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Phytophthora capsici: the diseases it causes and management strategies to produce healthier vegetable crops

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ABSTRACT

Vegetable crops are exposed to constant infection by numerous diseases, including those caused by the oomycete *Phytophthora capsici*. This microorganism is a polyphagous plant pathogen, capable of infecting dozens of plant species, including cultivated plants and weeds. The aim of this review is to address topics related to etiology and symptoms of the diseases caused by this oomycete (leaf blight, root rot, crown rot and fruit rot), as well as the integration and application of different control alternatives, such as genetics, cultural, physical, biological, and chemical. Crops such as sweet pepper (*Capsicum annuum*), chili pepper (*Capsicum* spp.), tomato (*Solanum lycopersicum*), eggplant (*S. melongena*), cucurbits (*Cucumis sativus, Cucurbita* spp.), among others, are subject to considerable economic losses induced by this pathogen. High soil humidity, high temperatures, resistance structures of the pathogen (oospores), scarce availability of resistant cultivars and a reduced range of effective fungicides are conditions that difficult the management of diseases caused by *P. capsici* in the field. Despite the irrefutable importance of this pathogen, the existing information regarding its integrated management is limited. Therefore, a successful management will depend to a great extent on its knowledge and its control. Thus, the joint application of different control strategies seeks to maintain the pathogen at low population levels and also keeping the epidemics under the threshold of economic loss. At the end, an integrated pest management approach for *P. capsici* could result in higher economic returns, long-term sustainable harvests, reduction of the environment impact and better quality products for consumers.

Keywords: Solanaceae, Cucurbitaceae, integrated disease management, oomycete, soil borne pathogen.

RESUMO

***Phytophthora capsici*: as doenças que causa e estratégias de manejo para produzir hortaliças mais saudáveis**

As hortaliças estão expostas a constantes infecções por inúmeras doenças, incluindo as causadas pelo oomiceto *Phytophthora capsici*. Este microrganismo é um patógeno vegetal polífago, capaz de infectar dezenas de espécies de plantas cultivadas ou invasoras. O objetivo desta revisão é abordar tópicos relacionados à etiologia e sintomas das doenças causadas por este oomiceto (queima de folhas, podridão da raiz, podridão da coroa e podridão dos frutos), bem como também a integração e aplicação de diferentes alternativas de controle como genética, cultural, física, biológica e química. É assim que, culturas como pimentão (*Capsicum annuum*), pimenta (*Capsicum* spp.), tomate (*Solanum lycopersicum*), berinjela (*S. melongena*), cucurbitáceas (*Cucumis sativus*, *Cucurbita* spp.), entre outras, estão sujeitas a perdas econômicas consideráveis. Elevada umidade do solo, altas temperaturas, estruturas de resistência do patógeno (oósporos), baixa disponibilidade de cultivares resistentes e reduzida disponibilidade de fungicidas eficazes são condições que dificultam o manejo de doenças causadas por *P. capsici* no campo. Apesar da importância irrefutável deste patógeno, as informações existentes sobre seu manejo integrado são limitadas. Portanto, uma gestão bem sucedida das lavouras dependerá em grande parte de seu conhecimento e controle. Assim, a aplicação conjunta de diferentes estratégias de controle visa manter o patógeno em níveis populacionais baixos e também manter a epidemia sob o limiar de danos econômicos. No final, um manejo integrado para *P. capsici* poderá gerar maiores retornos econômicos, colheitas sustentáveis de longo prazo, redução do impacto ambiental e produtos de melhor qualidade para os consumidores.

Palavras-chave: Solanaceae, Cucurbitaceae, manejo integrado de doenças, oomiceto, patógeno transmitido pelo solo.

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The plant pathogen *Phytophthora capsici* is a highly destructive oomycete, causing various symptoms such as root, stem, fruit and crown rot in vegetables, mainly in the Solanaceae and Cucurbitaceae families (Dunn *et al*., 2014). It was isolated and first reported in New Mexico by Leonian (1922) from pepper plants (*Capsicum annuum*). For several years this pathogen was associated with species of the genus *Capsicum* as the sole hosts. However, current reports indicate that there are several plant species that can be infected by this oomycete, including tomato, eggplant, cucurbits (cucumber, watermelon, melon and squash), as well as some legumes such as broad beans, common beans, runner beans and strawberry, totaling 49 botanical families (Reis *et al*., 2007; Lamour *et al*., 2012; Barboza *et al*., 2017; Petry *et al*., 2017a; Abeysekara *et al*., 2019; Parada-Rojas & Quesada-Ocampo, 2019; Farr & Rossman, 2020). This makes *P. capsici* one of the most destructive and widespread soil-borne pathogens, limiting the production of many species of agricultural importance worldwide, especially in host plants within the Solanaceae and Cucurbitaceae families (Castro *et al*., 2014; Reis *et al*., 2018).

Diseases caused by *P. capsici* can reduce productivity up to 100% when the infection occurs early in the season and conditions favor the disease (Liu *et al*., 2014). This pathogen can survive for many years (>24 months) in the absence of a host through resistant structures called oospores, a condition that makes its management very challenging (Gandariasbeitia *et al*., 2019). Temperatures between 25 and 28°C and high humidity (>80%) favor fungal infection and disease spread promoting large epidemics (Granke *et al*., 2009). Soils with high humidity are ideal for the primary inoculum (oospores) to initiate infection on susceptible plants (Gandariasbeitia *et al*., 2019).

