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Phytophthora capsici on chilli pepper (*Capsicum annuum* L.) and its management through genetic and bio-control: a review

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Abstract

Phytophthora capsici is the most destructive pathogen of vegetables that represents a serious threat to chilli pepper plants. We discussed the control of *P. capsici* through manipulation of genetic architecture of chilli plant and endophytic microorganisms. The function of various genes encoding transcriptional regulatory and defense related putative proteins such as pathogen-related protein (PR), anti-microbial peptides (AMPs), polygalacturonase-inhibiting proteins (PGIPs), lipid transfer protein (LTP), pectin methylesterase (PME), leucine-rich repeat proteins (LRRs), osmotin-like and thaumatin-like protein, in *Capsicum* was also analyzed. The bio-control of *P. capsici* by using various strains of Bacillus, Trichoderma, Pseudomonas, Chryseobacterium and Rhizobacteria was demonstrated. We also discussed the enhanced resistance to *P. capsici* infection by treatment with a variety of abiotic and biotic inducers that act on defence signalling pathways involved in disease resistance. We highlighted the vulnerability of chilli crop with reference to its genetic resources against Phytophthora blight. Disease control through chemicals is becoming problematic, so we proposed other ways to control the disease severity. This review highlights the economic significance of chilli pepper (*Capsicum annuum* L.) along with disease management strategies against *P. capsici*. This pathogen has posed a serious threat to chilli crop worldwide.

Keywords: biotic and abiotic inducers, genetic resources, proteins, transcriptional regulatory.

Introduction

Chilli pepper (*Capsicum annuum* spp.) is an essential horticultural crop grown worldwide, particularly in Asia (Tariq et al., 2014). This perishable vegetable is consumed as fresh, dry or processed spices as well as in medicines. Its hot taste is due to a compound capsaicinoid (C18H27NO3) which resides in the placental tissues, pericarp and internal membrane. Capsaicinoid compound administers its role in various ethno-pharmacological applications including anticancer therapy, anti-obesity treatment, body temperature regulation, pain therapy, antimicrobial agent and antioxidant (Meghvansi et al., 2010). Moreover, chilli fruit is not only cholesterol free but also a precious source of folic acid, potassium, vitamins A, B, C, phenolics and carotenoids. It also possesses antimicrobial activity (Materska, Perucka, 2005). Chilli belongs to the 3rd most economically important and valuable plant family known as *Solanaceae* containing more than 3000 species (Mueller et al., 2005). New world tropics and subtropics are its places of origin. *Capsicum annuum*, *C. pubescens*, *C. frutescens*, *C. chinense* and *C. baccatum* are the major cultivated species of the genus *Capsicum* for edible purpose (Sanatombi et al., 2010). Several pathogens comprising viruses, bacteria, fungi and nematodes cause disorder in chilli's normal metabolic pathways. Anthracnose, downy mildew, Phytophthora blight, collar rot, purple blotch, fruit and root rot are the most alarming diseases of *Capsicum* that cause severe yield losses in chilli production (Yin et al., 2012). Of these diseases the most damaging one is Phytophthora blight which is triggered by the infection of oomycete pathogens called *Phytophthora capsici* (Lee et al., 2008). These fungal diseases also make run short of the capsaicin contents in the chilli fruits. It has many applications as prospective medicinal plant like other plant species.

Plant pathological disorders can be controlled through chemical, mechanical and biological ways. Among these, disease control through pesticides is most widespread and popular among the farming community although it has generated several environmental problems. Fungal diseases in chilli are usually controlled by fungicides such as mencozeb, metalaxyl, mefenoxam, phenylamides or by cultural practices like soil treatment, mulching and water management (Matheron, Porchas, 2002). Disease management through fungicides and pesticides is also becoming difficult due to augmented resistance in pathogens.

Ecological pollution and health hazards are the prospective threats to the healthy food chain and human survival. Chemicals also destroy the beneficial bacteria that upsurge soil fertility. Scientists strongly discourage

the application of pesticides and fungicides against pests. So, there is instant need for evolving schemes to control plant diseases in environment friendly way (Parra, Ristaino, 2001). To alleviate the trend of chemical usage, numerous antagonistic strains of bacteria have been used against various pathogens to manage disease. These microorganisms induce the genes of resistance against infection or secrete the toxic enzymes against pathogens to control the disease. Some plant growth promoting bacteria also help the plants by strengthening their defense mechanisms. Bacteria can control the plant disease either by producing different hydrolytic enzymes such as β-1,3-glucanase and chitinase or inducing different plant defense genes, resultantly plants produce different antifungal extracellular proteins, mycoparasitism and enzymes (Fester, Hause, 2005).

Severity of the disease can be reduced or eradicated at the best level by the incorporation of all possible ways. Manipulation of disease resistant genes by genetic engineering or conventional plant breeding methods is very significant for plant improvement. The introduction of next-generation sequencing (NGS) and molecular markers are very useful in conventional plant breeding methods or genetic engineering to manipulate resistant genes from different sources (Ramchiary et al., 2014).

Persistent efforts have been made in understanding the functional and molecular basis to induce simple and polygenic resistance in plants to produce long-lasting protection against pathogens (Pflieger et al., 2001). Manipulation of resistant genes has become very common for producing disease resistant crops with better yield (Ali et al., 2014 b). A PCPME6 gene encoding pectin methylesterase (PME) is considered to be responsible for the pathogenesis of *P. capsici* on pepper (Feng et al., 2010). Genetic control of disease is an efficient, long term, competitive, cost effective and environment friendly way to control pathogens. Single gene-mediated resistance against plant pathogens is an effective tool for plant breeders.

