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Biological Control of Oomycetous Plant Pathogens: A Review

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Abstract
Oomycetes are generally known as water molds, and include diverse plant pathogenic organisms. In this review, we summarized plant diseases mainly caused by oomycetes and highlighted ongoing trends in controlling and managing these pathogens using eco-friendly ways.

Key words: antagonistic microorganisms, biological control, oomycet

Introduction
Oomycetes, commonly known as water molds (Winter 1880) are detrimental plant pathogens infecting a wide range of host plants such as native weeds, ornamental plants, and trees (Erwin & Ribeiro 1996, Margulis & Schwartz 2000, van West *et al.* 2003, Sanogo & Ji 2012). The pathogenicity of oomycetes is rendered by their spore production, development of infecting structures, and dispersal of spores (Endo & Colt 1974, Kramer *et al*. 1997). In molecular aspects, effector proteins recognized by signature amino acid motifs RxLR (arginine, any amino acid, leucine, arginine), and dEER (a string of acidic amino acids followed by arginine) are known to facilitate the oomycetes virulence in host plant (Kale & Tyler 2011, Tyler 2011).

Oomycetes are being controlled by numerous approaches which include clean nursery stock, use of resistant varieties, chemical, physical, and systemic fungicides. Biological control agents (BCAs) are also used to suppress oomycetes and their related diseases (Pal & Gardener 2006, Lee *et al*. 2005, Sang & Kim 2012). Aside from these, however, various *Pythium*- and *Phytophthora*-causing diseases exhibited the resistance to BCAs such as propamocarb, mefenoxam, and metalaxyl, no longer (Titone *et al*. 2009, Moorman & Kim 2004, Parra *et al*. 2001). Therefore, development of more advanced and efficient biological control is of utmost necessity for future success to control oomycetes. This mini review summarized major diseases caused by oomycetous pathogens, efficient BCAs against oomycetous diseases, and their relevant mechanisms.

Major diseases caused by oomycetes
The plant pathogenic oomycetes contains many taxa and exhibit remarkably diverse lifestyles ranging from obligate biotroph to necrotroph (Agrios 2011). General life cycle of these pathogens can be exemplified by *Phytophthora capsici* (Fig 1a). Few representative disease symptoms caused by them are shown in (Fig 1b). The diseases caused by major genera such as *Phytophthora*, *Pythium*, *Peronospora*, *Albugo*, and *Aphanomyces* are summarized in (Table 1). Species of *Pythium*, *Phytophthora*, *Aphanomyces* and *Rhizoctonia*, etc. are known to cause damping-off disease (Agrios 2011). *Albugo candida* causes white rust on *Erysimum crassicaule* (Mirzaee *et al*. 2009).

Soil borne *Phytophthora* and *Pythium* spp. are also widespread and cause major losses on crops of soybeans (Schmitthenner 1985) and avocados (Cohen 1981, Darvas *et al*. 1984). In addition, *Phytophthora* and *Pythium* spp. were responsible for many pre- and post-harvest problems on fruits and vegetables, including brown rot of citrus (Cohen 1981a, b, 1982, Gutter 1983), and black pod of cocoa (McGregor 1983, 1984). Recently, new diseases are emerging caused by these oomycetes; for example, severe rotting and blight of seedlings of soybean (Tomioka *et al*. 2013), root rot disease of legumes (Gaulin *et al*. 2007), etc. New species were also reported in many crops: *Pythium solare* (wilt and death of adult plants of *Phaseolus vulgaris*) (de Cock *et al*. 2008), *Pythium myriotylum* (root and crown necrosis) (Serrano *et al*. 2008), *Phytophthora bisheria* (raspberry, rose, and strawberry diseases) (Abad *et al*. 2008), *Pustula* sp. (sunflower white rust) (Rost & Thines 2012), *Pythium echinogynum* (severe "damping-off pathogen" to tomato and cucumber seedlings) (Balghouthi *et al*. 2013), etc. Some other oomycetes such as *Phytophthora gallica* (Jung & Nechwatal 2008), *Pythium indigoferae*, and *Pythium irregulare* (Souli *et al*. 2011) caused diseases in oak and apple trees, respectively.

