Chapter

Phytophthora capsici on *Capsicum* Plants: A Destructive Pathogen in Chili and Pepper Crops

Anthony A. Moreira-Morrillo, Álvaro Monteros-Altamirano, Ailton Reis and Felipe R. Garcés-Fiallos

Abstract

Capsicum from tropical and subtropical America, is an important genus for the nutritional, economic and cultural values of its species. At the same time, the *Capsicum* species are affected by diseases caused by viruses, bacteria, fungi and pseudofungi, in particular the oomycete *Phytophthora capsici*. This phytopathogen causes great damage and losses in different *Capsicum* species, because it infects all plant organs causing root, crown and fruit rot; and, leaf blight. The polycyclic dispersion through zoospores and sporangia, the limited availability of resistant genotypes, and the reduced diversity of effective oomyceticides (fungicides), make *P. capsici* one of the most complex phytopathogens to be managed worldwide specially in field conditions. However, successful management of *P. capsici* depends on the knowledge of the pathogen, its interaction with the susceptible host and the methods of control used. Thus, this chapter addressed the etiology, symptomatology, occurrence and management of the disease. Additionally, the cycle of the disease is discussed in a holistic and simple way.

Keywords: *Capsicum* spp., root and crown rot, leaf blight, fruit rot, *Phytophthora capsici* cycle, disease management

1. Introduction

Capsicum is a genus native to tropical and subtropical America [1], where species such as *C. annuum* L., *C. baccatum* L., *C. chinense* Jacq., *C. frutescens* L., and *C. pubescens* R. & P. [2, 3] excel for its great nutritional, economic [4], and cultural value in the gastronomy of several countries [5]. These vegetables, also commonly known as sweet peppers or hot peppers, can reach a global production of 38 million tons [6]. However, like other crops, peppers are not exempt from disease attacks, caused mainly by viruses, bacteria (leaf spots and vascular wilts), fungi (cercosporiosis, powdery mildew and anthracnose), and mainly pseudofungi (rot of roots, stems and fruits; and, leaf blight) [7].

Phytophthora capsici is an oomycete present in several parts of the world, being reported as the causal agent of countless diseases in different crops of agricultural importance such as Cucurbitaceae, Rosaceae, Fabaceae, Liliaceae and Solanaceae [8]. This phytopathogen in *Capsicum* can cause damage of up to 100% due to its rapid spread in field conditions and represents around $100 million in losses [9, 10] for which it is considered the fifth most destructive oomycete in the world [11]. Due to the reach of aerial tissues, its polycyclic characteristic makes *P. capsici* one of the most complex phytopathogens to be managed [12].

Resistant plants can generally activate different biochemical, structural and molecular defense mechanisms against the infection of *P. capsici* [13, 14]; conversely, susceptible plants can be infected and colonized by the pathogen. Since most of the common commercial genotypes of *Capsicum* are susceptible, i.e. Chinese Giant (CG), California Wonder (CW), Osh Kosh (OK) and Yolo Wonder (YW), farmers use a considerable amount of oomyceticides to control its attack [3]. However, there are other measures that can be used in an integrated manner to drastically reduce infection of *P. capsici* i.e. crop rotation, irrigation management, use of biocontrole agents, among others. For example, the rate of progress of collar rot in *Capsicum* plants can be reduced considerably by applying *Trichoderma harzianum* [15, 16]. Therefore, due to the importance of *P. capsici* in *Capsicum* spp., this chapter address the etiology, symptomatology, worldwide occurrence and biological cycle of the pathogen in the different plant tissues; and, finally describes the disease management measures to be used either in isolation or integrated approach.

2. Etiology

Phytophthora capsici belongs to the Phylum: Oomycota, Class: Oomycetes, Order: Peronosporales, and Family: Peronosporaceae (**Figure 1**). Under laboratory conditions, the phytopathogen can grow in culture media based on V8 juice [17, 18], carrot, tomato, and water agar. Although the growth pattern of the oomycete can be different between isolates, the shape of the colonies is generally rounded and whitish [19], standing out those with a slightly stellate pattern (**Figure 1A**). The phytopathogen characteristics are: elongated, coenocytic hyphae (**Figure 1B**); stretched cells with several nuclei [20], measuring between 3 and 8 μm wide [21]; oospores with a diameter between 25.6 and 52.4 μm (**Figure 1B**) [22]. Its sporangia (**Figure 1C**) are abundant and formed individually or branched, flaccid or closely spaced [21], mainly spherical (globose, ellipsoid and ovoid), pear-shaped (obpiriform and obturbinate), lemon (limoniform), and/or in some cases irregular (distorted) [19], measuring between 32.1 and 51.3 μm long and 23.3–37.1 μm wide [20]. The main pedicel has a length of 38.3 to 84.4 μm [22]. The zoospores released from the sporangia (**Figure 1D**) have a diameter between 5.84 and 11.3 μm [20]. Although resistance structures such as chlamydospores can also be formed by some *Phytophthora* species [21], it is not common in *P. capsici* [18].

