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ORIGINAL PAPER

Phytophthora capsici the Causal Agent of Phytophthora Blight of *Capsicum* spp.: From Its Taxonomy to Disease Management

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ABSTRACT

Capsicum, a genus native to tropical and subtropical America, holds immense nutritional, economic and cultural significance due to its diverse species. However, these valuable crops face a constant threat from various diseases caused by viruses, bacteria, fungi and especially the notorious *Phytophthora capsici*. *P. capsici*, first identified as a pepper pathogen in New Mexico by L.H. Leonian in 1922, is a devastating Oomycete wreaking havoc on vegetable, ornamental and tropical crops worldwide. This pathogen thrives in both temperate and tropical environments and possesses an arsenal of abilities that make it a formidable adversary. *P. capsici*'s high genetic diversity allows it to readily overcome fungicides and host resistance, while the formation of long-lasting oospores ensures its persistence in soil. Its ability to rapidly differentiate into infectious zoospores in the presence of water fuels epidemics and its broad host range amplifies economic losses and renders crop rotation less effective. The severity of *P. capsici*-induced diseases and the complex management challenges have spurred extensive research efforts. Here, we delve into recent discoveries regarding the biology, genetic diversity, disease management strategies and effector biology of this formidable Oomycete.

Keywords: *Phytophthora capsici*, Phytophthora blight, *Capsicum* spp., sustainability, management practice

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INTRODUCTION

Originating from tropical and subtropical America, *Capsicum* species like *C. pubescens* R. & P., *C. frutescens* L., *C. chinense* Jacq., *C. baccatum* L., *C. annuum* L., hold immense nutritional, economic , and cultural significance in global gastronomy. These vegetables, also known as sweet peppers or hot peppers, contribute to a staggering worldwide production of 38 million tons (Moon *et al.*, 2023). However, similar to other crops, peppers are susceptible to various diseases caused by viruses, bacteria (vascular wilts and leaf spots), fungi (anthracnose, powdery mildew and cercosporiosis) and primarily pseudofungi (leaf blight) (Parisi *et al.*, 2020).

Phytophthora capsici, a globally distributed Oomycete (Saltos *et al.*, 2021), has been identified as the culprit behind numerous diseases affecting economically crucial crops across diverse families like *Solanaceae*, *Liliaceae*, *Fabaceae*, *Rosaceae*, and *Cucurbitaceae* (Reis et al., 2018). In Capsicum, this notorious pathogen can cause devastating losses of up to 100% due to its rapid spread in field conditions (Barchenger *et al.*, 2018). The staggering $100 million in annual losses attributed to *P. capsici* makes it the world's fifth most destructive Oomycete (Kamoun *et al.*, 2015). Its ability to reach aerial plant tissues and its polycyclic nature further complicate management strategies, solidifying its reputation as one of the most challenging plant pathogens to control (Santos *et al.,* 2023 and Sharma *et al.*, 2023).

Resistant Capsicum plants activate various biochemical, structural and molecular defense mechanisms to counter *P. capsici* infection. Conversely, susceptible cultivars like Chinese Giant, California Wonder, Osh Kosh and Yolo Wonder succumb to infection and colonization by the pathogen (Barchenger *et al.*, 2018 and Acharya *et al.,* 2023). This susceptibility necessitates substantial oomyceticide use by farmers, prompting the exploration of alternative control methods. Integrating strategies like crop rotation, irrigation management, and biocontrol agents (e.g., *Trichoderma* spp. and *Bacillus* spp. which significantly reduce collar rot progression) can drastically reduce *P. capsici* infection (Liu *et al.*, 2019; Saltos *et al.*, 2021; Muthu *et al.*, 2022 and Quesada-Ocampo *et al.,* 2023). Given the significance of *P. capsici* in *Capsicum* spp., this chapter delves into the pathogen's etiology, symptomatology, worldwide occurrence and biological cycle across different plant tissues. Finally, it explores disease management measures applicable both independently and in an integrated approach.

