) to survive the winter and fallow periods. It should take at least 2 years to obtain isolates with full resistance (homozygosity of the co-dominant alleles) based on studies to determine the plausibility of young (weeks old) oospores contributing to overall genetic diversity within a single cropping season (e.g., continental United States for vegetables). These studies indicate that there is a strong dormancy period, and germination of what appear to be fully formed oospores led to the resulting "progeny" being identical to one or the other parent isolate (A1 or A2 mating type) (Donahoo and Lamour 2008; Hurtado-Gonzales and Lamour 2009), referred to as apomixis. Yet, full resistance (homozygosity) occurred within a single growing season. Detailed population genetic analyses revealed genetically isolated sexual populations, no clonal overwintering, fungicide application and resistance strongly correlated, and a curious caveat: newly resistant populations maintained a high level of genetic diversity (Lamour and Hausbeck 2001). Many in vitro crosses demonstrated that meiosis alone (due to sexual oospore dormancy) could not drive the rapid development of fully resistant, genotypically diverse populations (Erwin and Ribeiro 1996). A significant insight was gleaned performing reverse genetics on *P. capsici*: An induced point mutation could rapidly become homozygous (or disappear) in asexual zoospore progeny of a mutagenized sample (Hulvey et al. 2010). At this point, there were no whole genome resources, and consequently, the process was poorly understood. The first whole genome sequence, based on a scheme of backcrossing to reduce heterozygosity, revealed a novel phenomenon known as loss of heterozygosity (LOH)

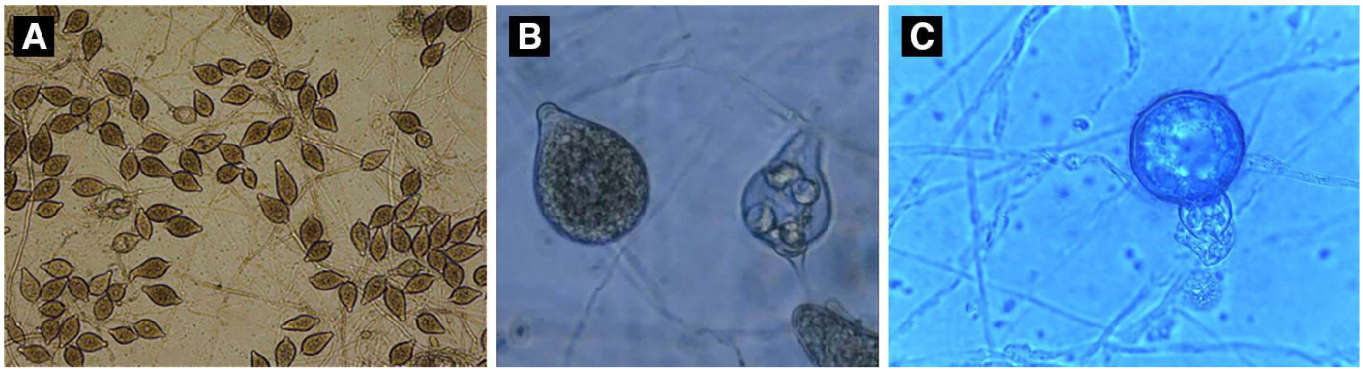

FIGURE 3
Structures formed by *Phytophthora capsici*: **A and B,** sporangia, with zoospores visible in the sporangium on the right in B. **C,** An oospore. Photo credits: A and C, Parada-Rojas and L. Quesada-Ocampo and B, S. Sanogo.