The management of diseases caused by *P. capsici* is expensive and difficult (Granke *et al*., 2012a). Chemical control still plays a prominent role in controlling crop pests in spite of its innumerable problems such as changes in physical-chemical properties of soils, accumulation of toxic compounds in fruits and fungicide resistance on pathogen populations (Dunn *et al*., 2010; Hung-Wan & Liew, 2020). This is why the combined application of control methods, such as genetic, physical, cultural, biological and chemical (use of fungicides / oomiceticides of synthetic origin) from an integrated management approach constitutes the best option to reduce economic losses in any crop, besides being more environmental friendly (Majid *et al*., 2016).

The use of diversified and integrated disease management practices minimizes the disturbance of the natural dynamics of an agro-ecosystem (ecological niches, microbiome), with a positive effect for sustainable agricultural production (Abrol & Shankar, 2012). Therefore, this review into each of the topics related to the integrated management of *P. capsici*, aimed to provide the reader with current technical information, in order to avoid and / or reduce damage to horticultural production systems associated with it.

Symptoms associated with *Phytophthora capsici*

Regardless their species, plants may be affected during any phenological stage and symptoms can appear in various organs (Hung-Wan & Liew, 2020) (Figure 1), these being dependent on environmental conditions, pathogen's virulence and host resistance levels (Reis *et al*., 2007; Granke *et al*., 2012b; Barchenger *et al*., 2018; Saltos *et al*., 2021). Young and immature tissues are often more susceptible to infection (Roberts *et al*., 1999).

Symptoms of *P. capsici* on adult plants begin with sudden yellowing and wilting of the leaves as a consequence of the collapse of the water-conducting tissues of the roots and stems (Figure 1A) (Ristaino & Johnston, 1999; Barchenger *et al*., 2018). Roots present small, dark-colored lesions that expand rapidly until complete rotting (Figure 1B) (Ristaino & Johnston, 1999; Reis *et al*., 2007; Lamour *et al*., 2012). In advanced stages of the disease, dry, dark brown or black lesions are developed on the cortical tissue of the crown near the soil line (Figure 1C). Symptoms of leaf blight include dark, watery spots that rapidly increase in size and become necrotic in appearance (Figure 1D) (Ristaino & Johnston, 1999; Walker & Bosland, 1999). The fruits first show water-soaked lesions with clear centers, which expand rapidly, usually covered with white structures of the pathogen, and completely rot the fruit in a few days (Figures 1F to 1J) (Ristaino &

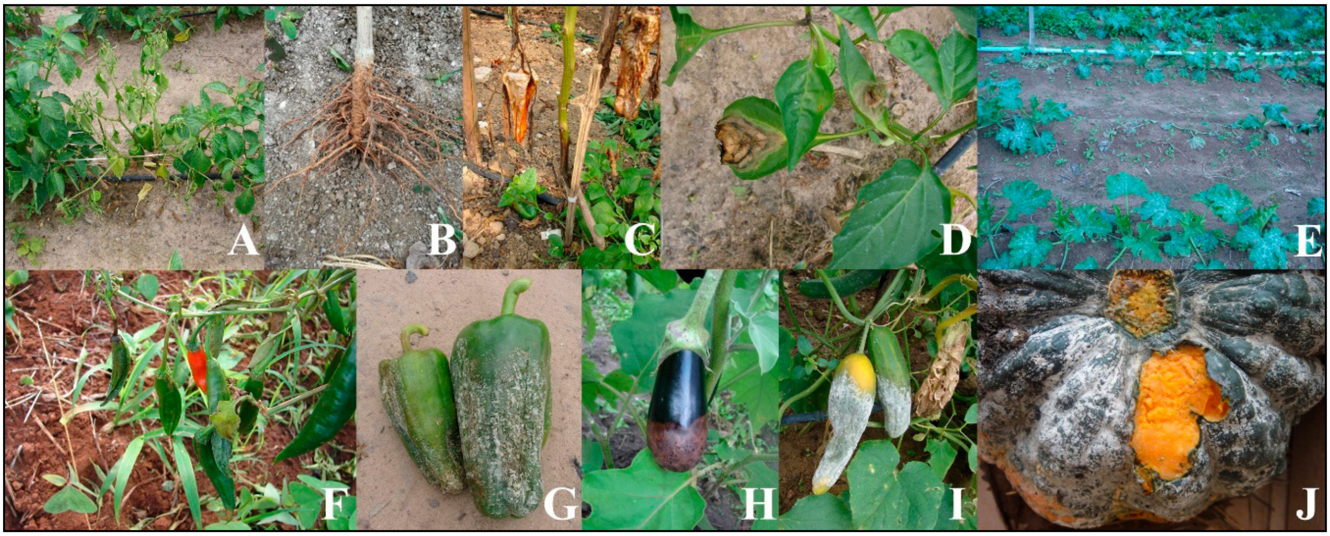

Figure 1. Symptoms caused by *Phytophthora capsici* in cucurbits and solanaceous plants: (A) wilt, (B) root rot, (C) crown and stem rot, and (D) leaf blight on sweet pepper (*Capsicum annum*); (E) damping-off on zucchini plants (*Cucurbita pepo*); Fruit rot on (F) chili and (G) sweet pepper (*Capsicum* spp.), (H) eggplant (*Solanum melongena*), (I) cucumber (*Cucumis sativus*) and (J) pumpkin (*C. maxima*) plants. Source: Unpublished photographs from the authors. Ecuador, Technical University of Manabí, 2018-2020.