ETIOLOGY

The genus *Phytophthora* comprises a collection of destructive plant pathogenic species that cause significant economic damage to essential crops worldwide. Historically classified within the *Pythiaceae* family of Oomycetes, *Phytophthora* was later reclassified under the *Peronosporaceae* family following ribosomal analysis. Advancements in molecular biology have enabled the clarification of these relationships and the identification of new genera, including *Phytopythium*. Currently, a total of 365 species and subspecies have been described within the genus *Phytophthora* and this number continues to grow (Lamour *et al.,* 2011; Ho, 2018). *Phytophthora capsici* belongs to Kingdom Chromista; Phylum Oomycota; Class Oomycetes; Order Peronosporales; Family Peronosporaceae; Genus *Phytophthora*. Oomycetes are a diverse group of eukaryotic organisms that encompass a vast array of plant pathogens. Unlike true fungi, Oomycetes belong to the kingdom Chromista and share closer evolutionary ties with brown algae. These microscopic organisms are notorious for causing devastating plant diseases, with some species capable of wiping out entire crops (Ho, 2018 and Smith *et al.*, 2019).

Phytophthora capsici is among the top five most important plant pathogenic Oomycetes, causing widespread damage to a variety of crops worldwide. These Oomycetes targets plants from the *Solanaceae* family, including peppers and tomatoes and *Cucurbitaceae* family, encompassing cucumbers and pumpkins. The destructive nature of *P. capsici* was first documented in 1922 by Leon Hatching Leonian, who identified it as a new pathogen infecting pepper plants (*C. annuum*). The pathogen causes a range of disease symptoms, including root rot, stem and fruit blight, seed rot, and ultimately, plant wilting and death (Ho, 2018 and Jayawardena *et al.*, 2020).

HOST RANGE

Phytophthora capsici exhibits a broad host range, encompassing over forty-nine plant species. Among the major hosts of *P. capsici* are red and green peppers (*Capsicum annuum*), beet (*Beta vulgaris*), watermelon (*Citrullus lanatus*), swiss-chard (*Beta vulgaris* var. *cicla*), cantaloupe (*Cucumis melo*), lima bean (*Phaseolus lunatus*), honeydew melon (*C. melo*), turnip (*Brassica rapa*), cucumber (*Cucumis sativus*), velvet-leaf (*Abutilon theophrasti*), spinach (*Spinacia oleracea*), cauliflower (*Brassica oleracea* var. *botrytis*), eggplant (*Solanum melongena*), black pepper (*Piper nigrum*), tomato (*Lycopersicon esculentum*), zucchini squash (*Cucurbita pepo*), yellow squash (*C pepo*), processing pumpkin (*C. moschata*), gourd (*C. moschata*), acorn squash (*C. moschata*), and blue hubbard squash (*C. maxima*) (Tian and Babadoost, 2004; Reis *et al.*, 2018; Saltos *et al.*, 2022 and Cui *et al.*, 2023).

Egyptian Journal of Phytopathology, Vol.52,No.1,pp 1-10

SYMPTOMATOLOGY

Symptoms caused by *P. capsici* vary depending on the infected plant part, degree of resistance and environmental conditions. Symptom development is not uniform, influenced by factors such as host resistance and prevailing weather patterns. In drier regions, *P. capsici* primarily attacks roots and crowns, leaving a distinctive black/brown lesion visible at the soil line. In areas with abundant rainfall, the pathogen infects all plant parts, including roots, crowns, foliage and fruits. Root infections cause damping-off in seedlings, leading to rapid decline and collapse. Older plants may exhibit stunted growth, wilting, and eventual death. Despite severe root damage, compensatory adventitious root growth may emerge above the infected taproot, allowing stunted plants to persist. Infected roots display small, dark-colored lesions that rapidly expand until complete rotting occurs. Leaf blight symptoms include dark, watery spots that enlarge and turn necrotic. In adult plants, *P. capsici* infection triggers sudden leaf yellowing and wilting, resulting from the collapse of water-conducting tissues in roots and stems. This disruption of water transport marks the final disease stages, leading to plant death (Lamour *et al.,* 2011; Barchenger *et al.,* 2018 and Santos *et al.,* 2023).