Epidemiology and disease cycle of causal agent *Phytophthora capsici*

"Phytophthora" is a Greek word meaning "destroyer of capsicums". *Phytophthora capsici* L. belongs to class Oomycetes of kingdom Chromalveolata, closely related to Kingdom Fungi. These are also called pseudofungi and about 60 species of genus Phytophthora are known currently to be responsible for various diseases in many crop plants. The prevalence of Phytophthora blight has increased worldwide infecting crowns, stems, roots, fruits and foliar parts of plant (Oelke et al., 2003; Hausbeck, Lamour, 2004; Bosland, 2008; Quesada-Ocampo et al., 2011). A PCPME6 gene encoding PME is responsible for pathogenesis of *P. capsici* on pepper (Feng et al., 2010). The reproductive part of *P. capsici* is called sporangium containing spores (antheridium or oogonium) by which further zoospores are formed (Fig. 1).

Two mating types of Phytophthora species have been identified. Some are homothallic (self-fertile) while others are heterothallic (out-cross). A single isolate in homothallic is able to complete sexual stage to form bi-motile zoospores whereas heterothallic requires mating types labelled as A1 and A2 to complete this stage. At sexual stage, each parent produces sporangia contain both male (antheridium) and female (oogonium) spores (Fig. 2). *P. capsici* is heterothallic, completes sexual stage (out-cross) regularly in the United States (Sholberg et al., 2007).

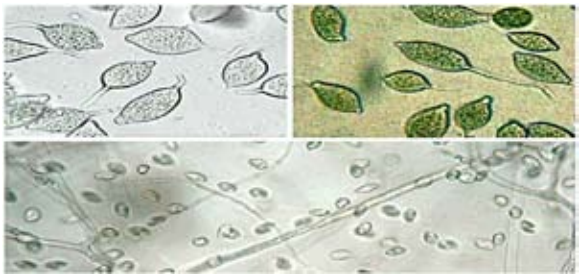

Figure 1. Microscopic diagram of spore containing sporangia of *Phytophthora capsici*

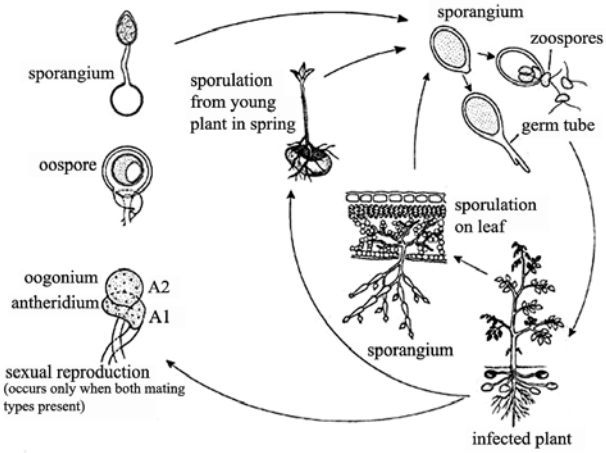

Figure 2. Life cycle of *Phytophthora capsici*

Like many other species of Phytophthora, warm humid weather is conducive to growth of *P. capsici* and it spreads rapidly around the fields of host plants due to multiple spore production and infection cycles. Roots and crowns are its favourite targeting sites (Esfahani et al., 2014). *P. capsici* grows normally between 25–30°C with 60–80% relative humidity. In optimum environment, it carries potential for rapid polycyclic disease development from a limited amount of inoculum. Inflicted wounds in humid conditions, water trigger the infection that may happen during cultural agronomic practices. Water is inevitable for the dispersal and detachment of the sporangia, rainfall has been the most influential environmental factor for disease incidence (Gevens et al., 2007; Sanogo, Ji, 2013).

P. capsici has wide host range like Solanaceae, Cucurbitaceae and Fabaceae families. It infects watermelon, cucurbits, tomato, pumpkin, eggplant, cocoa, red pepper, black pepper, lima beans, snap beans, soya beans, common beans, squash, cucumber (Fig. 3) and poses a serious threat to food security.

All plant parts, vegetative as well as reproductive, are highly vulnerable to *P. capsici* at different growth stages. It attacks roots during seedling stages. The disease results in stunted plant growth or sudden wilt. Affected chilli plants often show brown to black discoloration in roots, crown or fruits (Fig. 4). Infection of *P. capsici* on chilli usually starts at the soil line show water soaked areas and dark lesions on stems. These lesions spread around the stem and result in plant death. Small round or irregular leaf spots may be formed and enlarged with time. Crown rot that results in rapid blighting of newly emerged leaves or stems is also very common in pepper plant. Infected fruits appear dark green and further become brown (Fig. 5) by pathogenic attack (Roberts et al., 2008).

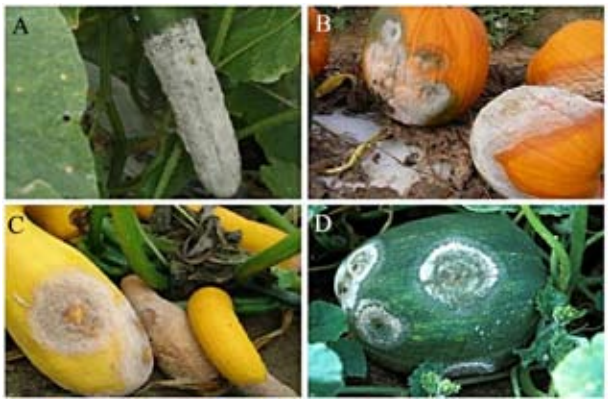

Figure 3. Symptoms of *Phytophthora capsici* attack on cucumbers (A), pumpkins (B), squashes (C) and watermelon (D) fruits