(Lamour et al. 2012). Accordingly, diverse contiguous genomic regions of the oospore progenies' genomes had "converted" to homozygosity, but not through the process of meiosis, which was performed as predicted by Mendelian inheritance across the remainder of their genomes. In essence, all the oospore progenies had at least some portion of their genomes where meiotic recombination could not have produced the resulting allelic configurations (e.g., a length of contiguous Aa alleles sexually recombined with aa genotypes produced long stretches of AA genotypes). This phenomenon was not confined to one portion of the genome, and it was estimated that approximately 30% of the entire genome was impacted by LOH when assessing the progeny cumulatively. It was also shown that sequence coverage across the LOH regions did not support loss of a chromosome—simply that one haplotype was retained and the other lost (Lamour et al. 2012). Not surprisingly, the resulting sexual progeny displayed diverse phenotypes, including dramatic changes in virulence and pathogenicity.

Further investigation of the stability of the *P. capsici* genome during asexual growth and sporulation (in the laboratory and within countries with large and long-lived clonal populations such as Peru and China) revealed that LOH was not limited to sexual crosses and was a common factor for asexual progeny (Gobena et al. 2012; Hu et al. 2013; Hurtado-Gonzales et al. 2008). Interestingly, whole genome sequencing of single-zoospore progeny revealed samples with regions that appeared to have variable ploidy, generally ranging from diploid to triploid, and further, continued growth of these samples could plausibly result in higher ploidy regions "collapsing" to the diploid state, thus revealing how an induced (or natural) recessive mutation (in an organism famous for its ability to quickly generate millions of sporangia and hundreds of millions of motile zoospores) could quickly bring an advantageous allele to the state of homozygosity (Hu et al. 2020). This underscores the impact of LOH within the context of asexual and sexual reproduction. There are no new alleles—simply the mitotic propagation of progeny with regions that were initially heterozygous and are now homozygous. The most basic challenge to scientific inquiry is being able to replicate experiments where it is crucial that the isolate (or isolates) under investigation retains the genomic structure (e.g., complement of heterozygosity) that exists while they are in the field or while being used in laboratory, greenhouse, or field studies. This work clearly shows that mitotic progeny are not always faithful copies of the clonal parent; instead, they are composed of many genomic variations, which can lead to rapid changes in growth morphology, chemical sensitivities, and virulence and pathogenicity (Hu et al. 2020). For example, in the work of Hu et al. (2020), the investigation of 241 A2 mating type isolates revealed that 74% had switched to the A1 mating type (the A2 is reported to be controlled by a mating type region in the heterozygous state). The A1 mating type was stable. It is common when sharing isolates with other research groups to have them "ask for another copy" as the isolates being used are no longer able to perform as they did previously (Lamour 2013).

The occurrence of the phenomenon of LOH during sexual and asexual processes has significance in the genetic diversity of *P. capsici*. From several studies, it has emerged that *P. capsici* does not persist clonally over multiple years in regions with a fallow or winter period (e.g., North America), and it may form geographically distinct populations with minimal gene flow among populations, restricting sexual reproduction to within geographically distinct populations of *P. capsici* (that may be relatively closely located, as close as 1 hectare distance) (Dunn et al. 2010; Lamour and Hausbeck 2002; Quesada-Ocampo et al. 2011; Siegenthaler et al. 2022).

Several phenotypic markers have been employed to assess variation in populations of *P. capsici* and other plant pathogens, including response to temperature and fungicides, mating types, and virulence attributes. Using response to temperature, Bowers et al. (2007) were able to separate temperate and tropical isolates of *P. capsici* into two distinct groups. Separation based on temperature response was supported by amplified fragment length polymorphism analysis, with low genetic diversity among temperate isolates and high genetic diversity among tropical isolates. Some studies found no correlation between phenotypic markers and molecular markers (Silvar et al. 2006).

Within *P. capsici*, several physiological races or virulence groups have been identified using host differentials in pepper (Barchenger et al. 2018; da Costa Ribeiro and Bosland 2012; Glosier et al. 2008; Jiang et al. 2015; Monroy-Barbosa and Bosland 2011; Oelke et al. 2003; Sy et al. 2008). In many vegetable growing areas, both mating types of *P. capsici* (A1 and A2) are present in production fields, and consequently, new races may arise as a result of recombination between mating types. The existence of physiological races or virulence groups and mating types represents a serious challenge to the durability of genetic resistance to *P. capsici*.