Johnston, 1999; Reis *et al*., 2007). Symptom development is not uniform, depending, among other factors, on the degree of resistance of the host (Drenth & Sendall, 2001).

Description of the pathogen

Phytophthora capsici belongs to the Kingdom Chromist (Stramenopile), Phylum Oomycota, Class Peronosporea, Order Peronosporales and Family Peronosporaceae (Roskov *et al*., 2016). It has coenocytic mycelium and produces ovoid, ellipsoid and papillate zoosporangia which contains reniform and biflagellate zoospores (Vélez-Olmedo *et al*., 2020) which are released quickly, isolated or grouped, and are chemotactically and electrostatically attracted to the surfaces of host plants (Fawke *et al*., 2015).

The pathogen is a heterothallic species, with isolates having one of two mating types (designated A1 and A2). Both mating types are required in close proximity for mating to occur (Lamour *et al*., 2012). It produces a male gametangium (antheridium), and a female gametangium (oogonium). The antheridium is amphigynous in *P. capsici*. Following by the formation of the antheridium and oogonium, meiosis occurs within the gametangia, and plasmogamy and karyogamy result in the formation of oospores (sexual spores). Oospore usually go through a rest period, and it serves also as an overwintering structure (Ristaino & Johnston, 1999). The oospores diameter ranges between 15 μm and 40 μm. They germinate after a period of rest (Erwin & Ribeiro, 1996). Under favorable environmental conditions, *P. capsici* will often produce massive numbers of sporangia on the surface of infected tissue (Lamour *et al*., 2012). They also may be produced *in vitro* in V8-agar culture medium. Sporangia can have ovoid, elliptical, papillate or semi-papillate shapes (with sizes in a length:diameter ratio of 2.1:1.3). This oomycete rarely produces chlamydospores (resistance structures), but when these are produced they may be of different types: intercalary (formed between hyphae); terminal (at the end of the hypha) with a size ranging from 20.0 μm to 27.5 μm in diameter (Islam *et al*., 2004); and globose with long pedicels (Vélez-Olmedo *et al*., 2020).

Like other *Phytophthora* species, under favorable conditions, *P. capsici* can spread rapidly between plants throughout the field due to multiple sporangium production and infection cycles. It has the potential for rapid polycyclic disease development from a limited amount of inoculum (Majid *et al*., 2016). Rainfall plays an important role for the release and dispersal of sporangia, therefore, the rapid increase of the epidemic in the field (Sanogo & Ji, 2013).

Plant-pathogen relation

Phytophthora capsici is a hemi-biotrophic pathogen, initially displaying a biotrophic lifestyle, followed by a change to a necrotrophic phase (Jupe *et al*., 2013). High humidity in the soil favors the germination of oospores producing germination tube or sporangium (Hausbeck & Lamour, 2004). Through the germination tube, the pathogen can penetrate directly through the tissues of the susceptible host or by zoospores produced from sporangia (Waterhouse *et al*., 1983). Biflagellate mobile zoospores move to the surface of the host and initiate the infection process (Fawke *et al*., 2015). However, all plants present preformed structural and biochemical barriers that represent a limitation for the penetration of the pathogen (Kale & Tyler, 2011).

During the initial events of the plant-pathogen interaction, the oomycete releases an array of biological weapons, called elicitors (Elicitins, NLPs, CRNs, SCRs) and pathogen-associated molecular patterns (PAMPs) (Hein *et al*., 2009). These are recognized by specific receptors located in the plant cell membranes, giving rise to an immunity triggered by PAMP (PTI). PTI constitutes the first line of defense that must be overcome by the pathogen for a successful colonization of the tissues. This is achieved through virulence determinants, called effectors, which suppress the plant innate immunity (Jupe *et al*., 2013). Effector-triggered susceptibility (ETS) includes the suppression of PTI, which represents the first phase of events at the molecular level in the plant-pathogens interaction (Hein *et al*., 2009). Resistance proteins (PR) represent the second molecular barrier that detects effectors (avirulence proteins, AVRs), conferring immunity to the pathogen that may be successful in suppressing PTI. The effector-triggered immunity (ETI) constitutes the second line of defense at the molecular level between the plant and oomycete (Hein *et al*., 2009). Once all these restrictions have been overcome, the penetration of tissues by the oomycete is inevitable, thus initiating the infectious process.

Subsequently, the hyphae invade and colonize the tissues intercellularly and haustorium is emitted, which can infect the cells of the cortical and vascular tissue of different plant organs (Fawke *et al*., 2015). Finally, under optimal conditions (25-30°C and high relative humidity) the sporulation phase (production of sporangia) occurs outside the tissues, ≈90 hours after infection (Lamour *et al*., 2012).

***Phytophthora capsici* diseases methods of control**

The integrated management strategy to control any plant disease, not differently from those caused by *P. capsici*, is fundamentally based on the selection and implementation of genetic, cultural, physical, biological and chemical measures, aiming to avoid, reduce and / or maintain disease severity below the economic threshold of damage to crops (Abrol & Shankar, 2012).

Genetic control

Genetic resistance of the host constitutes the main approach of any integrated program for *P. capsici* management, although it usually cannot be considered as the sole control measure (Hausbeck & Lamour, 2004; Granke *et al*., 2012a).