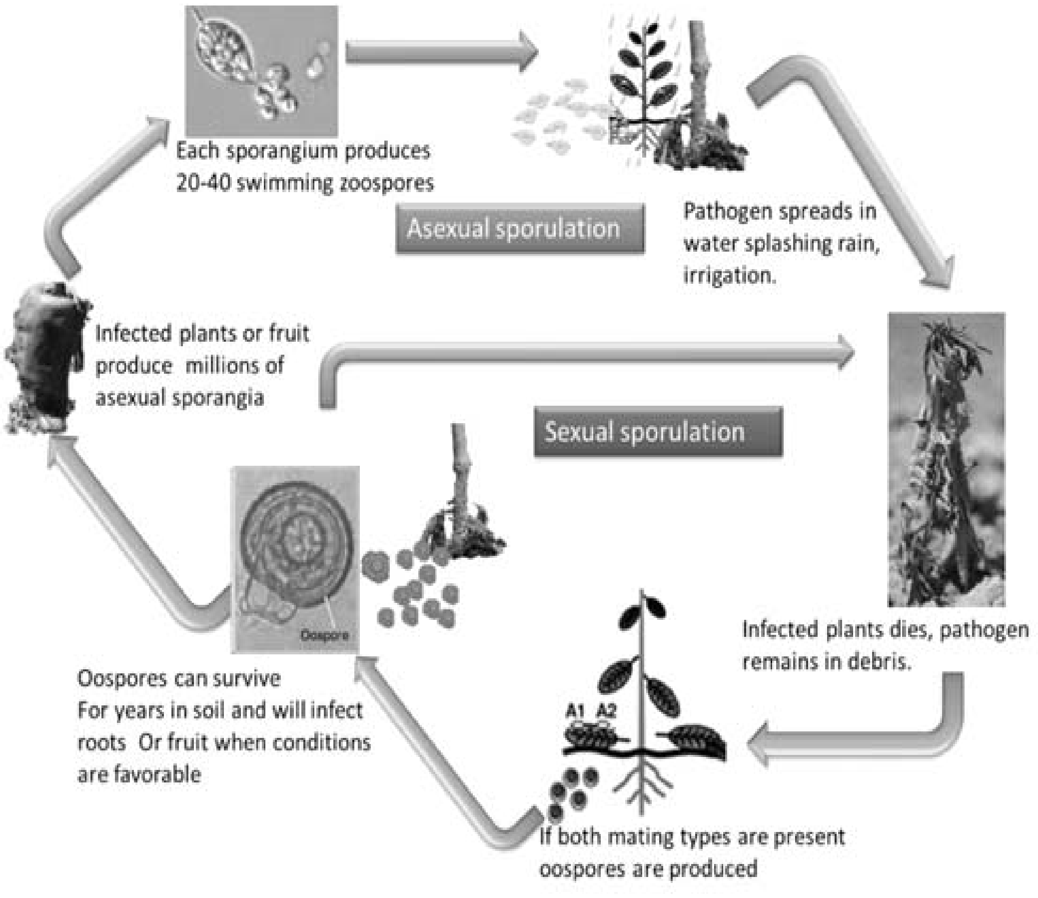

Fig. 1a. Diagram depicting the life cycle of *Phytopthora capsici.*
Life cycle figure was provided by C.D. Smart, Cornell University, with some modifications.
Oospores; Reproduced by permission, from Gallup, C. A., Sullivan, M. J., and Shew, H. D. 2006. Black shank of tobacco. The Plant Health Instructor. DOI: 10.1094/PHI-I-2006-0717-01.
Photo courtesy Zoospores: Fred Brooks, University of Hawaii at Manoa, Bugwood.org.