Resistance and Susceptibility of Plant Hosts

With the goal of using host resistance in managing Phytophthora blight, numerous studies have been conducted on understanding the susceptibility and resistance of crops to *P. capsici*. Some important components of this effort have been the identification of sources of resistance, inheritance patterns, and genes associated with resistance. Multiple sources of resistance to *P. capsici* (root and fruit rot resistance) have been reported in the literature in species of *Capsicum*, *Cucurbita*, and *Citrullus* (Candole et al. 2010; Kousik et al. 2012, 2014b, 2018, 2021; Meyer and Hausbeck 2013; Naegele and Hausbeck 2020; Ortega et al. 1991; Walker and Bosland 1999). Identification of the resistance and susceptibility of various hosts is based on a wide array of symptomatic reactions following natural and artificial inoculations with *P. capsici* under field and controlled-environment conditions. Observed symptomatic reactions were correlated with plant and fruit characteristics.

In *Capsicum* spp., the most prominent resistance source is 'Criollo de Morelos 334', a landrace from Mexico (Ortega et al. 1991; Walker and Bosland 1999). At Texas A&M University, the resistance selection program has been focused on the wild *C. annuum* accession 'Fidel'. This is due to less linkage drag experienced in F_2 and backcross families for fruit quality traits and yield. Multiple families have been developed with this line crossed with elite Anaheim, cayenne, ancho, and jalapeño parents. Resistance expression appears to be recessive as less than 10% of F_2 plants were resistant after inoculation with highly virulent strains of *P. capsici* (Gonzalez-Paredes 2004).

Many other potential sources of resistance in *Capsicum* have been reported (Barchenger et al. 2018; Candole et al. 2010; Parada-Rojas and Quesada-Ocampo 2019). The focus in all screening efforts has been the identification of resistance to root rot, foliar blight, and fruit rot (Barchenger et al. 2018). Naegele and Hausbeck (2020) evaluated pepper lines for *P. capsici* resistance, comparing root rot resistance to fruit rot resistance and genetic structure. Pepper accessions with resistance to root and fruit rot belonging to different genetic subpopulations were identified and are candidates for partial-resistance loci to incorporate into new cultivars.

In *Citrullus*, although Phytophthora fruit rot of watermelon was described in the 1940s, sources of resistance were identified only in 2012 (Kousik et al. 2012). Germplasm for use in breeding programs (Kousik et al. 2014b) with broad resistance to *P. capsici* isolates from across the United States (Kousik et al. 2021) has also been developed from these resistance sources. Fruits of the resistant germplasm are resistant to *P. capsici* at all stages of development (Kousik et al. 2018). These resistant germplasm lines belong to *Citrullus mucosospermus* and can be easily crossed with cultivated watermelon (*C. lanatus*). However, it has been a challenge to incorporate this resistance into usable germplasm lines.

Fruit rot has also been the focus of screening germplasm for resistance to *P. capsici* in *Cucurbita*. Alzohairy et al. (2020) used scanning electron microscopy imaging to show a high correlation between a thickened cuticle and epidermis in maturing winter squash fruit and disease resistance, indicating that a structural barrier forms as fruit matures. Pathogen hyphae were observed to penetrate susceptible Chieftain butternut (*C. moshata*) fruit exocarp at 7 days post-pollination (dpp) directly from the surface 6 h postinoculation (hpi), degrading the fruit cell wall within 48 hpi; resistant fruit (14, 21 dpp) was unaffected. Mature fruit of pumpkins with hard, gourd-like rinds is less susceptible to Phytophthora fruit rot than pumpkins producing conventional rinds (McGrath and Superak 1999). Middle Eastern squash is less susceptible than yellow summer squash and thus is a potential alternative crop and source of resistance in breeding (McGrath et al. 1994).