Some sources of resistance to *P. capsici* have been found in tomato, sweet and chili pepper, muskmelon and squash (Padley *et al*., 2009; Foster & Hausbeck, 2010; Quesada-Ocampo & Hausbeck, 2010; Dunn *et al*., 2014; Pontes *et al*., 2014; Petry *et al*., 2017b). However, the majority of commercial varieties currently available, independent on the host species, lack resistance (Ando *et al*., 2009; Lamour *et al*., 2012; Krasnow *et al.*, 2017), because introgression of resistance genes from wild species onto commercial genotypes is usually complex. Examples of resistant commercial pepper genotypes to *P. capsici* are: Nathalie (Figure 2), Criollo de Morelos 334 and Paladín (Dunn *et al.*, 2014; Dunn & Smart, 2015; Saltos *et al.*, 2021). In a recent work carried out in Ecuador by Saltos *et al.* (2021), *Capsicum* genotypes Nathalie, ECU-12831, ECU-9129, Código 5, and ECU-1296 were found to be resistant to root and crown rot.

There are great challenges in the plant breeding of vegetable crops to confer resistance to *P. capsici*; among them, different inheritance models have been reported in different sources of resistance (Barchenger *et al.*, 2018). Resistance to *P. capsici* is expressed in different ways in *Capsicum* spp., for instance, the resistance of the cultivar Criollo de Morelos 334, was associated with the expression of two genes (Sy *et al.*, 2005), whilst other studies related resistance to only one dominant gene, as well as resistance of multiple genes with additive or epistatic effects (Barchenger *et al.*, 2018).

Some genes confer resistance to root rot, crown rot or leaf blight, while others provide resistance to fruit rot (syndrome-specific resistance), as has been demonstrated for *Capsicum* spp. (Sy *et al.*, 2005). On the other hand, the resistance of a genotype varies according to the virulence of the *P. capsici* isolate (race-specific resistance, associated with a qualitative gene model); a cultivar may be resistant to one strain but susceptible to another genetically different (Glosier *et al.*, 2008; Ribeiro & Bosland, 2012). Ontogenetic, developmental, or age-related resistance has also been highlighted, wherein plants or plant organs change their state of susceptibility to one of resistance as a result of changes in development (Mansfeld *et al.*, 2020). Plants develop PTI to detect nonspecific MAMPs and ETI which is resistance specific and accompanied by a hypersensitive response (Du *et al.*, 2021).

Grafting is another control strategy within genetic resistance (Gisbert *et al.*, 2010; Sanogo & Ji, 2012). In this technique, the scion of a genotype with high productive potential is grafted onto rootstocks from another line or resistant cultivar. Grafting is a technique that has gained remarkable momentum and is used as important practice to reduce the incidence of many diseases caused by soilborne pathogens, such as *P. capsici*. For example, Jang *et al.* (2012) found that grafted pepper plants showed greater resistance to both *P. capsici* and *Ralstonia solanacearum*, without a reduction in yield and fruit quality. These highest levels of resistance to *P. capsici* were obtained with the combination of peppers “Nokkwang”, “Saengsaeng Matkkwari”, and “Shinhong”, grafted onto breeding lines “PR 920”, “PR 921”, and “PR 922”.

Other source of resistance has been discovered in the wild relative of tomato *Solanum habrochaites* (accession LA407), which showed resistance to a variety of *P. capsici* isolates, while other genotypes (Ha7998, Fla7600, Jolly Elf and Talladega) exhibited moderate resistance (Quesada-Ocampo & Hausbeck, 2010). Black pepper has also displayed resistance in its wild species *Piper colubrinum* (Suraby *et al.*, 2020). In cucurbits, there are few wild species such as *C. pepo* (accessions PI 169417, PI 181761, PI 512709 and Table Ace) with resistance to *P. capsici* (Krasnow *et al.*, 2014). On the contrary, species under the genus *Solanum* (Petry *et al.*, 2017b) or *Capsicum* (Glosier *et al.*, 2008), wild genotypes with complete resistance have been identified, although with unfavorable horticultural characteristics (Granke *et al.*, 2012a). Partial resistance to *P. capsici* was also found in habanero (*C. chinense*) pepper accessions (Soares *et al.*, 2019). In muskmelon, wild accesses with good resistance sources to root and stem rot were identified in Brazil (Pontes *et al.*, 2014). Sources of resistance to crown rot caused by *P. capsici* have also been identified in *Cucurbita* germplasm (Brune & Lopes, 1994).

Despite the high number of genebank accessions evaluated for resistance, mostly wild species, they do not present satisfactory agronomic characteristics, such as high yields and fruit quality. However, they represent important genetic resources to be explored and considered in plant breeding to improve resistance to *P. capsici*,