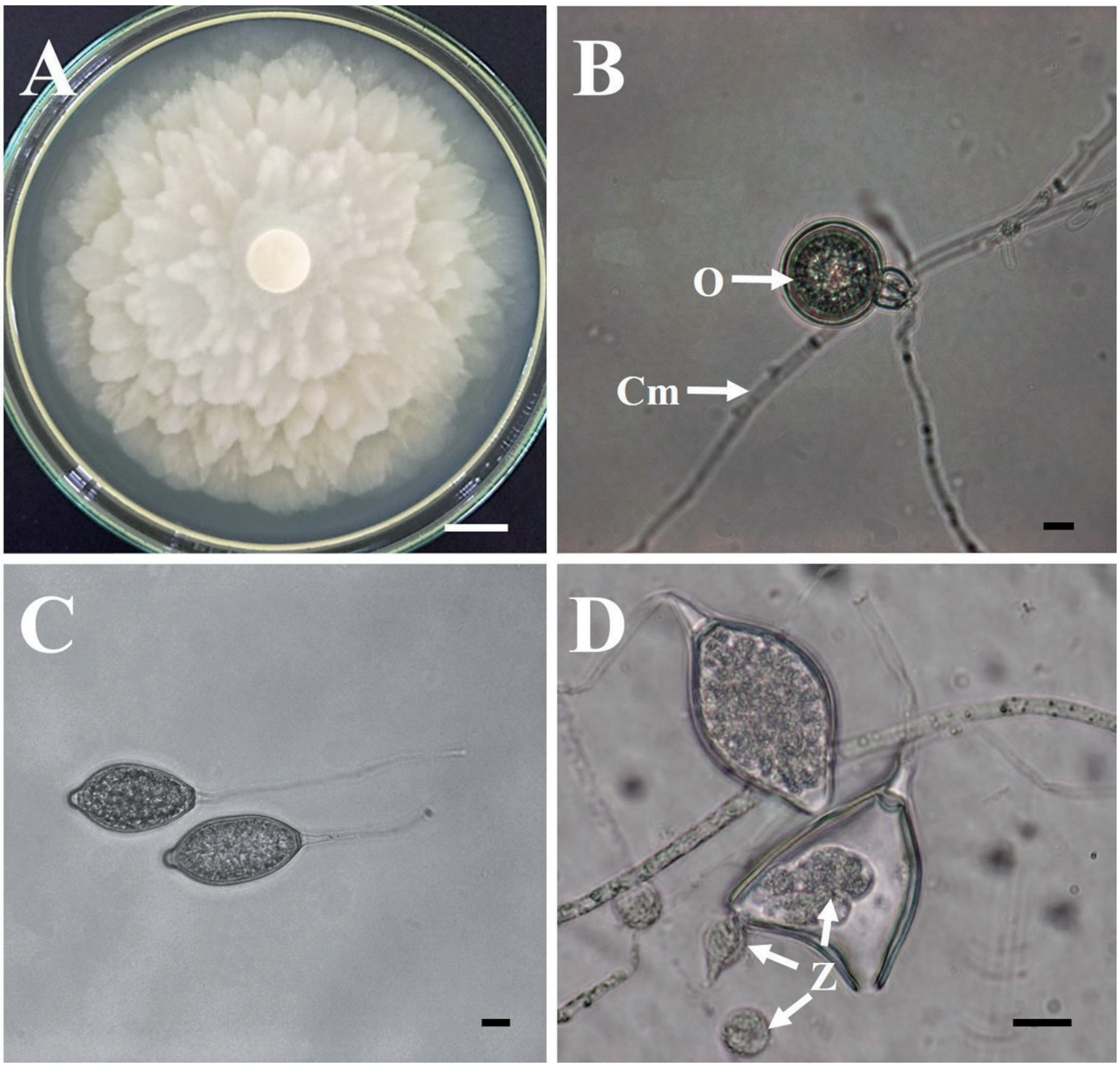

Figure 1.
Morphological structures of Phytophthora capsici*: A) Colony morphology after 14 d growth at 24 ± 3°C on potato dextrose agar; B) Coenocytic mycelium, and oospore; C) Papillate limoniform sporangia; D) Zospores inside and outside of sporangia. Cm: Coenocytic mycelium; O: Oospore; Z: Zoospores. Bars: 1 cm (A) and 10 μm (B-D). Source: Unpublished photographs from the authors.*