Histological, cytological, and biochemical changes in susceptible and resistant hosts have been described in several studies (Piccini et al. 2019). For example, in the *Capsicum-Phytophthora capsici* pathosystem, in susceptible hosts, *P. capsici* colonizes all cortical and vascular tissues of secondary roots and taproots, with a high number of hyphae shown on these roots; in contrast, in resistant hosts, colonization is limited to a few secondary roots with the presence of very few hyphae (Dunn and Smart 2015). Additionally, deposition of callose in the xylem of roots was reported to be denser in infected, resistant plants than in noninfected, resistant plants, whereas such deposition was not observed in susceptible infected and noninfected plants (Piccini et al. 2019).

Extensive research has been conducted on the differential expression of several plant-defense genes during infections of susceptible and resistant plants by *P. capsici* (Ayala-Doñas et al. 2021; Bagheri et al. 2020; Richins et al. 2010). Additionally, several genes have been demonstrated to be expressed during the occurrence of induced resistance to *P. capsici* as mediated by colonization of plants by nonpathogenic microorganisms such as species of *Trichoderma* and by application of plant activators such as acibenzolar-S-methyl (Bae et al. 2011; Bellini et al. 2021).

Inheritance studies have elucidated the genetic system of host–parasite interactions in various pathosystems (Ortega et al. 1991; Walker and Bosland 1999). Resistance to *P. capsici* is complex and may be controlled by multiple dominant and recessive genes (Barchenger et al. 2018; Crosby et al. 2012; Gonzalez-Paredes 2004). Additionally, in *Capsicum* spp., there is evidence that expression of disease resistance may be hampered by the presence of inhibitor genes (Reeves et al. 2013). Advances in genomics have led to the characterization of quantitative trait loci (QTLs) associated with resistance in *Capsicum* using linkage analysis (Lozada et al. 2021a). A genome-wide association study was also previously implemented, and the short arm of pepper chromosome 5 has been pinpointed as a major genomic region harboring *P. capsici* resistance QTLs (Siddique et al. 2019). Evidence from meta-QTL analysis (Lozada et al. 2021b) and transcriptomics (Du et al. 2021) further identified chromosome 5 for resistance to *P. capsici*. Marker-assisted selection could therefore be targeted at this chromosomal region for the genetic improvement of *P. capsici* disease resistance in *Capsicum* spp.

Management Approaches

When Leonian completed his description of *P. capsici* in 1922, he recommended two main control measures: seed selection and application of fungicides. Research conducted since then has led to the identification of multiple strategies that may be used to reduce the impact of *P. capsici* in various crops.

Knowledge of the field history is of paramount importance in the mitigation of Phytophthora blight. Planting in fields with no history of the occurrence of *P. capsici* is ideal. However, care must be exercised to prevent the introduction of the pathogen into such fields by cleaning farm equipment used in infested fields, by hand sanitation after handling fruits in fields with high incidence and severity of the disease, and by avoiding infested irrigation water from ponds and rivers.

In fields with a history of the pathogen, risk mitigation centers on the reduction of inoculum potential (Sanogo 2019) and maintaining it at nonthreatening levels through water management, crop rotation, fungicide application, and integrated systems. Water management is a key component for mitigating the risk posed by *P. capsici* (Sanogo and Ji 2013). This component involves using high-quality irrigation water, minimizing saturation conditions in soil by using water-efficient irrigation systems such as drip irrigation, and growing plants in raised beds. When transplanting into raised beds, it is critical to ensure the hole is filled with soil so water cannot pool around the plant stem. All of these efforts can be thwarted by intense rainfall events, which are predicted to become more common with climate change.