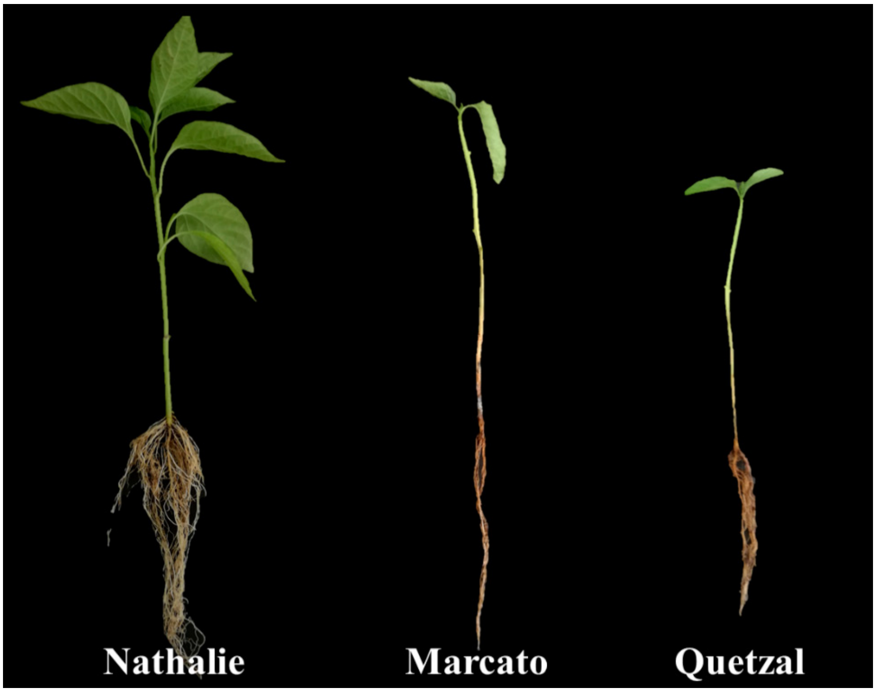

Figure 2. Commercial hybrids of sweet pepper (*Capsicum annuum*) Nathalie (resistant), Quetzal and Marcato (susceptible) showing a differentiated response to *Phytophthora capsici*. Source: Unpublished photographs from the authors. Ecuador, Technical University of Manabí, 2018-2020.

especially in species of Solanaceae and Cucurbitaceae. On the other hand, the scarce sources of resistance encountered so far, in few resistant cultivars (or none in the case of tomato, melon and pumpkins) available on the market, is probably due to complex genetic control, governed by few or several genes.

Cultural control

The use of adequate cultural practices that favor the plant and disfavor the pathogen contributes substantially to the reduction of plants affected by *P. capsici* (Narayanasamy, 2013). Continuous cropping of susceptible cultivars in the same field favors the increase of inoculum levels in the soil over time (Bowers & Mitchell, 1991). Crop rotation with non-host species is recommended for the reduction of plant pathogens. However, the survival of *P. capsici* oospores for more than 36 months makes rotation not completely effective and viable when both pathogen mating types are present in the field (Babadoost & Pavon, 2013). However, the natural presence of both mating types in a field and on an infected plant is rare (Ristaino, 1991; Erwin & Ribeiro, 1996). Kim (1989) observed a reduction in the incidence of leaf blight in chili peppers in rotations with peanuts (*Arachis hypogaea*) and sesame (*Sesamum indicum*). It was shown that a four-year crop rotation program with non-host species and effective weed control are recommended for management of Phytophthora blight of peppers, for significantly reducing the level of inoculum (oospores) in the field (Babadoost *et al*., 2015).

Intense rains or excess moisture in the soil due to excess irrigation water (ponding), provide ideal conditions for the pathogen (Café Filho *et al*., 2019) (Figure 3). Thus, irrigation should limit to soil saturation because accumulation and movement of water within the field contribute to the spread of *P. capsici* (Ristaino, 1991; Granke *et al*., 2012a).

In zucchini (*Cucurbita pepo* var. *melopepo* cv. Early) the effect of a 7-day interval irrigation resulted in more incidence of *P. capsici* than a 14 or 21 interval (Café Filho *et al*., 1995). Xie *et al*. (1999) observed less damage by *P. capsici* in peppers when drip irrigation was used than of gravity irrigation. Usually, irrigation in high-frequency increases fruit yield in crops such as chili pepper (Ristaino, 1991). In addition, it creates unfavorable conditions for spreading the pathogen in the field (Xie *et al*., 1999).

Damage caused by *P. capsici* may be reduced with the establishment of crops in soils with good drainage, low compaction and adequate irrigation system (Ristaino & Johnston, 1999; Café Filho *et al*., 2019). Raised beds also minimize the probabilities of moisture accumulation at the base of the plants. During the rainy season, it is advisable to remodel the planting beds with a slight angle of inclination to promote the displacement of excess water towards leakage areas (Granke *et al*., 2012a; Ristaino & Johnston, 1999). In this sense, the use of natural (wheat, rice or other leftovers) or synthetic (plastic) mulch, is also a good strategy for the management of *P. capsici* (Hausbeck & Lamour, 2004).

Plant covers can significantly reduce epidemics caused by soilborne *Phytophthora* spp. avoiding water splashes (an important factor of dispersal of the pathogen) on infested soils. For example, the use of wheat stubble on bell peppers established under a zero-tillage cultivation system avoided splash generated by water and reduced both the spread and incidence of the *Phytophthora* blight (Ristaino *et al*., 1997). Madden & Ellis (1990) also observed a reduction in the incidence of leather rot caused by *P. cactorum* on strawberries. The use of cover affects the physical, chemical and biological dynamics of the soil, with a positive impact on the spatial and temporal progress of epidemics caused by *P. capsici* (Liu *et al*., 2007).

The black polyethylene plastic cover is a variant of the vegetal cover (Figure 4), but it works under the same principle; reduce the dispersion of inoculum by water splashes on bare soils and also prevents the growth of weeds that serve as hosts of the pathogen

Figure 3. Sweet pepper plants (*Capsicum annuum*) affected by *Phytophthora capsici* under field conditions: (A) plant affected in a plantation with a drip irrigation system, (B) high incidence of wilt in pepper plants due to improper use of gravity (furrow) irrigation, and (C) excessive application of water in a gravity irrigation system. Source: Unpublished photographs from the authors. Ecuador, Technical University of Manabí, 2018-2020.