3. Symptomatology

Several symptoms (**Figure 2**) may be caused by *P. capsici* in different phenological stages of the plant [23], which can vary depending on host resistance, affected tissue and/or climatic conditions [24]. In susceptible plants, the initial symptoms can appear between four and seven days after inoculation (DAI), and can die at approximately 10 DAI [25, 26]. Meanwhile, in resistant plants after 10 DAI, slight lesions appear, mainly due to the ability to counteract the advance of colonization [3, 27].

The root system is the first affected tissue (**Figure 2A**), showing a brown rot [3]. Later, brown lesions with a rough shape can be observed on the crown tissues (**Figure 2A**) [28]. Other symptoms observed in adult plants are stunting (**Figure 2B**) and generalized wilting (**Figure 2C**) [9, 26, 29]. In the foliar area, leaf blight may be

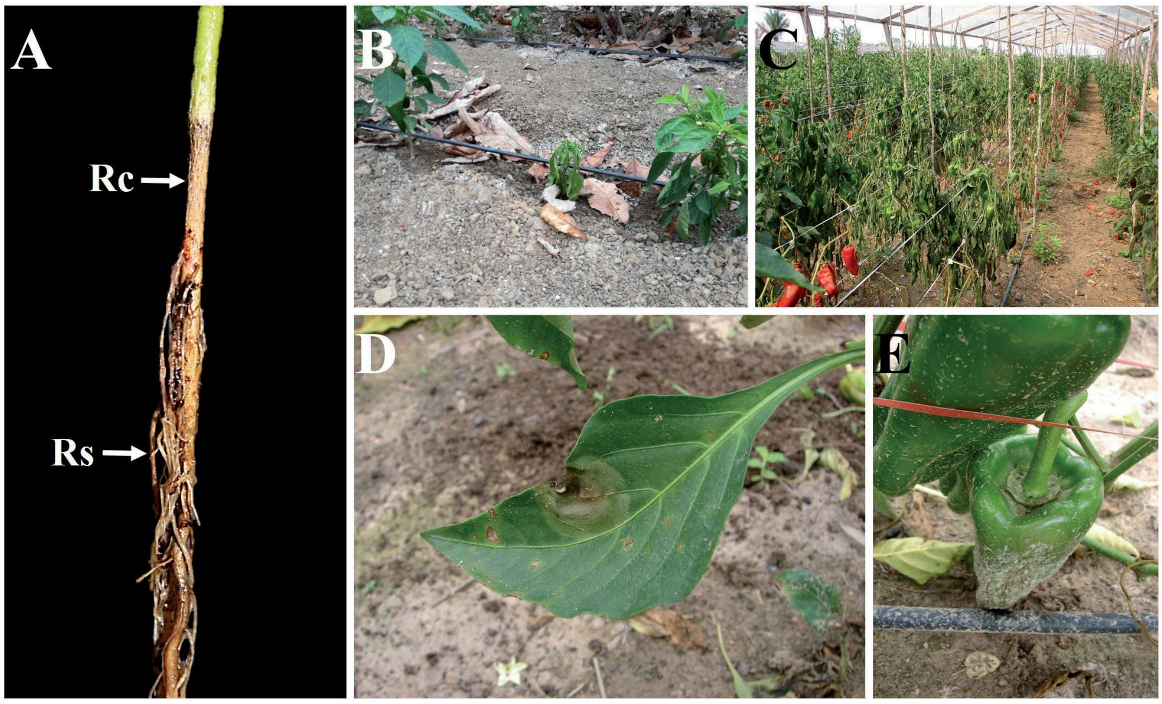

Figure 2.
Symptoms caused by Phytophthora capsici *on different organs of* Capsicum *plants: A) root and crown rot; B) dwarf; C) wilting; D) leaf blight; E) fruit rot. Rc: Root crown. Rs: Root system. Source: Unpublished photographs from the authors.*

observed (**Figure 2D**) starting with small dark water-soaked lesions, which later become necrotic with a light brown center and dark edges [30, 31]. Fruits are also affected by the oomycete, initially, minute lesions with clear whitish centers are observed in the tissue [32, 33], advancing rapidly until this organ completely rots (**Figure 2E**) [18]. This last symptom is often presented in young fruits, compared to mature fruits that present more resistance to *P. capsici* [34].