Figure 4. Chilli plants affected by *Phytophthora capsici*

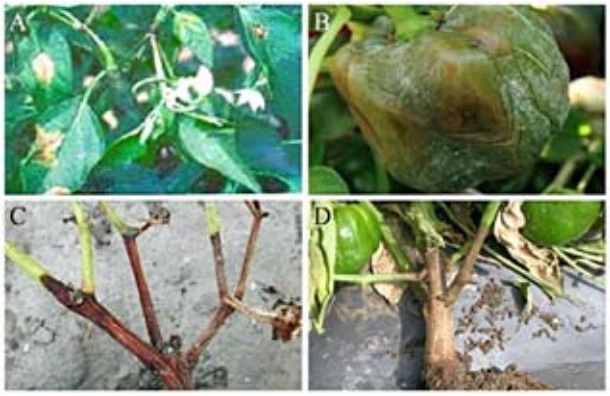

Figure 5. Symptoms of disease caused by *Phytophthora capsici* including: leaf blight and lesions (A), fruit rot (B), stem rot (C) and root rot (D)

Genetic resistance in *Capsicum annuum* spp. against *Phytophthora capsici*

Chilli pepper (*Capsicum annuum* L.) possesses various groups of valuable genes that can be transferred to other plant species and also keep functions. Disease resistant genes related to quantitative traits are more effective (Ortiz et al., 2010; Dang et al., 2014). We can overcome the shortfall of our traditional plant breeding by manipulating the vast variety of genes present in chilli plant through genetic engineering. In *C. annuum*, about 292 genes related to sterility, morphology, physiology and resistance against numerous diseases had been recognized, by the year 2006 (Wang, Bosland, 2006). *C. annuum* genome comprises a rich source of genes against various pathogens and a locus on chromosome five confers resistance against oomycetes pathogens in chilli. Moreover, six chromosomal regions have been identified that have genes involved in resistance against *P. capsici*. These chromosomal regions are Phyto4.1, Phyto5.1, Phyto5.2, Phyto6.1, Phyto11.1 and Phyto12.1 existing on different chromosomes (Gurr, Rushton, 2005).

C. annuum has hypersensitive response (HR) genes against *P. capsici* that can be induced by numerous environmental factors. These factors stimulate plant defense mechanisms in various pathways, resultantly different proteins are formed in plants creating immunity (Hong et al., 2008 b; Choi, Hwang, 2015).

A huge number of the gene sequences and expressed sequenced tags are easily accessible in pepper. Genetic variation for several traits also exists in *Capsicum* that needs to be exploited by researchers. For the rapid identification of resistant genes in chilli plants, molecular markers may be helpful to save money and time (Ali et al., 2014 a; Ji et al., 2014). Simple sequence repeat (SSR) type molecular markers are very helpful due to their co-dominant and multi-allelic nature. Transformation of resistant genes in the disease susceptible varieties is the best tactic to control disease. Virus induced gene silencing, gene transformation and quantitative real time PCR have been used to determine gain and loss of function of the genes against oomycete pathogens (Ko et al., 2007). The identification and transformation of pathogen resistant genes, have led to the development of various transgenic chilli cultivars resistant to diseases. Categorization and location of quantitative trait loci (QTL) has led to the understanding of the functional roots of polygenic inherited resistance in chilli and a QTL on chromosome 5 is considered as a major promoter of resistance against diseases (Liu et al., 2014). Other than constitutive resistance, systemic acquired resistance (SAR) or inducible resistance arises after the contact of plant with the pathogens. It offers long-term complete immunity to the plants and its economic status for plant disease control cannot be denied. Several exogenous inducers are available to induce defense-related gene expression and endogenous hormonal signalling throughout SAR development in pepper plants (Choi, Hwang, 2011). Anti-microbial peptides (AMPs) having biological activities against pathogens are economical and reachable source. AMPs of 12–100 amino acids are very valuable against various pathogens. Genes encoding AMPs in chilli plant have been explored and being expressed against various pathogens (Fernando et al., 2014). The exploration and research on the promoters of defense-related genes is very essential for the transcriptional activation and stress signalling pathways, during pathogenic infection (Castro Rocha et al., 2012).

Capsicum genes transferred to other plant species

Various genes from genus *Capsicum* have been transferred to other plant species for different functions. A gene CAPOA1 was transferred in tobacco plant to produce transgenic tobacco. This was done to explore the role of antioxidant enzyme ascorbate peroxidase in reaction to pathogens and abiotic stresses (Sarowar et al., 2005). This resulted in high level of gene expression in tobacco plant with amplified peroxidase activity and plant growth. This process revealed the involvement of gene CAPOA1 in oxidative stress tolerance in plant and

resistance against oomycete pathogens. Overexpression of pepper gene CaSAR82A in transgenic *Arabidopsis* plant showed earlier plant growth and improved resistance against salt, drought, oxidative stresses and fungal pathogens (Lee, Hwang, 2006). Pepper gene CaPMEI1 encoding pectin methylesterase (PME) was also transferred in *A. thaliana* to observe its expression level (An et al., 2008). Two potential pepper genes CABPR1 and CAPOA1 encoding PR1 also gave marvellous results in tomato plant. Transgenic tomato plants exhibited improved tolerance against *P. capsici* (Sarowar et al., 2006). Pepper esterase (PepEST) gene introduced in bentgrass confirmed resistance in plant against pathogens like *P. capsici* and *Rhizoctonia solani*. The PepEST gene stopped the development of fungal hyphae. Moreover, the disease severity on transgenic plants inoculated with *P. capsici* showed only 10% fungal growth while more than 50% fungal activity was detected in non-transgenic plants. More accumulation of PepEST was found in ripe chilli fruits. Therefore, ripe chilli fruit is testified to be a rich source of PepEST and finally more resistant to fungi as compared to unripe chilli fruits (Ko et al., 2005; Cho et al., 2011).