Phytophthora capsici wreaks havoc on fruits, causing a rapid and devastating form of rot. The initial signs of infection manifest as water-soaked lesions with distinct clear centers. These lesions swiftly expand, often enveloping the entire fruit surface in a white, cottony growth of the pathogen. Within a few days, the affected fruit succumbs to complete decay. In contrast to *Pythium* infections, *P. capsici* infections typically do not exhibit hyphae emerging from infected plants or fruits. Instead, sporangia, the pathogen's reproductive structures, are the primary visible elements on the surface of infected plants. The rapid progression of *P. capsici* fruit rot underscores the pathogen's ability to inflict significant damage on crops. Understanding the distinct symptoms and mechanisms of this disease is crucial for developing effective control strategies and minimizing crop losses (Saltos *et al.,* 2021 and Saltos *et al.,* 2022).

ECONOMIC IMPORTANCE

Phytophthora capsici poses a significant challenge to growers due to its broad host range, long-lived dormant sexual spores, extensive genotypic diversity and explosive asexual disease cycle (Barchenger *et al.,* 2018). The emergence of novel control strategies is becoming increasingly urgent to protect food production from *P. capsici* and other Oomycetes. Given its ease of growth, mating, and manipulation in the laboratory, and its ability to infect a wide range of plant species, *P. capsici* serves as a robust model organism for research, particularly in areas related to sexual reproduction, host range and virulence (Kamoun *et al.,* 2015 and Saltos *et al.,* 2022).

Phytophthora capsici can cause devastating damage to crops, with the potential to inflict losses of up to 100% in uncontrolled situations. Its rapid spread and ability to inflict significant economic losses, estimated at around $100 million annually, have earned it the dubious distinction of being the fifth most prevalent plant pathogenic Oomycete worldwide (Kamoun *et al.,* 2015). The pathogen's presence in aerial tissues, coupled with its polycyclic nature, poses a formidable challenge for agricultural management. Polycyclic diseases, characterized by multiple infection cycles within a single growing season, make *P. capsici* particularly difficult to control (Barchenger *et al.,* 2018).

Understanding the intricate biology and diverse modes of attack employed by *P. capsici* is crucial for developing effective control strategies and safeguarding crop yields from this relentless pathogen.

OCCURRENCE OF *Phytophthora capsici* WORLDWIDE

Since its initial discovery in 1922 on pepper plants in New Mexico, the Oomycete *P. capsici* has spread to numerous countries and infects a wide range of plants. Despite lacking the ability to disperse through the air, *P. capsici* thrives in diverse environments, from tropical to temperate regions. Flooding and human activities are believed to facilitate its long-distance spread, enabling this vegetable pathogen to establish itself across North America, most of South and Central America, parts of Africa, Europe, Asia and Australia (Fig. 1) (Quesada-Ocampo *et al.*, 2023).

Fig. (1): A global map highlights the widespread presence of *Phytophthora capsici*, with green-colored countries indicating confirmed reports of the pathogen affecting both field- and greenhouse-grown vegetables and ornamentals from 1918 to 2022 (Barchenger *et al.*, 2018).

DISEASE CYCLE

The life cycle of *P. capsici* (Fig. 2) begins with its survival in various sources. Mycelium can persist in soil, plant debris, or even on weeds serving as alternative hosts. Additionally, oospores can endure long periods in the soil (Lamour *et al.*, 2011). These structures then give rise to sporangia, which primarily spread through water (rain or irrigation) reaching nearby or distant crops (Hudson *et al.*, 2020). Under favorable conditions (high humidity and 27-32°C), sporangia release motile zoospores that swim through water to infect plant tissues. While wind dispersal has been suggested, its role remains uncertain (Hyder *et al.*, 2018).

Sporangia of *P. capsici* can directly germinate on the plant surface, forming a germ tube that pierces the outer walls of root cells. Alternatively, zoospores released from within the sporangia can encyst on various plant tissues, then germinate and form an appressorium to penetrate epidermal cells. This hemibiotrophic pathogen initially exhibits biotrophic behavior, acquiring nutrients from living cells via haustoria, before transitioning to a necrotrophic phase (Reis *et al.*, 2018). Vegetative hyphae and haustoria branch out, colonizing cells intracellularly and on the surface. Ultimately, *P. capsici* extensively infects epidermal, vascular (phloem, xylem) and parenchymal cells. The entire infection and colonization process, known as the latent period, can last between four and seven days (Piccini *et al.*, 2019).