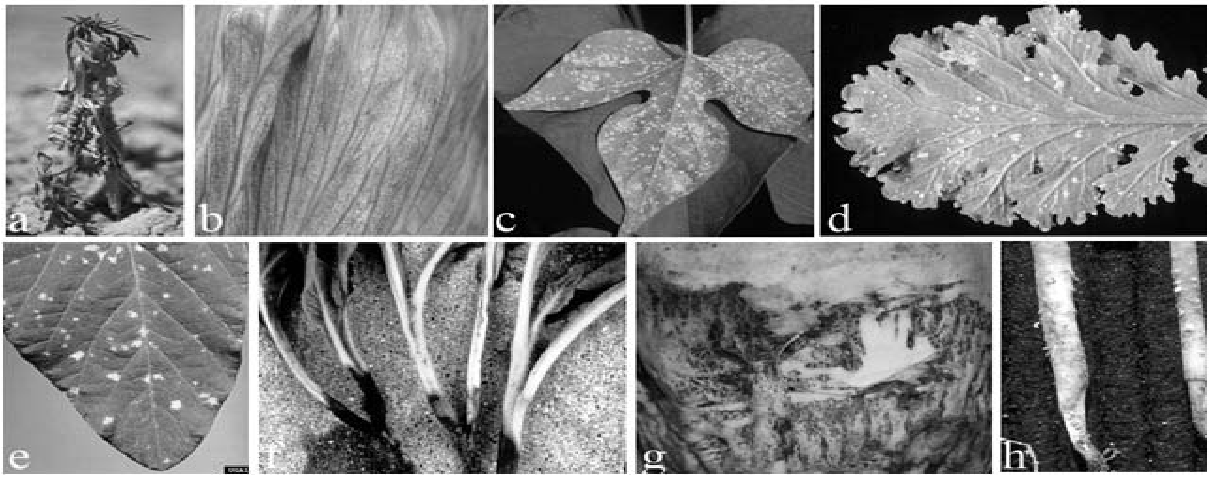

Fig. 1b. Representative photographs of some disease symptoms caused by oomycetes:
a) Symptoms of Phytopthora blight on pepper plant with characteristic wilting due to *Phytopthora capsici* leonian, b) Downy mildew on lettuce plant by *Bremia lactucae*, c) White rust on morning glory leaf with heavy sporulation of white rust caused by *Albugo ipomoe panduratae*, d) White rust on mustard with white rust pustules on the leaf underside due to *Albugo candida*, e) Downy mildew on soyabean caused by *Peronospora manshurica*, f) Damping off of tobacco with characteristic large and wet lesions caused by *Pythium* sp. pringsh., g) Damping off characterized by root rot external symptoms on mature beet, superficial scaring caused by *Aphanomyces cochlioides*, and h) Damping off of common bean caused by *Pythium* spp.
Photo courtesy; a, b, c, d; Gerald Holmes,Valent USA Corporation, Bugwood.org.
e; Clemson University, USDA Cooperative Extension Slides Series, Bugwood.org.
f; R. J. Reynolds, Tobacco Company Slide Set, Bugwood.org.
g; Oliver T. Neher, The Amalgamated Sugar Company, Bugwood.org.
h; Howard F. Schwartz, Colorado State University, Bugwood.org.

Table 1. Important plant pathogenic oomycetes and diseases caused by them

Pathogen	Disease caused	References
Phytopthora species	Root rot pathogen of soybean	Tyler 2007, Souli *et al*. 2011, Sang *et al*. 2013
	Root and crown necrosis of bean	Abad *et al*. 2008
	Damping off disease	Agrios 2011
	Root rot on ginseng	Sang *et al*. 2006
Pythium species	Damping-off, root-rot	Cohen 1981a, Cohen 1981b, Cohen 1982 Van West *et al*. 2003, Schmitthenner 1985, Cohen 1981a
	damping-off pathogen” to tomato and cucumber seedlings	Balghouthi *et al*. 2013
	Root rot disease of legumes	Cohen 1981b, Cohen 1982, Gutter 1983, de Cock *et al*. 2008, Serrano *et al.* 2008, Balghouthi *et al*. 2012
		Souli *et al.* 2011
Peronospora Bremia, Plasmopara	Various downy mildews	Agrios 2011
Albugo species	White blister	Abbasi & Mohammadi, 2009
	Sunflower white rust	Rost & Thines, 2012
Aphanomyces	Damping off disease	Agrios 2011, Gaulin *et al.* 2007

Biological control of oomycetes and mechanisms involved

Microorganisms from different sources such as rhizosphere and phylloshere can potentially reveal biological control effects against different plant pathogenic oomycetes. In mechanistic basis, these microorganisms control the target pathogens by antibiotic production, root colonization, nutrient competition, induced systemic resistance, plant growth promotion, mutualism, mycoparasitism, and predation. Some of the common bacteria, fungi, and actinomycetes against oomyceteous pathogens were summarized (Table 2). The most effective bacterial isolates were *Pseudomonas*, *Bacillus*, *Lysobacter*, *Enterbacter*, and *Paenibacillus*. Fungi such as *Trichoderma*, endophytic *Fusarium*, and *Ganoderma* spp. also controlled oomycetes. Moreover, about 9% of the total number of isolated bacteria identified as Firmicutes, α-Proteobacteria, γ-Proteobacteria and Actinomycetes exhibited anti-oomycetic activity (Bibi *et al*. 2012).