4. Occurrence of *Phytophthora capsici* worldwide

Phytophthora capsici has been reported affecting various crops in several countries, however, we focus on the pathogen's reports on *Capsicum* spp. (**Figure 3**). The first report of the oomycete dates back to 1922 in New Mexico, attacking branches and fruits of chili plants [35]. Subsequently, the pathogen was reported in the Netherlands [28], Bulgaria [36], Brazil [37], South Africa [38], Korea [39] and Tunisia [40], all affecting pepper.

From 2002 onwards, the oomycete was reported affecting *Capsicum* spp. crops in different countries and regions such as Egypt [41], Spain [42], and Italy [43], China [44], Canada [45], Taiwan [46], Peru [47], Algeria [48], Mexico [49], Laos PDR [29], Pakistan, [50], Bhutan [22], Indonesia [51], Trinidad and Tobago [20] and Ecuador [52]. Despite the oomycete's reported geographical distribution affecting mainly chili and sweet peppers, some other countries could be affected, but official reports are missing. [9].

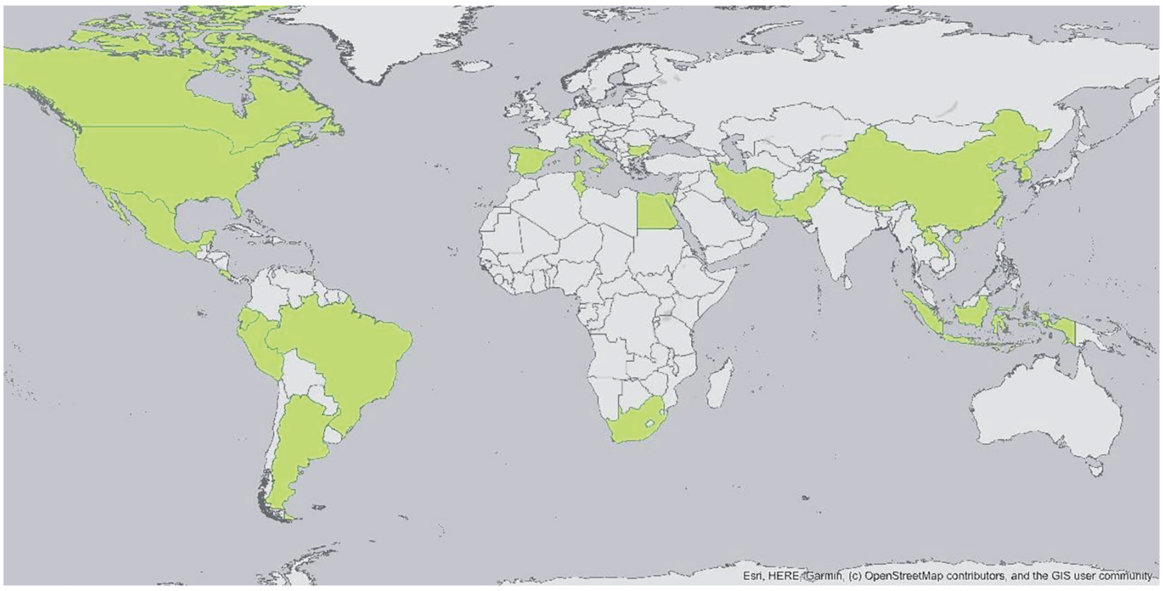

Figure 3.
Global geographic distribution of Phytophthora capsici *affecting tissues of* Capsicum *plants. This figure was developed with the help of the BioRender platform. Source: Unpublished photographs from the authors.*

5. Disease cycle of *Phytophthora capsici*

Every disease begins with the survival of the phytopathogen (source of primary inoculum); in the case of *P. capsici* (**Figure 4**) the mycelium can survive in the soil and cultural debris, or in the weeds that serve as facultative hosts. Besides, the oospores