Capsicum genes encoding lipid transfer protein (LTP)

Many *Capsicum* genes that can be induced due to infection by *P. capsici* or *Xanthomonas campestris* were recognized in pepper tissues. These genes in chilli plants encode diverse putative lipid transfer protein I and II, osmotin (PR-5), thionin, chitinase, SAR 8.2, stellacyanin, leucine-rich repeat protein, auxin-repressed protein and β-1,3-glucanase. Furthermore, various fungus hindering plant proteins and peptides have been known recently. A lipid transfer protein (LTP) having size of 9 kDa, from the seeds of *C. annuum* is known as Ca-LTP_1. It results in the morphological deformation and changes in the cells of pathogens. It usually resides in the dense vesicles and displays antifungal activity (Fernando et al., 2014). These proteins encoded by different genes prevent fungus growth. Osmotin is another important pathogenesis-related protein formed after the introduction of plants to the biotic and abiotic stress conditions (Hong et al., 2008 a). A plant peptide termed as CaTI was found in the seeds of *C. annuum*, it not only inhibits the trypsin and chymotrypsin but also the progression of *Kluyveromyces marxiannus*, *Candida albicans* and *Saccharomyces cerevisiae* by cellular, cytoplasmic and morphological, alterations. This peptide also induces the assembly of nitric oxide in plant tissues (Ribeiro et al., 2012). A gene CaTin2 encoding putative and pathogenesis related protein was isolated through differential screening of a cDNA library of hot peppers (*C. annuum*). It was observed that only one copy of gene CaTin2 amino acid sequences existed in the pepper genome having resemblance with the signal sequence. This protein accumulates in the cell wall of inoculated pepper plant leaves by producing a fusion protein (Shin et al., 2003). Storage proteins are also involved in plant defense mechanism because of their insecticidal and antimicrobial actions. It also has been observed that a gene PepTLP encoding thaumatin-like protein in pepper plants during the days of fruit ripening, increased the total soluble sugars along with improved resistance against Phytophthora blight and anthracnose (De Souza Cândido et al., 2011).

Pathogen-related proteins (PR), polygalacturonase-inhibiting proteins (PGIPs) and extracellular peroxidase-2 ($CaPO_2$) encoding genes

In plants genes encoding PR proteins or anti-microbial peptides (AMPs) are very important to develop resistance against fungi and bacteria (Khaliluev, Shpakovskii, 2013). About 17 families of pathogen-related protein (PR) from PR-1 to PR-17 have been reported in plants that are controlled by several genes (Soh et al., 2012). These PRs genes can be induced through biotic and abiotic stresses such as signalling compounds ethylene, jasmonic acids, salicylic acids, or non-pathogenic bacteria (Van der Ent et al., 2009). Genes encoding transcriptional regulatory and pathogen-related (PR) proteins, also play a vital role in plants. The expression pattern of gene encoding a protein PR-1 involved in defense mechanism was examined against *P. capsici*, in three cultivars of pepper exhibiting different levels of resistance. The results revealed that PR-1 up-regulated all the genes present in susceptible and resistant cultivars. Difference was observed in the duration and level of defense response (Silvar et al., 2008). Pepper plants inoculated with *Fusarium oxysporum* against *P. capsici* were examined. Pathogen biomass was found in the stems and roots of infected plants but not in the leaves of plants. The results showed that PR-1 protein is related to five different genes (Silvar et al., 2009). Polygalacturonase-inhibiting proteins (PGIPs) are proteins present in the cell walls of plant cells and also act as fungal endopolygalacturonases inhibitors (Wang et al., 2013 b).

$CaPO_2$ for extracellular peroxidase-2 in *C.annuum* plays an efficient role during biotic and abiotic stresses. Transgenic *Arabidopsis* plants having $CaPO_2$ gene showed drought, salt and oxidative stress tolerance along with fungal resistance. This pleiotropic effect of $CaPO_2$ gene showed resistance against biotic and abiotic stresses in plants (Choi, Hwang, 2012). In resistant pepper plants, pathogenic stress generally increases the quantity of hydrogen peroxide (H_2O_2) and phenylalanine ammonia-lyase (PAL) that act against pathogens (Zheng et al., 2005).

Genes induced by chemicals or other abiotic stress

Various chemical compounds such as abscisic acid, methyl jasmonate, indole-3-acetic acid (IAA), hydrogen peroxide (H_2O_2), salicylic acid, ethylene, or abiotic stress like drought and high salinity also induce resistant genes in chilli plants before pathogenic attack. Plants either produce these compounds under stress response or by manual treatment that activates the promoter regions of genes.

The CaPMEI1 pepper gene promoter region was functionally analysed in the transformed tobacco plants. Through the treatment of ethylene and methyl jasmonate, 958 bp promoter was regulated functionally and CaPMEI1 promoter region from 754 to 958 bp was found liable for the expression of stress-response (An et al., 2009). Another gene CALRR1 encoding leucine-rich repeat proteins (LRRs) always expressed in plants affected by *Colletotrichum coccodes*, *P. capsici* and *X. campestris* but never expressed in healthy plants. It was also identified in the leaves of pepper plant treated with

ethylene, methyl jasmonate, salicylic acid, IAA, abscisic acid, H_2O_2, drought and high salinity stresses (Jung, Hwang, 2007). Among plants, pepper (*C. annuum*) has the highest quantity of ascorbate that is a natural anti-oxidant. The gene expression and activity of the pepper ascorbate oxidase (pAO) enzyme was studied through Northern and Southern blotting that confirmed its existence after araquidonic acid (AA) application (García-Pineda et al., 2004). Moreover, the systematic acquired resistance (SAR) can be created with the systematic generation and accumulation of H_2O_2 in oxidative burst, as well as through the induction of defense-related genes in pepper plants (Lee, Hwang, 2005).