Table 2. Biological control agent (BCA) and some commercial microbial inoculants for control of plant disease

Name of BCAs	Target disease(s)/ pathogen (s)	Product name (if available)	Mode of action	Reference
Bacteria				
Bacillus licheniformis	Turfgrass diseases	Ecogurad^{TM}		Nelson 2004
*Bacillus lentimorbus*WJ5a17 mutants	Pythium root rot		Radiation	Lee *et al*. 2003
Bacillus pumilus	Soybean seed, and root rots (*Pythium*)	GB34^{TM}		Nelson 2004
Bacillus subtilis	Various foilar, and root diseases	Kodiak^{TM}		Nelson 2004
Burkholderia cepacia	Seed, seedlings, and root rots (*Pythium*)	Avogreen^{TM}, Deny ^{TM}		Nelson 2004
Bacillus amyloliquefaciens,and *Pseudomonas aeruginosa*	*Pythium aphanidermatum*			Elazzay *et al*. 2012
Chryseobacterium wanjuense, strain KJ9C8	Phytopthora blight of pepper, *Phytopthora capsici*		Colonization, and antibiosis; production of HCN with swarming effect	Kim *et al*. 2012
Enterobacter cloacae, and *Erwinia herbicola*	Pythium seed rot, and pre-emergence damping-off of cotton		Competition for nutrient (fatty acid)	Nelson 1988,van Dijk & Nelson 2000
Flavobacterium johnsoniae strain GSE09	*Phytopthora capsici*		Volatile organic compound 2,4-di-ter-butylpheonl inhibits mycelial growth, sporulation, zoospore formation, and colonization	Sang & Kim, 2012
Fluorescent *Pseudomonad* spp	*Pythium ultimum,*			Mezaache *et al*. 2010
Lysobacter sp strain SB-K88	Damping off, *Peronosporomycetes*, *Aphanomyces cochlioides*		Colonization, and antibiosis	Islam *et al*. 2005
Lysobacter antibioticus HS124	Phytopthora blight of pepper		Antibiosis; production of secondary metabolite 4-hudroxyphenylacetic acid	Ko *et al*. 2009

Lysobacter enzymogenes 3.1 T8	Pythium root rot in cucumber, *Pythium aphanidermatum*		Colonization; root of cucumber plant	Folman 2003,
Lactic acid bacterial strains	*Pythium ultimum*		Production of organic acids such as propionic or lactic acid, and decrease in pH, accumulation of H_20_2; antimicrobial compounds	Lutz *et al*. 2012
Novosphingobium capsulatum strain YJR107	Phytopthora blight of pepper, *Phytopthora capsici*		Effective selection procedure, colonization, and inhibition of mycelial growth	Sang *et al*. 2013
Pseudomonas corrugate (CCR80), and *Chryseobacterium indologenes* ISE14	Phytopthora blight of pepper, *Phytopthora capsici*		Antagonism, inhibition of mycelial growth	Sang *et al*. 2008
Pseudomonas fluorescens EBL 20-PF	*Pythium aphanidermatum*		Antagonism; inhibition of mycelial growth; Induce systemic resistance	Muthukumar *et al*. 2011
Pseudomonas cepacia	Pythium damping off, and Aphanomyces root rot of peas		Seed colonization	Parke *et al*. 1991
Pseudomonas fluorescens F113	*Pythium ultimum* damping-off of sugar beet		2,4-diacetylphloroglucinol; a natural phenol renders antiphtyopathogenic action	Dunne *et al*. 1998
Pseudomonas flourescens CV69 and V11	Cucumber root, and crown rot by *Phytopthora dreschsleri*		Antibiosis, production of siderophores, and indole-3-acetic acid (IAA)	Maleki *et al*. 2010, Maleki *et al*. 2011
Pseudomonas marginalis	*Pythium ultimum* or *Pythium aphanidermatum*		Inhibition of mycelial growth	Gravel *et al*. 2005
Pseudomonas chlororaphis	Turfgrass diseases	AtEze™, Cedomon™		Nelson 2004
Pseudomonas aeruginosa strain 7NSK2	Pythium damping off of tomato		Antibiosis due to siderophere mediated compound	Buysens *et al*. 1996,
Pseudomonasv sp	Rhizoctoina, and Pythium root of wheat		Antagonism,	Williams & Asher1996
Paenibacillus polymyxa GBR-462	*Phytopthora capsici*		Inhibition of mycelium growth, and zoospore formation	Kim *et al*. 2009
Paenibacillus polymyxa	*Phytopthora palmivora,and Pythium aphanidermatum*		Biofilm formation, and niche exclusion	Timmusk *et al*. 2009
Paenibacillus lentimorbus WJ15	*Phytopthora capsici,and Pythium ultimum*		Production of antifungal metabolites	Lee *et al*. 2008