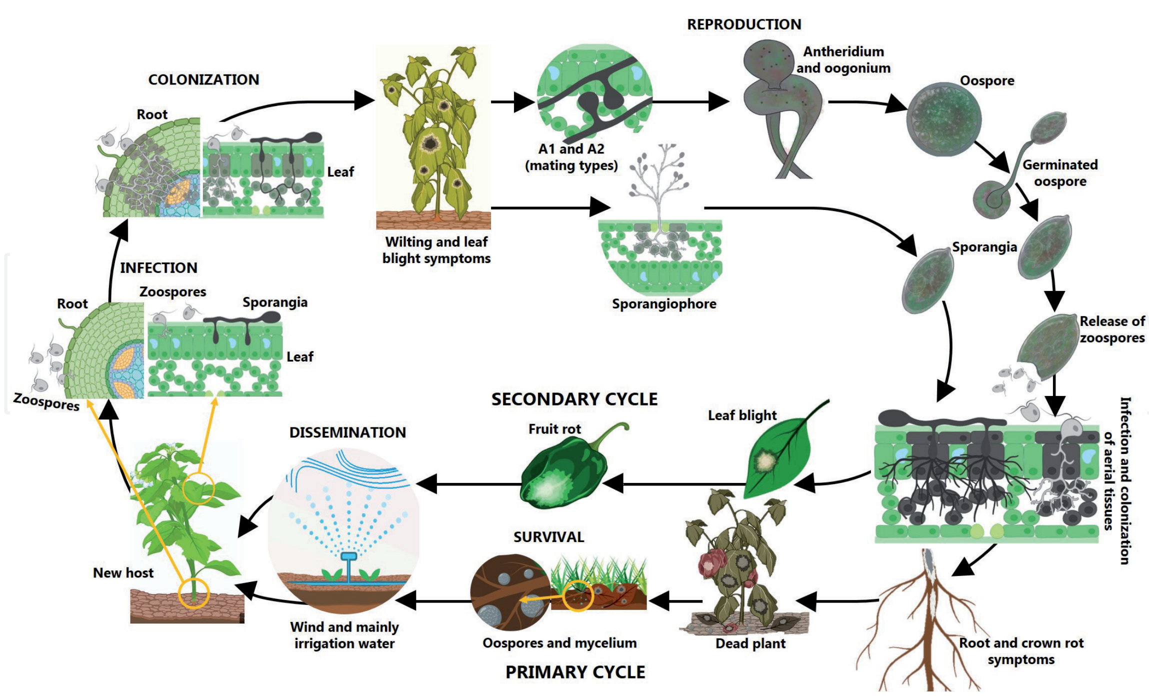

Figure 4.
Biological cycle of Phytophthora capsici *causing root, crown and fruit rot, and foliar blight in* Capsicum *plants. This figure was developed with the help of the BioRender platform. Source: Unpublished photographs from the authors.*

can persist for long periods in the soil [16, 53, 54]. From these structures, sporangia are formed, which spread towards the tissues of the host located in near or distant crops, mainly through water (rainfall or irrigation) [18]. Under conditions of high relative humidity and between 27 and 32°C, the sporangia release motile biflagellate zoospores that swim through the irrigation water until they reach plant tissues [12, 55]. Although it is mentioned that the wind is also a disseminating factor of the pathogen [56], this is not fully accepted yet.

Sporangia can germinate directly on the plant surface, forming a germ tube that penetrates the anticlinal walls of rhizodermal cells [12]. Likewise, they can do it indirectly through zoospores released from the interior of sporangia that encyst on the surface of root, crown and leaf tissues, subsequently producing a germ tube, and finally an appressorium used to penetrate epidermal cells [55–57]. *Phytophthora capsici* is a hemibiotrophic phytopathogen, which initially presents a biotrophic lifestyle, followed by a necrotrophic phase [58]. In fact, once the penetrating hyphae of the oomycete enter plant tissues intercellularly, these structures form haustoria to remove nutrients from the cells [57, 58]. Subsequently, vegetative hyphae and haustoria are formed in the form of lateral branches that colonize intracellularly and epicuticularly [27]. Finally, *P. capsici* intensely colonizes epidermal, vascular (phloem, xylem) and parenchymal cells [16]. Both the infection and colonization processes (latent period) can last between four and seven days [3].