Genes induced by microorganisms or other biotic stress

Plants also activate defense related mechanisms in response to biotic stress. Aphid attack stimulates the plant resistance mechanisms to cope with pathogens (Hong, Kim, 2005).

Plant pathogens Tobacco mosaic virus (TMV) or treatment with *X. campestris* and rhizospheres induced different genes in pepper plants that can be isolated (Hong, Kim, 2005). A pepper gene CAPIP2 was induced by the infection of *X. campestris* in pepper plants and analysis exposed that the elements that induced gene expression are mainly located in the promoter regions of that gene (Lee et al., 2007). Another gene CADEF1 encoding a putative protein was identified from the pepper leaves inoculated by a virulent strain Bv5-4a of *X. campestris*. A cDNA clone named as basic-1,3-glucanase (CABGLU) was also isolated from the wounds of infected pepper leaves. The transcriptional factors of CABGLU gene were induced less in compatible interactions and more in incompatible interactions. Its mRNAs were particularly expressed only in the roots. It was assumed that this gene may be prompted due to pathogenic attack (Mee Do et al., 2004). Many other genes have been identified in chilli pepper plants that were induced by various biotic or abiotic stresses and acted against *P. capsici* as given in Table 1.

Table 1. *Capsicum* genes related to resistance against *Phytophthora capsici*

Gene	Accession No.	Gene size	Induced by	Gene product (protein)	Phenotype (resistance)	References
CaRGA2	GU116570.1	3,018 bp	*P. capsici*	108.6 kDa blight resistance protein	*P. capsici*	Castro Rocha et al., 2012; Zhang et al., 2013
CaHIR1	DI139028.1	1,052 bp	*Pseudomonas syringae* infection	hypersensitive induced reaction (HIR) protein	*P. capsici*	Jung, Hwang, 2007; Jung et al., 2008
CaPGIP1	JN180922.1	798 bp	methyl jasmonate, salicylic acid and wounds	polygalacturonase-inhibiting proteins (PGIPs)	*P. capsici*	Wang et al., 2013 b
CAPR-10	JF345171.1	1500 bp	compost water extracts	β-1,3-glucanase, chitinase and peroxidase (PO)	*P. capsici*	Sang et al., 2010
CaPGIP2	JN180923.1	1038 bp	methyl jasmonate, salicylic acid and wounds	polygalacturonase-inhibiting proteins (PGIPs)	*P. capsici*	Wang et al., 2013 b
CAChi2	AY775335.1	2,619 bp	compost water extracts	β-1,3-glucanase, chitinase and peroxidase (PO)	*P. capsici*	Hong, Hwang, 2006; Sang et al., 2010
CaPGIP3	JN180921.1	843 bp	methyl jasmonate, salicylic acid and wounds	polygalacturonase-inhibiting proteins (PGIPs)	*P. capsici*	Wang et al., 2013 b
CanPOD	FJ596178	1353 bp	pathogen, abiotic stresses and salicylic acid	peroxidise (POD)	*P. capsici*	Wang et al., 2013 a
CAPO1	AF442386.1	1222 bp	compost water extracts	β-1,3-glucanase, chitinase and peroxidase (PO)	*P. capsici*	Sang et al., 2010
CaBGLU	AF227953.1	1332 bp	*Fy-11 Bacillus amyloliquefaciens*	β-1,3-glucanase	*P. capsici*	Yang et al., 2014
CaPO2	DQ632587.1	1,121 bp	abscisic acid, high salt, drought and oxidative stress	extracellular peroxidase 2	biotic and abiotic stress	Choi, Hwang, 2012
CaPR4	JX030397.1	686 bp	*Fy-11 Bacillus amyloliquefaciens*	*Capsicum annuum* pathogenesis-protein 4	*P. capsici*	Yang et al., 2014
CASAR82A	DI023421.1	258 bp	biotic and abiotic stresses	SAR8.2 protein	phytopathogenic fungi and *P. capsici*	Lee, Hwang, 2006
CaMsrB2	EF144172.1	952 bp	compatible or incompatible pathogens	methionine-R-sulfoxide reductase B2 protein	*P. capsici* and *P. infestans*	Oh et al., 2010
CaPMEI1	DQ640309.1	834 bp	pathogen infection, methyl jasmonate and ethylene	pectin methylesterase inhibitor	bacterial and oomycete pathogens	An et al., 2009
CATHION1	AF112869.1	548 bp	bacterial infection	gamma-thionin 1 precursor	*P. capsici* and *Xanthomonas campestris* pv. *vesicatoria*	Lee et al., 2000
CABPR1	AF053343.2	805 bp	ethylene and *P. syringae* pv. *tabaci*	basic PR protein 1	pathogen, environmental and abiotic stresses	Hong et al., 2005
CABGLU	AF227953.1	1332 bp	ethephon and methyl jasmonate	β-1,3-glucanase	*P. capsici* and *X. campestris*	Jung, Hwang, 2000
CAOSM1	AY262059.1	985 bp	Bv5-4a of *Xanthomonas* and *P. capsici*	osmotin-like protein	*P. capsici* and *Colletotrichum coccodes*	Hong et al., 2004
CAPOA1	AF442387.1	1138 bp	oxidative stress and pathogens	ascorbate peroxidase (PO)	*P. capsici*	Sarowar et al., 2005
CALRR1	AY237117.1	888 bp	*P. capsici*, abscisic acid (ABA) and wounding	leucine-rich repeat protein	*P. capsici* and *X. campestris*	Kim et al., 2014 a
pAO	KC176709.1	1,838 bp	wounding or cellulose	pheophorbide A oxygenase	pathogen and resistance	García-Pineda et al., 2004
CaERFLP1	AY529642.1	1032 bp	biotic and abiotic stress	ethylene-responsive factor like protein 1	salt stress and *P. syringae*	Lee et al., 2004