In a quest for developing effective irrigation water treatments, Granke and Hausbeck (2010) evaluated the efficacy of several algaecides containing active ingredients such as sodium hypochlorite, copper sulfate, chelated copper, or sodium carbonate peroxyhydrate on the infectivity of zoospores of *P. capsici*. Zoospores were no longer motile within 3 min of water treatment, and zoospore mortality was increased to over 80% in some treatments and reached 100% in others. Water may also be effectively treated using synthetic nonionic surfactants and biosurfactants (rhamnolipid and saponin), which have been demonstrated to be highly effective against diseases caused by zoosporic pathogens, including *P. capsici*, in recirculating hydroponic systems (Nielsen et al. 2006; Pagliaccia et al. 2007; Stanghellini et al. 1996). On the other hand, Lewis Ivey and Miller (2013) found that chlorine dioxide injected into irrigation water at concentrations designed to inhibit coliform bacteria did not reduce *P. capsici* mycelial growth or sporangial germination and reduced zoospore populations by less than 50%.

Phytophthora blight may be reduced with crop rotation, at least for 4 years, and management inputs such as bioactive crop residues from Brassicas with high glucosinolate content (McGrath and Menasha 2013) and other agricultural byproducts including organic materials from non-host crops, yard-waste compost, or brewery-waste compost (Babadoost and Pavon 2013; Lujan et al. 2021; McGrath and Rangarajan 2002; Tian and Babadoost 2004) and biopesticides. The use of vegetable crops in the Brassicaceae family as biofumigants must be considered carefully. Members of this family have not been considered as hosts for *P. capsici*. However, Krasnow and Hausbeck (2015) observed that *P. capsici* reduced the fresh weight of all *Brassica* spp. evaluated and killed *B. juncea* 'Pacific Gold' plants, commonly recommended for biofumigation. Thus, using Pacific Gold mustard as a biofumigant might not reduce soil populations of *P. capsici* (Krasnow and Hausbeck 2015).

Host resistance is important to the management of Phytophthora blight. Screening efforts have identified several sources of genetic resistance that may be incorporated in the development of commercial cultivars. However, progress has been made only in *Capsicum* pepper, especially in bell pepper. Resistance is to root and crown rot. The evaluation of bell pepper breeding lines and cultivars with intermediate or high resistance to *P. capsici* has led to the commercial development and release of resistant cultivars and improved bell pepper production in regions where *P. capsici* remains a significant threat (Wyenandt and Kline 2019). The release and adoption of bell pepper cultivars resistant to *P. capsici* have provided a powerful tool to pepper growers in many parts of the United States. In 1996, the Phytophthora-resistant bell pepper 'Paladin' was released for commercial use and subsequently became the most widely grown bell pepper in states such as New Jersey (Ristaino and Johnston 1999). However, over the years, *P. capsici* resistance in Paladin has broken down in some fields in southern New Jersey. Since the release of Paladin, other bell pepper cultivars

with intermediate resistance to *P. capsici* have been released and widely adopted by bell pepper growers in New Jersey and other states. However, as the use of these resistant cultivars increased, the development of "silvering" or skin separation in harvested fruit has become an issue for some growers over the past two decades. Research in New Jersey has demonstrated that neither N fertility nor the type of production system affects the development of "silvering" in fruit but that it is more related to genotype (Kline et al. 2011; Wyenandt et al. 2017). Resistant cultivars commercially available in 2022 include sweet bell types ('Archimedes', 'Aristotle', 'Bayonet', 'Cortes', 'Currier', 'Declaration', 'Galileo', 'Ilyn', 'Intruder', 'Lulton', 'Majestic Red', 'Mercer', 'Paladin', 'Playmaker', 'Remarkable', 'Revolution', 'Sailfish', 'Snapper', 'Tarpon', 'Telestar', 'Turnpike X5R', and 'Vanguard') and hot types ('Becan', 'Don Matias', 'Durango', 'Legendario', 'Sargento', 'Sequoia', 'Spitfire', 'Tzotzil', and 'Unique').