Figure 4. (A and B) Preparation of raised beds with plastic mulch for the establishment of pepper (*Capsicum annuum*), (C) tomato (*Solanum lycopersicum*) and (D) watermelon (*Citrullus* sp.) crops with plasticulture system. Source: Unpublished photographs from the authors. Ecuador, Technical University of Manabí, 2018-2020.

within rows or seed beds (Ploetz & Haynes, 2000). A notable decrease in leaf blight epidemics, high yields and higher quality fruits have been obtained in pepper by using this system (Roe *et al*., 1994; Ristaino & Johnston, 1999).

Organic amendments can also contribute to the maintenance of low levels of diseases caused by soil-associated pathogens by providing a natural biocontrol through increasing the diversity of microorganisms in the soil (Bonanomi *et al*., 2007). This practice has been effective in the cultivation of bell pepper by the addition of compost (obtained from solid urban and biodegradable waste) to the soil, reducing neck rot caused by *P. capsici* (Gilardi *et al*., 2013). This practice is low-cost and contributes to the improvement of soil fertility, to be considered an alternative for organic farming.

Physical control

Plant pathogens cause disease within an ideal temperature range and are sensitive to extreme modifications compromising their survival status (Kanaan *et al*., 2017). This is the principle of soil solarization, which may be used in the management of pathogens such as *Phytophthora* spp. and *Pythium ultimum* (Gamliel & Stapleton, 1993; Hartz *et al*., 1993). Soil solarization is a special mulching process that causes hydrothermal disinfection and changes in the biological composition of soils with benefits for the health and growth of plants (Kanaan *et al*., 2017). This effective strategy used in pre- and post-sowing is compatible with chemical treatments and biological amendments (Gandariasbeitia *et al*., 2019). The effectiveness of solarization is directly related to the availability and duration of direct sun exposure and to the thickness of the plastic sheet, with better results being observed with low thickness plastics (25 μm), compared to those with greater thickness (between 50 μm and 100 μm) (Souza, 1994).

Solar collectors to disinfest substrates or transparent plastic polyethylene film can be found in the market (Ghini *et* *al*., 2000; May-de-Mio *et al*., 2002). The latter is based on covering the soil surface (in a state of high humidity; saturation) with a plastic film for 6 weeks. In this period, solar radiation increases the temperature of the soil to levels where most pathogens are unable to survive, thus reducing the inoculum density (oospores) and the potential danger of a disease (Gandariasbeitia *et al*., 2019). Most oomycetes may be eliminated in soil at temperatures above 40°C. In contrast, several beneficial microorganisms survive and occupy the soil niche more quickly than the pathogens (Etxeberria *et al*., 2011), thus providing a natural biological control.

Soil solarization may be complemented with the application of organic amendments (Gamliel *et al*., 2000; Núñez-Zofío *et al*., 2010). The combination of both practices controls pathogens in several ways: (i) accumulation of volatile toxic compounds resulting from the decomposition of organic matter; (ii) creation of anaerobic soil conditions; and (iii) increased suppression of soil pathogens due to high levels of microbial activity (Gamliel *et al*., 2000). According to Núñez-Zofío *et al*. (2011), the incorporation of semi or non-decomposed compost mixtures followed by the use of transparent plastic reduces the incidence of root and crown rot up to 86% in pepper by partially reducing the viability of oospores in the soil. Cabbage cropping amendments plus solarization produce a significant control of *Phytophthora nicotianae* and *P. capsici* up to a depth of 10 cm (Coelho *et al*., 1999). Soil solarization is a significant advance in the non-chemical management of many soil-related pathogens, but it is limited to areas where climatic conditions are favorable.

Biologic control

Biological control agents (BCAs) can be viable alternative strategies to manage diseases caused by soil-associated pathogens (Diánez *et al*., 2015). These act through different modes of action, such as hyperparasitism, antibiosis, competition or induced resistance and priming in plants (Köhl *et al*., 2019). The most widespread and used BCAs in the biological control of pathogens include fungi (*Trichoderma* spp.) and bacteria (*Bacillus* spp., *Streptomyces* spp. and *Pseudomonas* spp.), isolated from the rhizosphere or endosphere (Zohaib *et al*., 2019). The range of commercial biological products registered for diseases control caused by *Phytophthora* sp. is reduced. Currently, there is increasing research where the biological action of many strains of fungi and bacteria has been demonstrated against *P. capsici* (Das *et al*., 2019; Santos *et al*., 2019; Syed-Ab-Rahman *et al*., 2019; Abbasi *et al*., 2020; Bhusal & Mmbaga, 2020; Li *et al*., 2020; Tomah *et al*., 2020). Sometimes, certain BCAs can be used in a compatible way with some oomiceticides, expanding the control spectrum (Widmer, 2019).

The aqueous extracts obtained from compost is another option for plant diseases control. These extracts are constituted by diverse microbial populations to control *Phytophthora* spp. as alternative to the use of synthetic oomycitecides (Koné *et al*., 2010). These substances have suppressive properties and antagonistic activity against plant pathogens (Noble & Coventry, 2005). For instance, Marín *et al*. (2014) observed positive effect on the development of chili and pepper plants infected by *P. capsici* and *P. parasitica*, when non-aerated compost tea extract was applied. This practice can also be used as an alternative to the use of synthetic fertilizers and oomycitecides, due to the stimulation of plant growth, sanitary protection and increased fruit yield in *Capsicum* spp.