Biocontrol of *Phytophthora capsici*

Biological control of plant pathogens through other microorganisms has emerged during recent years. For this purpose, several bacterial strains have been widely used as biological agents for the management of soil borne diseases. It is the best alternative to the chemical fungicides because it is harmless to environment and human health (Chung et al., 2008; Cimen et al., 2009). Microbial metabolites such as validamycins, blasticidin spolyoxins and kasugamycin with antifungal activity as microbial fungicides have an impact on crop protection worldwide. The recent advancement in microbial fungicides such as fludioxonil, fenpiclonil and syntheic derivatives of strobilurins is very important (Guetsky et al., 2002).

About 0.3 million plant species exist on the Earth; each individual plant is host to one or more endophytes (Massart, Jijakli, 2007). In red pepper, Pseudomonas and Bacillus species of rhizospheres have been used to diminish *P. capsici*. Various bacterial strains are responsible for the production of a large number of antibiotics that show antifungal activity and are antagonistic to different fungal diseases such as sheath blight, root rot and stem rot (Chatterton et al., 2004).

Various species and strains of bacteria are useful in controlling fungus related diseases in chilli plants.

Bacillus strain

Bacillus strains have widespread marvelous bio-control activity against fungal pathogens in chilli plants. *B. vallismortis* strain BS07 was found to be a potential bio-control agent particularly against Phytophthora blight and anthracnose disease of chilli plants. Plants treated with this rhizobacterium also showed significant increase in chlorophyll contents of leaves and increased fruit yield. SB10 also has showed 72.2% ability to decelerate disease incidence in chilli plants (Rajkumar et al., 2005; Jiang et al., 2006).

Trichoderma harzianum bacterial strains also have antagonistic effect on *P. capsici* of chilli plants. The seed and root treatment of chilli with the spores of *T. harzianum* has a positive effect on the *P. capsici*. It has been observed by various researchers that necrosis caused by *P. capsici* was reduced in plants that were treated with different doses (Ezziyyani et al., 2007).

Pseudomonas strains. A single strain of *Pseudomonas* can produce several different antibiotics. A similar spectrum of antibiotic production has been described in different strains. *P. fluorescens* strain Pf-5 has been demonstrated to synthesize different antibiotics such as 2,4-diacetylphloroglucinol, phenazines, pyoluteorin, pyrrolnitrin, rhamnolipids, cepaciamide A, ecomycins, cepaciamide A and hydrogen cyanide (Aravind et al., 2009; Anand et al., 2010). It has been observed that *P. corrugata* strains CCR04 and CCR80 residing in chilli roots suppressed Phytophthora blight disease more effectively as compared to *Escherichia coli* DH5α and MgSO4 solutions (Lee et al., 2003 a). Pf1 of fluorescent *P. aeruginosa* strain GC-B26 exhibited increased plant growth and maximum check to the growth of fungi as observed by Lee et al. (2003 c). The ability of Pf1 isolate against fungal pathogens was further investigated. It also triggers the production of defense-related enzymes and chemicals that increase the activity of defense-related genes and accumulation of phenolics in plants.

Chryseobacterium strains. *Chryseobacterium* sp. (R98) was also found to be a bio-control agent against *P. capsici*. This was the first strain of *Chryseobacterium* species reported to act as endophytic against fungal diseases (Ristaino, Johnston, 1999).

Antagonistic rhizobacteria. Rhizobacterium species also revealed huge scale antifungal features especially against Phytophthora blight. Rhizobacteria is mostly effective in the growth of the plants but some bacterial strains like ISE14, CCR80, R13 and R33 proved antagonistic to fungal attack in chilli plants (Emmert, Handelsman, 1999). Plant growth-promoting rhizobacteria (PGPR) not only increased the production of pepper (Kim et al., 2008; Reddy et al., 2016), but *Bacillus vallismortis* strain BS07 and *B. subtilis* CAS15 were found as a potential bio-control agent particularly against Phytophathora blight, Fusarium wilt and anthracnose disease of chilli plants. Plants treated with this rhizobacterium also showed significant boost in chlorophyll contents of leaves and increased fruit yield (Rajkumar et al., 2005).

Some strains of *Actinomycetes* and *Streptomyces* were also found to act as bio-control agents that effectively inhibited *P. capsici* on chilli plants. Table 2 shows various bacterial strains identified that induce resistance in chilli plants against *P. capsici*.

Table 2. Endophytic microorganisms used against *Phytophthora capsici* in chilli pepper