Egyptian Journal of Phytopathology, Vol.52,No.1,pp 1-10

The final stage of the primary disease cycle involves the pathogen's reproduction, occurring on the host's external surface. *P. capsici*, a heterothallic species with two mating types (A1 and A2), forms male (antheridia) and female (oogonia) gametangia. These fuse to produce sexually derived oospores, featuring thick walls for enduring winter and harsh conditions. These reproductive structures undergo a dormant period, ensuring the pathogen's survival. Asexual reproduction also occurs, characterized by sporangiophores generating sporangia. Optimal sporangial production happens between 25-30°C, under high humidity, and approximately 90 hours post-infection. Subsequently, cytoplasmic cleavage within the sporangia yields zoospores (Saltos *et al.*, 2021).

While root and crown rot are monocyclic, other diseases like leaf blight and fruit rot are polycyclic. Therefore, *P. capsici* sporangia act as secondary inoculum, spread by water splashes to aerial tissues. This initiates new infection cycles, repeating the previously mentioned phases of infection, colonization, and reproduction. The pathogen's ability to reach virtually all plant tissues complicates its management (Saltos *et al.*, 2022).

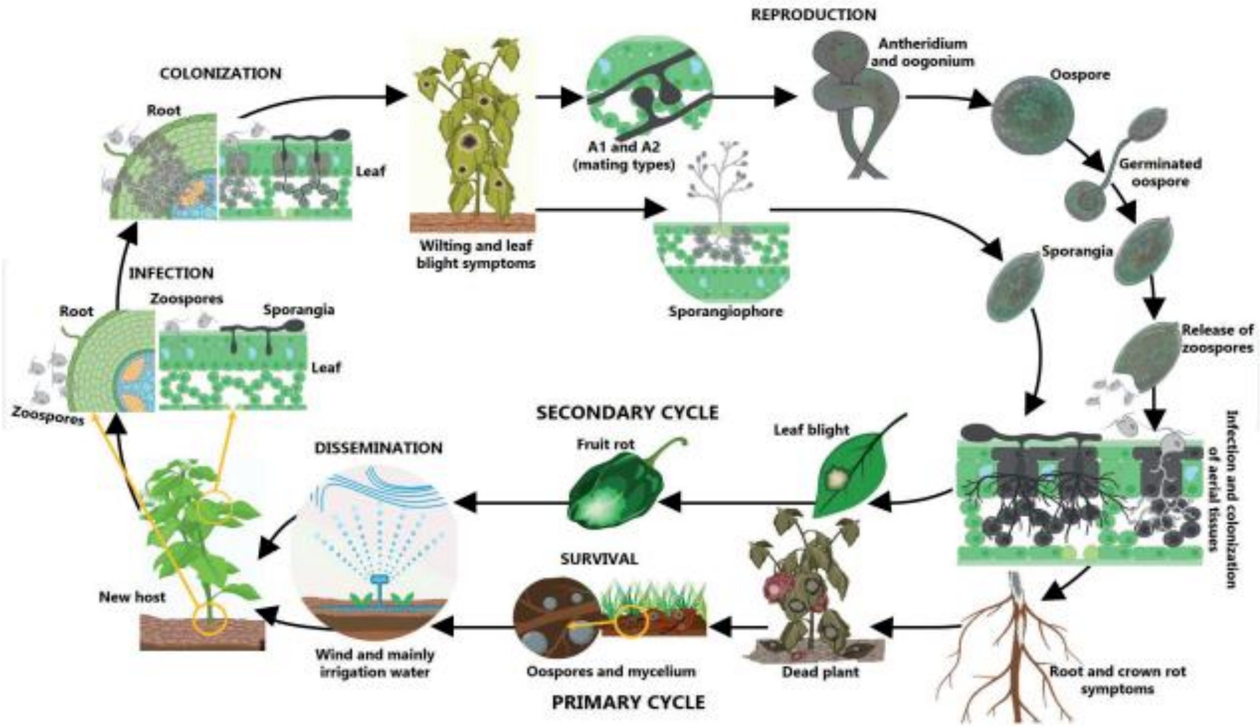

Fig. (2): Life cycle of *Phytophthora capsici* in *Capsicum* spp. hosts (Moreira-Morrillo *et al.*, 2022).