The last phase of the primary cycle of the disease is completed with the reproduction of the pathogen, which occurs on the external surface of the host. *Phytophthora capsici* is a heterothallic species that has one of two mating types called A1 and A2, producing a male gametangium (antheridium) and a female gametangium (oogonium), resulting in sexual spores called oospores, with thick walls adapted to survive winter and unfavorable weather conditions [30, 55, 59]. These reproductive structures go through a rest period and serve for the survival of the phytopathogen [53]. There is also asexual reproduction that is characterized by the formation of sporangia from branched sporangiophores [30, 55]. The production of sporangia occurs between 25 and 30°C, under conditions of high relative humidity, and ≈90 hours after infection, which will produce zoospores by cytoplasmic cleavage [24, 55].

Although root and crown rot are monocyclic diseases, others such as leaf blight and fruit rot would be polycyclic. Thus, the sporangia of *P. capsici* would function as a secondary inoculum [53, 57]. These structures or propagules would reach the aerial tissues through water splashes, initiating a new infectious cycle [53, 60, 61], repeating the previously mentioned phases of infection, colonization and reproduction. The ability of the phytopathogen to reach practically all plant tissues makes its management complex.

6. Disease management

The management of diseases caused by *P. capsici* may be very difficult and economically expensive, especially due to the excessive use of oomyceticides (formerly called fungicides). However, there are different alternatives which used in an integrated manner during the pre-sowing, production and post-harvest stages could reduce damage and losses in *Capsicum* crops. These alternatives are: the use of resistant cultivars, well-drained soils, crop rotation, soil treatments, tillage methods, irrigation control, improvement of irrigation water quality, and use of plastic mulches [12]. In any case, the infection of different plant organs of *Capsicum* (**Figure 2**) by

P. caspici makes the integrated implementation of measures by farmers, complex but worthwhile [16, 18].

6.1 Genetic control

Obtaining resistant germplasm of *Capsicum* to *P. capsici* is a complex task, requiring different breeding techniques and germplasm screening including landraces as sources of resistance [9]. So far there are some resistant commercial cultivars such as Nathalie, Paladin, Ungara, Violeta, Ayesha, Violeta 1, Sempurna, and Ayesha Ungu, which are being used worldwide [3, 51]. Likewise, there are different resistant landraces such as CM-334, (*C. annuum*) ECU-12831 (*C. baccatum*), ECU-9129, (*C. chinense*) Code 5 (*C. frutescens*), ECU-1296 (*C. frutescens*), found in Ecuador and Mexico [3, 62] that could be used in breeding programs.

In one hand, *P. capsici* has developed different mechanisms to attack plants and to obtain its necessary nutrients, while on the other hand, plants have developed a complex defense system that prevents the entry or limits the advance of the oomycete in plant tissue, including physical, biochemical and molecular mechanisms [13, 14, 63]. One of the first barriers in pepper plants (*C. annuum*) limiting *P. capsici* infection is a thick cell wall and a high content of phenolics and flavonoids [16], such as the soluble phenols chlorogenic acid, luteolin glycoside, apiosil glucoside of luteolin, and aglycone apigenin [64, 65]. Other mechanisms include the synthesis of antimicrobial phytoalexins, the induction of hydrolytic enzymes such as chitinase and glucanase, and the production of proteins rich in hydroxyproline, reactive oxygen species (ROS), and capsidiol [66, 67]. Regarding the latter mechanism, this *Capsicum* phytoalexin could inhibit oomycete development [66, 67]. These and other mechanisms make *Capsicum* plants prevent or considerably delay the infection, colonization and reproduction of *P. capsici* in the different subterranean or aerial tissues.

6.2 Biological control

The current need to consume healthy foods, free of synthetic-pesticide residues [68], has led to the promotion of alternatives such as the use of effective biological control agents i.e. *Bacillus* spp., *Trichoderma* spp., among others, which if used under suitable climatic conditions will contribute significantly and economically to the prevention and management of diseases caused by *P. capsici*, in addition to promoting the growth of *Capsicum* [69, 70].

The use of microorganisms such as *Bacillus* spp. and *Trichoderma* spp. are highly valuable alternatives for the management of diseases caused by *P. capsici*. Under laboratory and green house conditions, *Bacillus amyloliquefaciens* (strain PsL) can reduce the mycelial growth of *P. capsici* by up to 46%, in addition to the growth promotion of *P. capsici* pepper plants [70]. *Bacillus subtilis* (isolates R13 and R33) can reduce the incidence of foliar blight between 71 and 87% [23]. *In vitro* and *in vivo* experiments of native *Trichoderma* strains against *P. capsici* isolates in *C. pubescens* plants, showed that *T. harzianum* inhibits the radial growth of the phytopathogen by 43%, and reduces plant mortality by 10% at 20 DAI [71].