Endophytic bacteria	Pathogenic fungi	Enzymes produced	References
1	2	3	4
Bacillus tequilensis (CNU082075)	*Alternaria panax*, *Fusarium oxysporum*, *Colletotrichum acutatum* and *P. capsici*		Abeysinghe, 2009; Paul et al., 2013
Actinomycete isolate 9p	*Alternaria brassiceae*, *Rhizoctonia solani* and *P. capsici*	β-1,3-glucanase, lipase, cellulose and chitinase	Sakure et al., 2015; Ali et al., 2014 a
Streptomyces isolates P8, P39, P115 and P42	*Colletotrichum truncatum*, *C. gloeosporioides* and *C. acutatum*		Jung et al., 2004; Shahbazi et al., 2013
Bacillus isolates SB10	*P. capsici*	fengycins, iturins and surfactins	Zheng et al., 2004
ISE14, CCR04 and CCR80	*P. capsici*	2,4-di-*tert*-butylphenol	Kamoun et al., 1999
GSE09	*P. capsici*	2,4-di-*tert*-butylphenol	Kamoun et al., 1999
Pseudomonas corrugate CCR80 and *Chryseobacterium indologenes* ISE14	*P. capsici*	2,4-di-*tert*-butylphenol	Emmert, Handelsman, 1999
Bacillus subtilis R13 and R33	*P. capsici*	hydrolytic enzymes and hydrogen cyanide (HCN)	Emmert, Handelsman, 1999; Lee et al., 2008
Burkholderia cepacia CNU082111	*A. panax*, *Fusarium oxysporum*, *C. acutatum* and *P. capsici*		Abeysinghe, 2009
Pseudomonas aeruginosa CNU082137 and CNU082142	*A. panax*, *F. oxysporum*, *C. acutatum* and *P. capsici*		Abeysinghe, 2009

Table 2 continued

1	2	3	4
Pseudomonas fluorescens Pf1	*Pythium aphanidermatum*	polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL) and peroxidase (PO)	Lee et al., 2003 c
Trichoderma harzianum spores	*P. capsici*	capsidiol	Ma et al., 2008
OA-B36 and GK-B15	*P. capsici*	radicle assay and plant assessments	Yánez-Mendizábal et al., 2012
Bacterial strains KJ1R5, KJ2C12 and KJ9C8	*P. capsici*	radicle assay and plant assessments	Bloemberg, Lugtenberg, 2001
Bacillus luciferensis strain KJ2C12	*P. capsici*		Lee et al., 1999
Chryseobacterium wanjuense strain KJ9C8	*P. capsici*		Shen et al., 2002
Pseudomonas strains YJR27, YJR92, YJR102 and YJR107	*P. capsici*		Chang et al., 2001
Streptomyces halstedii AJ-7	*P. capsici*	10 kDa	Chatterton et al., 2004
Bacilli PGPR strains SE52, SE76, INR7, IN937a and IN937b	*P. capsici*		Jiang et al., 2006
Bacilli strains BB11 and FH17	*P. capsici*		Sang et al., 2007
Bacillus amyloliquefaciens Fy11 and Zy44	*P. capsici*	crude lipopeptides	Shen et al., 2007
Chryseobacterium strain KJ9C8	*P. capsici*	protease and hydrogen cyanide (HCN)	Anith et al., 2003
Strains GSE09 and ISE14	*P. capsici* and *C. capsici*	2,4-di-*tert*-butylphenol	Rajkumar et al., 2005
Flavobacterium johnsoniae strain GSE09	*P. capsici*	2,4-di-*tert*-butylphenol	Compant et al., 2005
Bacillus vallismortis strain BS07	*P. capsici* and *C. capsici*	salicylic acid (SA)	Rajkumar et al., 2005
Pseudomonas corrugate CCR04 and CCR80	*P. capsici*	hydrogen peroxide (H_2O_2) and 2,4-di-*tert*-butylphenol	Rajkumar et al., 2005
Serratia plymuthica strain C-1	*P. capsici*		Cordier et al., 1998
Bacterium burkholderia sp. H-6	*P. capsici* and *Fusarium graminearum*		Howell, 2003
B1301, R98 and PX35	*P. capsici*	chitinase, cellulose, of siderophores and protease	Ristaino, Johnston, 1999
Pseudomonas fluorescens isolate PS119	*P. capsici*		Sid Ahmed et al., 1999
Bacillus subtilis (CBE4) and *Pseudomonas chlororaphis* (*BCA+*)	*P. aphanidermatum* (damping off)	phenylalanine ammonia lyase (PAL), peroxidase (PO), polyphenol oxidase (PPO) and β-1,3-glucanase	Chen et al., 2003
Pseudomonas fluorescens	*C. capsici*	peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL), β-1,3-glucanase, chitinase	Drider et al., 2006
GK-B15 and GK-B25	*P. capsici*		Benítez et al., 2010
OA-B26 and OA-B36	*P. capsici*		Benítez et al., 2010
PK-B09 and VK-B14	*P. capsici*		Benítez et al., 2010
Strain A1022 SC	*C. gloeosporioides* and *P. capsici*		Candela et al., 1995
Bacillus amyloliquefaciens Fy11 and Zy44	*P. capsici*		Khan et al., 2004
Bacillus subtilis CAS15	*Fusarium* wilt		Yin et al., 2012
Bacillus subtilis CA32 and *T. harzianum* RU01	*R. solani*		Yang et al., 2012
Streptomyces sp. AMG-P1	*P. capsici*	aminoglycoside antibiotics	Akgül, Mirik, 2008
Paenibacillus polymyxa E681	*P. capsici*	fusaricidin	Akgül, Mirik, 2008
Serratia plymuthica strain C-1	*P. capsici*		Roberts et al., 2010
Pseudomonas fluorescens strain IISR-6	*P. capsici*	pyoluteorin and pyrrolnitrin	Howell, 2003
Lysobacter antibioticus strain HS124	*P. capsici*	chitinase and β-1,3-glucanase	Fester, Hause, 2005
Paenibacillus ehimensis KWN38	*P. capsici*	β -1,3-glucanase	Hwang et al., 1997
Bacillus amyloliquefaciens Bg-C31	*P. capsici*	fusion protein	Selvaraj, Chellappan, 2006
Bacillus subtilis HS93	*P. capsicia* and *A. alternate*	chitinase	Veloso, Díaz, 2012; Ahmed et al., 2003
Bacillus licheniformis LS234, LS523 and LS674	*P. capsici* and *A. alternate*	chitinase	Ahmed et al., 2003
Bacillus strains BB11 and FH17	*P. capsici*		Ahmed et al., 2003
Bacillus amyloliquefaciens FZB42	*P. capsici*	lipopeptides and polyketides	Ahmed et al., 2003
Pseudomonas aeruginosa strain B5	*P. capsici*	rhamn olipid B	Zhang et al., 2010
Chryseobacterium wanjuense strain KJ9C8	*P. capsici*	protease and hydrogen cyanide (HCN)	Ryan et al., 2008
Paenibacillus polymyxa GBR-462	*P. capsici*		Akgül, Mirik, 2008
Bacillus amyloliquefaciens strain BS211	*P. capsici*		Chung et al., 2008
Trichoderma asperellum strains T2 and T31	*P. capsici*		Lee et al., 1999