DISEASE MANAGEMENT

Managing diseases caused by *P. capsici* can be challenging and costly, primarily due to the overuse of Oomyceticides (previously known as fungicides). However, integrating various alternative strategies during pre-sowing, production, and post-harvest stages can significantly reduce damage and losses in Capsicum crops (Santos *et al.*, 2023). These alternatives include: utilizing resistant cultivars, ensuring well-drained soil, implementing crop rotation, applying soil treatments, practicing appropriate tillage methods, managing irrigation effectively, improving irrigation water quality and employing plastic mulches (Hajji-Hedfi *et al.*, 2023a; Hajji-Hedfi *et al.*, 2023b; Hajji-Hedfi *et al.*, 2023c; Rhouma *et al.*, 2023a and Rhouma *et al.*, 2023b). While, the infection of diverse Capsicum organs by *P. capsici* necessitates complex integrated management, the potential benefits for farmers make the effort worthwhile (Santos *et al.*, 2023).

Oomyceticides, particularly those containing molecules with a direct impact on the pathogen, are widely used to manage *P. capsici* diseases in Capsicum plants (Wang *et al.*, 2016). Extensive laboratory and field trials have demonstrated the effectiveness of these synthetic Oomyceticides (Wang *et al.*, 2020). For instance, Mancozeb 64% + Metalaxyl 4%, Copper sulfate pentahydrate (soil application) and Potassium phosphonate (foliar application) can completely eliminate root and crown rot (Sharma *et al.*, 2023). Additionally, Fosetil Aluminum (soil drench) has been shown to reduce wilting in pepper plants by 100%. Other effective molecules against damping-off, leaf blight, and fruit rot include ametoctradine + dimethomorph, cyazofamid, dimethomorph, famoxadon + cymoxanil, fluazinam, fluopicolide, mandipropamide, mefenoxam, phosphonates, and zoxamide + mancozeb (Hua *et al.*, 2022).

While chemical control has achieved success against *P. capsici*, inappropriate use of certain molecules has led to the development of resistant isolates (Rhouma *et al.*, 2023a). This includes resistance to commonly used Oomyceticides like metalaxyl and mefenoxam. To mitigate these effects, alternative options like mandipropamide and dimethomorph are gaining traction, as they pose a low to medium risk of resistance development (Hua *et al.*, 2022). To further reduce selection pressure on the pathogen, farmers should employ a diverse arsenal of molecules, rotating them periodically and systematically throughout the crop cycle. Additionally, utilizing mixtures with both systemic and protective modes of action can enhance disease control (Wang *et al.*, 2020).

Cultural control methods aim to promote healthy crop development while hindering the growth and spread of the pathogen, ultimately reducing disease severity (Moreira-Morrillo *et al.*, 2022 and Rhouma *et al.*, 2023b). This includes strategies such as limiting soil saturation, preventing water accumulation in plots and avoiding the movement of infected plant debris or infested soil within a field. Crop rotation plays a crucial role in this approach, as it disrupts the pathogen's life cycle and limits its host availability. Implementing a three-year rotation can significantly reduce the population of *P. capsici* propagules, particularly oospores, which can persist in the soil for extended periods (Rhouma *et al.*, 2022; Hajji-Hedfi *et al.*, 2023a; Hajji-Hedfi *et al.*, 2023b and Quesada-Ocampo *et al.*, 2023).

The growing demand for healthy food free from synthetic pesticide residues has driven the exploration of alternative solutions, including the use of effective biological control agents. Promising candidates like *Bacillus* spp. and *Trichoderma* spp. (Santos *et al.*, 2023), when applied under favorable climatic conditions, can significantly and cost-effectively contribute to preventing and managing *P. capsici* diseases while promoting Capsicum growth (Ngo *et al.*, 2020).