Fungicides have been the focus of numerous research publications and are key tools in the management of *P. capsici* targeting soil, seed, and plant in various solanaceous and cucurbitaceous crops (Babadoost and de Souza 2019; Babadoost and Islam 2003; Hausbeck and Lamour 2004; Kousik et al. 2011, 2014a, 2017; Matheron and Porchas 2000, 2002, 2014; McGrath and Fox 2008; Miller et al. 2018; Sanogo and Ji 2012; Wyenandt 2014; Wyenandt and Kline 2014). Old and new chemistries used include mefenoxam, fluopicolide, oxathiapiprolin, dimethomorph, mandipropamid, and cyazofamid. However, in several regions, the development of populations of *P. capsici* resistant to fungicides has been observed for mefenoxam, fluopicolide, and cyazofamid (Dunn et al. 2010; Jackson et al. 2012; Parada-Rojas and Quesada-Ocampo 2018, 2022; Parra and Ristaino 1998, 2001; Keinath 2007; Kousik and Keinath 2008; Lamour and Hausbeck 2000; Wang and Ji 2021). Additionally, Siegenthaler and Hansen (2021) first reported resistance of *P. capsici* to oxathiapiprolin, a relatively new active ingredient.

Other avenues that have been researched for application in management of *P. capsici* include biopesticides and other biorational tools such as plant activators, botanical extracts, inorganic substances, and microbial formulations. Plant activators such as acibenzolar-S-methyl, botanical extracts such as phenolic extracts from pecan shell and husk, *Trichoderma hamatum* T382, and exposure to red light have been demonstrated to elicit induced resistance with a significant reduction in disease incidence and severity (Islam et al. 2002; Khan et al. 2004; Lujan et al. 2021; Matheron and Porchas 2002). Inorganic substances such as silicon have also been shown to reduce disease severity and to enhance plant growth in peppers (French-Monar et al. 2010). Research conducted on numerous microbial biopesticides documented that their efficacy has been inconsistent across crops, locations, and years (McGrath and Sexton 2019; Sanogo 2020; Sanogo and Lujan 2021). Microbial biopesticides, when used in conjunction with chemical fungicides, may provide an avenue for hampering the development of *P. capsici* strains resistant to chemical fungicides (Wan and Liew 2020). Although it is known that these avenues are used by growers in various regions, there have been no reports that document the extent to which each one is used.

Phytophthora blight must be managed using a combination of tactics, including varietal resistance, cultural practices, crop rotation, fungicides, and biopesticides. Combinations of tools have been the focus of several studies and are pivotal to the sustainable management of *P. capsici* (Babadoost et al. 2010; Foster and Hausbeck 2010; Granke et al. 2012; Hausbeck and Lamour 2004; Krasnow et al. 2017; Ristaino and Johnston 1999; Saltos et al. 2022; Sanogo and Ji 2012; Sanogo and Lujan 2021).

Concluding Remarks

Research conducted over the past 100 years has yielded a wealth of information on *P. capsici* that has increased our understanding of the biology and management of this global pathogen. Basic research is poised to continue to unravel the intricacies of the life cycle of *P. capsici* using emerging technologies in genetics, genomics, physiology and biochemistry, and soil ecology and biology. In particular, the plasticity of the *P. capsici* genome in the laboratory and the field presents significant challenges and requires further investigations. Applied research, especially focused on evaluating management tools in commercial and research fields, has been and continues to be challenging. Large in-field and year-to-year changes in disease occurrence in fields exacerbates effective blocking and research success. For example, fungicide treatments can be overwhelmed when an intensive rainstorm, especially occurring early in an experiment, creates highly favorable conditions for the development of Phytophthora blight. On the other hand, no disease may occur in the same research field when rainfall is limited despite use of excessive irrigation. Research aimed at increasing understanding of the spatiotemporal dynamics of the development of Phytophthora blight and the impact of mitotic genomic rearrangements (e.g., LOH) will be crucial for advances in the field evaluation of all management tools.

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