Table 2 continued

1	2	3	4
Trichoderma hamatum strain T25	*P. capsici*		Lee et al., 1999
Pseudomonas fluorescens strain MM-B16	*P. capsici* and *C. orbiculare*	aerugine	Lee et al., 2003 b
Streptomyces halstedii AJ-7	*P. capsici*		Suryanto et al., 2012
Streptomyces padanus IA70-5	*P. capsici*		Kim et al., 2014 b
Bacillus vallismortis ZZ185	*P. capsici* and *R. solani*	bacillomycin D	Park et al., 2013
Bacillus isolate SB10	*P. capsici*	iturins, surfactins and fengycins	Oh et al., 2011
Trichoderma hamatum 382 (T382)	*P. capsici*		Khan et al., 2004

Other management strategies for *Phytophthora capsici*

P. capsici is a soil born disease and it predominantly spreads through water. Effective irrigation management is crucial to control *P. capsici* inside a field. Development of disease resistant varieties is also a good strategy to control *P. capsici*. Several experiments conducted by grafting the bell pepper shoot on the resistant rootstock showed significant disease decline on *P. capsici* infected plants (Gilardi et al., 2013). Crop rotation with non-susceptible crops can minimize the chances of sporulation residing in the field. Infected chilli plants and fruits should be properly dumped in un-cultivated areas because pathogen can survive in the soil for several years. Fungicide application in the drenches is more effective as compared to foliar application. Combined fungicides with diverse mode of actions should be applied at dissimilar intervals to break the resistance in *P. capsici*. Essential oils such as myrtaceae, red thyme, oregano and palmarosa also suppress the influence of *P. capsici*. Cultural practices such as mulching, raised beds, drip irrigation and the use of resistant varieties can minimize the *P. capsici* spreading in field (Sanogo, Ji, 2013). Application of dung and rice straws also can efficiently reduce the severity of Phytophthora fruit rot in chilli. Incorporation of bio-fumigation along with endophytic microorganism is also beneficial.

Future prospects and directions

Phytophthora blight disease is one of the main economic limitations to the vegetable crops worldwide. Integrated disease management strategies like host resistance, chemical control, cultural practices, and biological control should be combined to control diseases. Although the management and control of *P. capsici* are being comprehensively researched, all taxonomic facts about the pathogenic races of *P. capsici* and their whole biology must be known. We tried to focus on all recommended strategies that might be effective against this pathogen but there is still a need to discover more genes and antagonistic microorganisms against *P. capsici*. As chilli plant is a rich source of resistant genes that can be manipulated against *P. capsici* in other related plants. Many genes have been identified by researchers that confer resistance against *P. capsici*. These genes may help successfully for the development of resistant and more productive cultivars in the future. Use of antagonistic microorganisms against fungal pathogens is also a cheap and environment friendly way to manage the diseases. Research on physiology and pathogenesis of fungi can generate new targets specific to plant pathogens. Diverse approaches are also required for different pathogens having complementary activities.

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Genetinė ir biologinė *Phytophthora capsici* kontrolė aitriosios paprikos (*Capsicum annuum* L.) augalams: apžvalga

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Santrauka

Phytophthora capsici yra pats žalingiausias daržovių patogenas, keliantis grėsmę aitriųjų paprikų augalams. Straipsnyje aptariama *P. capsici* kontrolė atsižvelgiant į aitriosios paprikos genetinę struktūrą ir endofitinius mikroorganizmus. Analizuota įvairių genų transkripciją reguliuojančių ir atsparumą lemiančių proteinų funkcija. Aptarti su patogenu susiję baltymai, antimikrobiniai peptidai, poligalakturonazę slopinantys ir lipidus pernešantys baltymai, pektino metilesterasės, leucino turintys baltymai, panašūs į osmotiną ir taumatiną baltymai. Aprašyta *P. capsici* biologinė kontrolė naudojant įvairias *Bacillus*, *Trichoderma*, *Pseudomonas*, *Chryseobacterium* ir *Rhizobacteria* padermes. Aptartas atsparumo *P. capsici* infekcijai padidėjimas panaudojus įvairius abiotinius ir biotinius induktorius, kurie veikia gynybą sąlygojančius signalinius kelius. Išryškintas aitriųjų paprikų genetinių išteklių pažeidžiamumas sergant fitoftoroze. Cheminė ligų kontrolė tampa probleminė, todėl pasiūlyti kiti ligos intensyvumo kontrolės būdai. Apžvalgoje išryškinta aitriųjų paprikų ir *P. capsici* išplitimo valdymo strategijų ekonominė reikšmė. Nurodoma, kad patogenas kelia didelę grėsmę aitriųjų paprikų augalams visame pasaulyje.

Reikšminiai žodžiai: baltymai, biotiniai ir abiotiniai induktoriai/sužadintojai, genetiniai ištekliai, transkripcijos reguliatorius.

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