Microorganisms like *Bacillus* spp. (Ngo *et al.*, 2020) and *Trichoderma* spp. (Santos *et al.*, 2023) offer valuable alternatives for managing diseases caused by

Egyptian Journal of Phytopathology, Vol.52,No.1,pp 1-10

P. capsici. In controlled environments, *Bacillus amyloliquefaciens* has demonstrated its ability to reduce the mycelial growth of *P. capsici* by up to 46%, while also promoting the growth of Capsicum pepper plants. *Bacillus subtilis* showed significant potential, reducing the incidence of foliar blight by 71-87% (Liu *et al.,* 2019 and Ngo *et al.,* 2020). Furthermore, *in vitro* and *in vivo* experiments with native *Trichoderma* strains against *P. capsici* isolates in *C. pubescens* plants revealed that *T. harzianum* can inhibit the radial growth of the pathogen by 43% and reduce plant mortality by 10% (Santos *et al.,* 2023).

Endophytic microorganisms, such as *Nigrospora sphaerica*, *Enterobacter* sp. and *Dothideales* sp., can be harnessed as biocontrol agents against pathogens like *P. capsici* affecting *C. annuum*. In a recent study, *Nigrospora sphaerica* significantly reduced root rot in susceptible *C. annuum* seedlings compared to controls. Additionally, a metagenomic analysis revealed diverse fungal species within the mycobiome of resistant and susceptible hypocotyls, both infected and uninfected with *P. capsici*, suggesting potential for further exploration in biocontrol strategies (Ngo *et al.,* 2020; Muthu Narayanan *et al.,* 2022; Tiwari *et al.,* 2022 and Santos *et al.,* 2023).

Developing Capsicum germplasm resistant to *P. capsici* is a complex undertaking, demanding diverse breeding techniques and comprehensive germplasm screening, including the exploration of resistant landraces. Currently, several commercially available cultivars like Ayesha Ungu, Sempurna, Violeta 1, Ayesha, Violeta, Ungara, Paladin, and Nathalie offer resistance and are cultivated worldwide. Additionally, promising resistant landraces like ECU-1296 (*C. frutescens*), Code 5 (*C. frutescens*), ECU-9129 (*C. chinense*), ECU-12831 (*C. baccatum*), and CM-334 (*C. annuum*) have been identified in Ecuador and Mexico and hold potential for future breeding programs (Orton and Ayeni, 2022; Acharya *et al.,* 2023 and Bongiorno *et al.,* 2023).

Phytophthora capsici possesses a potent arsenal of mechanisms to attack plants and acquire nutrients. Conversely, plants like *C. annuum* have evolved a sophisticated defense system to thwart the entry and restrict the progression of the Oomycetes within their tissues (Wang *et al.,* 2016). This system encompasses physical, biochemical, and molecular barriers. One of the first lines of defense in pepper plants is their thick cell wall, rich in phenolic compounds and flavonoids such as chlorogenic acid, luteolin glycosides, and apigenin aglycone. Other defense mechanisms include the synthesis of antimicrobial phytoalexins, the activation of hydrolytic enzymes like chitinase and glucanase, the production of hydroxyproline-rich proteins, reactive oxygen species, and the Capsicum-specific phytoalexin capsidiol, which potentially inhibits Oomycete development. The combined action of these and other mechanisms allows Capsicum plants to prevent or significantly delay *P. capsici* infection, colonization and reproduction across various subterranean and aerial tissues (Barraza *et al.,* 2022).

Integrated disease management (IDM) aims to minimize the pathogen's biological activity and boost crop productivity. This approach employs various eco-friendly techniques, including soil and plant management, to address *P. capsici* diseases without relying heavily on chemical interventions. These techniques include soil amendments, solarization, crop cover, water treatment, seed treatment, etc. IDM strategies should be integrated within agroecological, conventional, or other production systems, as a single approach often proves insufficient. By combining these strategies, IDM aims to achieve effective and sustainable control of *P. capsici* in Capsicum crops (Liu *et al.*, 2019; Ngo *et al.*, 2020; Hua *et al.*, 2022; Muthu Narayanan *et al.*, 2022; Tiwari *et al.*, 2022; Acharya *et al.*, 2023; Quesada-Ocampo *et al.*, 2023; Santos *et al.*, 2023 and Sharma *et al.*, 2023).

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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