Beneficial microorganisms in compost extracts include bacteria, fungi, and protozoa, which form a physical barrier against disease-causing agents, creating a suppressive environment where pathogenic organisms reduce their activity, furthermore, they can induce growth and resistance (González-Hernández *et al*., 2021). Such microorganisms have been suggested to suppress plant pathogens through various mechanisms, including induction of resistance against pathogens (Hoitink *et al*., 1977), inhibition of spore germination and antagonism and competition by nutrients (Whipps, 2001). Aqueous extracts of compost have suppressed the infection caused by *P. capsici* in pepper by inducing systemic resistance in plants, promoting, for example, the expression of genes related to pathogenesis (*CABPR1*, *CABGLU*, *CAChi2*, *CaPR-4*, *CAPO1*, or *CaPR-10*), as well as the enzymatic activity of β-1,3-glucanase, chitinase and peroxidase, improving the defense response of plants against the attack of the pathogen (Sang *et al*., 2010). Although several studies have generated optimal results in the control of *P. capsici* as alternative methods, most of them were not adequately tested on large scale or under field conditions. However, the methods developed in such studies could in the future become successful or complementary tools in the control of *P. capsici*.

Chemical control

The chemical molecules (synthetic origin) are key components in the successful management of diseases caused by *P. capsici* under field conditions (Matheron & Porchas, 2014). However, when environmental conditions favor the development of the disease, no currently available fungicide has shown to fully control the pathogen (Granke *et al*., 2012a). Despite the limited efficacy of fungicides, they exert an extra degree of protection when combined with other management practices such as crop rotation, raised beds, and irrigation water management (Hausbeck & Lamour, 2004). Currently, the range of active ingredients available in the market for the control of *P. capsici* is scarce and with inadequate control efficacy (Table 1), with specific formulations for application to the soil and foliage. The different molecules for the control of oomycetes are applied in a preventive way, both to the soil and to aerial organs (Gisi & Sierotzki, 2015), because the applications of a curative type, after infection by *P. capsici*, are in most cases ineffective.

Fungicide application methods should be chosen based on the affected organ, for example, root or aerial infection. In this way, the control of root and crown rot caused by *P. capsici* is carried out with targeted applications through drip irrigation or

Table 1. Registered fungicides for use in the management of diseases caused by *P. capsici.* Ecuador, Technical University of Manabí, 2018-2020.

Active ingredients*†	Mode of action group (FRAC) ‡	Target site action (FRAC) ‡	FRAC code no. and group name‡	Chemical (sub-) group‡	Resistance Risk‡	Toxicological class
Cymoxanil*†	Unknown	Unknown	27	Cyanoacetamide-oxime	Low to medium	III
Copper preparations*†	**M:** Multi-Site Activity	Unknown	M01	Inorganic	Low	III
Dimethomorph	**H:** Cell wall biosynthesis	**H5:** Cellulose synthase	40	Cinnamic acid amides	Low to medium	III
Fosetyl-Al†	**P:** Host plant defence induction	Unknown	P07	Ethyl phosphonates	Low	III
Mancozeb*†	**M:** Multi-Site Activity	Unknown	M03	Dithiocarbamates	Low	IV
Mandipropami†	**H:** Cell wall biosynthesis	**H5:** Cellulose synthase	40	Mandelic acid amides	Low to medium	IV
Metalaxyl†	**A:** Nucleic acids metabolism	**A1:** RNA polymerase I	4	Acylalanines	High	III
Propamocarb*†	**F:** Lipid synthesis or transport / membrane integrity or function	**F4:** Cell membrane permeability, fatty acids	28	Carbamates	Low to medium	IV

*Active ingredients registered in Ministry of Agriculture, Livestock and Supply (MAPA-Brazil, 2021). †Active ingredients registered in the Ecuadorian Agency for the Quality Assurance of Agriculture (Agrocalidad 2021). ‡Fungicide Resistance Action Committee (FRAC 2020).

drenching, while foliar applications include spraying the aerial organs with equipment such as hydraulic function, centrifuge, etc. (Granke *et al*., 2012a).

The inappropriate use of fungicides can increase resistance of *P. capsici* which is an organism with high genetic plasticity and have developed insensitivity to molecules such as metalaxyl (Parra & Ristaino, 2001; Dunn *et al*., 2010; Wang *et al*., 2021). In fact, resistance of *P. capsici* to metalaxyl has been caused by the long-term intense use of this fungicide (Wang *et al*., 2001). A solution to dissipate this problem is the use of other active principles such as mandipropamid and dimethomorph, which act on the synthesis of lipids and membranes, as well as on the synthesis of cellulose and cell wall of oomycetes, and are considered as fungicides of low to medium risk of resistance (FRAC, 2020; Siegenthaler & Hansen, 2021). Another aspect to consider in the management of resistance to fungicides is to have a wide range of molecules applied in periodic and programmed rotation at the maximum amount of application per crop cycle (Castro *et al*., 2014). Other approach used to reduce the selection pressure of resistant phytopathogenic fungi populations is the mixture of systemic and protective fungicides. This practice is important due to the several reports of resistance outbreaks in populations of *P. capsici* to cyazofamid, fluopicolide, mefenoxam, metalaxyl, and oxathiapiprolin fungicides (Parra & Ristaino, 2001; Wang *et al*., 2020; Siegenthaler & Hansen, 2021; Wang *et al*., 2021; Wang & Ji, 2021).