Endophytic microorganisms can also be used in biological control. Some of them such as *Nigrospora sphaerica*, *Enterobacter* sp. and *Dothideales* sp. have been used as biocontrollers of pathogens affecting *C. annuum*, such as *P. capsici* [72]. *Nigrospora sphaerica* (isolate A22F1) was used to control *P capsici* in susceptible seedlings of *C. annuum* (cvs. California Wonder, Numex spring and Pepper cayene), observing a considerable reduction in root rot compared to control. Recently, a metagenomic study [73] found different fungal species that are used in the biological control of phytopathogens associated with the mycobiome of resistant and susceptible hypocotyls, infected or not with *P. capsici*.

6.3 Cultural control

Cultural control is based on the use of measures that favor the development of the crop, and at the same time, affecting the phytopathogen, in order to reduce the intensity of the disease [74]. Strategies include limiting soil saturation, water accumulation in plots, and movement of infected plant debris or infested soil within a field [18]. Crop rotation is another very important aspect to consider because it affects the survival of the phytopathogen and the host range [26] e.g. crop rotation for 3 years can considerably reduce the propagules (mainly oospores) of *P. capsici*, which have the ability to remain in the soil for long periods of time [16, 22].

6.4 Chemical control

The use of oomyceticides (previously called fungicides) is common in the management of diseases caused by *P. capsici* in *Capsicum* plants (Table 1), especially those that contain molecules with a direct mode of action on the phytopathogen [75]. The efficacy of these oomyceticides, of synthetic origin, has been demonstrated under laboratory and field conditions. For example, Mancozeb 64% + Metalaxyl 4% (7.5 g L^{-1}) or Copper sulfate pentahydrate (2.5 mL L^{-1}) applied to the soil, and Potassium phosphonate (5 mL L^{-1}) applied to the leaf area, can totally reduce the incidence of root and crown rot [47]. Also, the use of Fosetil Aluminum (2.5 kg ha^{-1}) applied to the soil (drench) can reduce up to 100% of wilting in pepper plants [76]. Other molecules such as ametoctradine + dimethomorph, cyazofamid, dimethomorph, famoxadon + cymoxanil, fluazinam, fluopicolide, mandipropamide, mefenoxam, phosphonates, and zoxamide + mancozeb, can also be used to control damping-off, leaf blight and fruit rot [26].

Despite the success achieved over the years with the use of chemical control, the inappropriate use of molecules has made some *P. capsici* isolates insensitive to commercial oomyceticides such as metalaxyl and mefenoxam [77, 78]. A solution to reduce these effects on the oomycete is the use of active ingredients such as mandipropamide and dimethomorph, considered molecules with low to medium risk of resistance [79, 80]. In order to reduce the selection pressure by the phytopathogen, the farmer must have a wide range of molecules applied in periodic and scheduled rotation during each crop cycle [81], and even use mixtures that have systemic and protective modes of action.

6.5 Integrated disease management

Integrated disease management (IDM) aims to minimize the biological activity of the pathogen and increase crop productivity, involving the use of various techniques in favor of the environment by avoiding the excessive use of chemical molecules and reducing control costs of *P. capsici* [80]. To effectively manage diseases caused by *P. capsici* in *Capsicum,* different management strategies should be integrated in either agroecological, conventional or other production systems [81]. Usually a single strategy is ineffective for the management of *P. capsici* [80]; for this, IDM is based on immunization, exclusion, eradication and crop protection mainly including soil and plant management through soil amendments, solarization, crop cover, water treatment, seed treatment (with a biofungicide to improve germination and reduce the incidence of damping-off), and others [82–84].

7. Conclusions

Without a doubt *Phytophthora capsici* is a dangerous pathogen for horticultural fields; negatively affecting both young and adult chili and sweet pepper plants. The versatility of this plant pathogen to spread in the field, and to infect and to colonize practically all the plant organs, make the management of the diseases a huge challenge. However, different control methods such as genetic, biological, cultural and chemical or integrated disease management may be integrated to mitigate damages and losses in *Capsicum* spp. production fields. Despite the advances already made around *P. capsici*, there is still much to study and learn about this phytopathogen.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this chapter.

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