Integrated management

The long-term risk of *P. capsici* infection in infested fields decreases when a disease management plan is applied using various tools in an integrated way from a sustainable approach, ranging from the use of resistant cultivars to proper soil operation, (Hausbeck & Lamour, 2004) (Figure 5).

The aim of integrated disease management is to minimize the activity of a causative agent and increase the yield of a given crop. The holistic and combined study of the soil and plant (Figure 5), which, within a conceptual framework operated as a whole, allows the development of strategies that help minimize the damage caused by pathogens such as *P. capsici* in vegetables (Sanogo & Ji, 2012). The principles of integrated disease management are based on the integration of the basic concepts of immunization, exclusion, eradication and protection of plants against pathogens in order to prevent the potential economic, environmental and health risks that can occur (Razdan & Gupta, 2009).

Usually, the adoption of only a single control practice is ineffective for the management of the diseases caused by *P. capsici,* regardless the host. Then farmers must be aware of the epidemiology of the disease and employ different strategies from early stages (pre-sowing) to the development and reproduction of the crop (Table 2).

Conclusions

The important economic losses

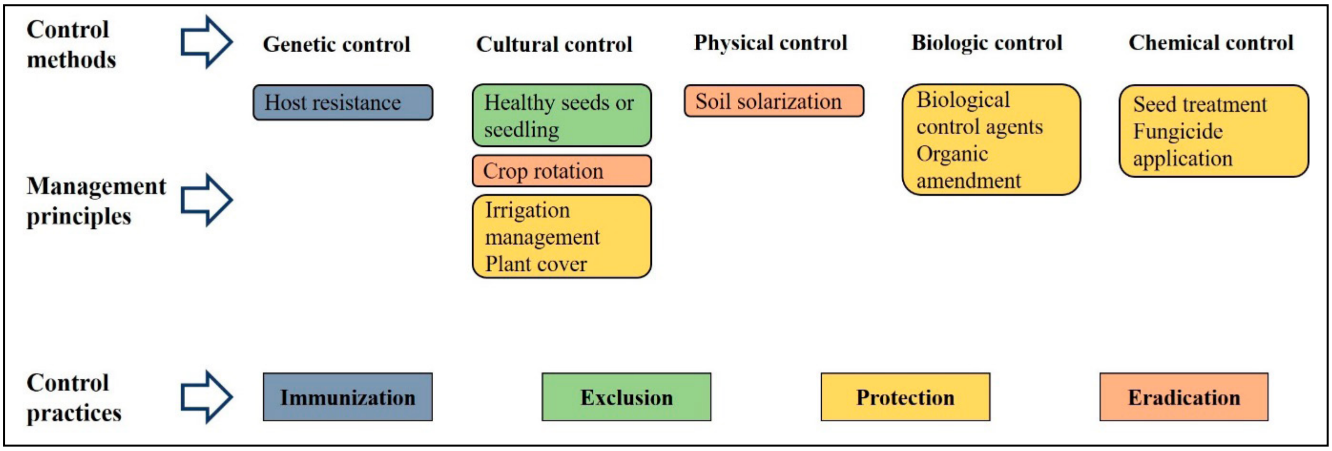

Figure 5. Management methods to reduce epidemics associated with *Phytophthora capsici* and to increment the fruit yield and the economic return in horticultural crops. Source: Unpublished figure from the authors. Ecuador, Technical University of Manabí, 2018-2020.

Table 2. Strategies for managing *Phytophthora capsici* infection in vegetables in addition to the chemical control. Ecuador, Technical University of Manabí, 2018-2020.

Plant stage	Strategies	References
Before planting	Protective seed treatment (chemical and biological)	Mao *et al.* (1998)
	Selection of resistant cultivars	Granke *et al.* (2012a)
	Choice of soils without a history of *P. capsici* Control of machinery and equipment movement between crop areas	Ristaino & Jonhston (1999)
	Sowing in raised beds	Ristaino & Jonhston (1999)
	Use of plastic or vegetable coverage	Núñez-Zofío *et al.* (2011)
Crop development and reproduction	Frequent monitoring of disease incidence	Hausbeck & Lamour (2004)
	Irrigation at long intervals, avoiding saturation of the soil	Café Filho *et al.* (1995)
	Irrigation water free of *P. capsici*	Granke *et al.* (2012a)
	Removal of infected plants and fruits	Hausbeck & Lamour (2004)
	Application of antagonistic microorganisms	Sanogo & Bosland (2013)

that may be caused by *P. capsici* must be considered before establishing any horticultural production system. The selection and combined application of the different disease management practices will guarantee the avoidance and the reduction of losses caused by this oomycete plant pathogen. Thus, the integrated management of *P. capsici* seeks to create unfavorable conditions for the development of epidemics in the field. Starting from the principle of exclusion, which aims to prevent the entry of the pathogen into the agricultural exploitation area, followed by cultural operations and protection (chemical or biological) in order to maintain pathogen populations at non-harmful levels, with crops in optimal health, so they can express their maximum yield potential. The benefits of integrated disease management include reducing the use of chemical molecules, obtaining high fruit yields, and reducing costs associated with the control of other plant pathogenic agents. Finally, the results obtained from a successful *P. capsici* management program are: high economic return, long-term sustainable harvests, reduced environmental impact, and high-quality products that are safe for consumer health.

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