Paenibacillus sp	Damping off (*Pythium*)		Indirect; Inducing plant systemic resistance by plant growth promotion	Li *et al*. 2007
Rhizobacteria	*Pythium ultimum*,and *Aphanomyces cochlioides* on sugar-beet seedlings		Colonization, and antifungal metabolites	Mavrodi *et al*. 2012
Rhizobium leguminosarum Jordan bv. Viceae	Pythium damping-off of pea, and sugar beet		Colonization	Bardin *et al*. 2004
Serratia plymuthica A21–4,	*Phytopthora capsici*		Inhibition of mycelium growth, and zoospore formation	Shen *et al*. 2002
Stenotrophomonas maltophilia W81	*Pythiumultimum*damping -off of sugar beet		Production of extracellular protease	Dunne *et al*.1997, Dunne *et al*. 1998
Fungi				
Chaetomium cupreum/*C. globosum*	Disease caused by Phytophthora	Ketomium (R) ^{TM}		Nelson 2004
Chaetomium globosum	*Phytopthora infestans*	Symbion C ^{TM}		Ramarethinam *et al*. 2008
Clonostachys rosea	*Pythium tracheiphilum*		PGP	Moller *et al*. 2003
Fusarium oxysporum EF119	*Pythium ultimum*, *Phytophthora infestans*,and *Phytophthora capsici*		Antioomycete activity; Antibiosis; Bikaverin, and fusaric acid	Kim *et al*. 2007, Son *et al*. 2007
Fusarium oxysporum Strain Fo47	*Pythium ultimum*		Direct; antibiosis and mycoparasitism, indirect; inducing systemic resistance	Benhamou *et al*. 2002
Glicocladium virens	Seed seedlings, and root rots (*Pythium*)	Soil Guard^{TM}, Gliomix^{TM}		Nelson 2004
Ganoderma appalantum	*Sclerospora graminicola*		Inhibition of sporangia, zoospore release, and zoospore motility,	Sudisha & Shetty 2009
Phoma nov.sp	*Phytopthora parasiticia*		*Phoma* impairs *P. parasitica* mycelium growth, and prevents *P. parasitica* infection of the leaf	French patent application (FR 1051767)
Trichoderma viride (TVA)	*Pythium aphanidermatum*		Induction of defense-related enzymes, and phenolic compound	Muthukumar *et al*. 2011
Trichoderma	Pythium damping-off			Yang *et al*. 2004
Actinomycetes				
Actinoplanescampanulatus, Micromonospora chalcea, and *Streptomyces spiralis*	*Pythium aphanidermatum* damping off disease of cucumber		Antibiosis; cell wall degrading enzymes, and inducing systemic resistance in cucumber plant	El-Tarabily *et al*. 2010, El-Tarabily *et al*. 2009, El-Tarabily 2006
Actinoplanes spp	*Phytophthora megasperma* f. sp. *Glycinea*		Antagonism	Filonow & Lockwood 1985
Streptomyces	Wilts, seed, and root rots	Mycostop^{TM}		Nelson 2004

Mechanisms of anti-oomycetic activity are mainly due to colonization, antibiotic production, hyphal lysis, sporangium abortion, oospore parasitism and siderophore production (Buysens *et al*. 1996, Broadbent *et al*. 1971, Drapeau *et al*. 1973, Honor & Tsao 1973, Broadbent & Baker 1974, Wynn & Epton 1979). Colonization of bacteria (e.g. *Enterobacter cloacae*) resulted in a competitive exclusion of nutrients from *Pythium*, *Phytopthora capsici*, and *Phytophthora cactorum* (Nelson 1988, Sang *et al.* 2007, Sang *et al*. 2006). Various antibiotics and lytic enzymes produced by microorganisms revealed antagonism against oomycetes (Dunne *et al*. 1997, Lee *et al.* 2003, Lee *et al.* 2008, Timmusk *et al.* 2009, Muthukumar *et al*. 2011). Recently, *Streptomyces* producing chitinase, ß-1, 3-glucanase, lipase and protease showed direct lysis of *Phytophthora capsici* hyphae (Nguyen *et al*. 2012). In addition, *Pseudomonas ûuorescens* and *Serratia plymuthi* showed the antagonisms to *Pythium aphanidermatum* and *Phytophthora capsici* (Muthukumar *et al*. 2011, Shen *et al*. 2002). The compounds originated from *Streptomyces koyangensis* and *Ganoderma appalantum* restricted the growth of oomycetes (Lee *et al*. 2005, Sudisha & Shetty 2009).

On the other hand, various BCAs were suggested to control oomycetes by modulating the induced systemic resistance (ISR) of host plants either directly or through volatile organic compounds produced by them (Benhamou *et al*. 2002, Sang & Kim 2012). Most of the BCAs reported are able to suppress more than one pathogen; however, some of them were pathogen specific and even some were host-specific showing selective influence of BCAs (Maurhofer *et al*. 1994, Van Dijk & Nelson 2000, Mavrodi *et al*. 2012, Sang *et al*. 2013). Combination treatment of bacteria-fungi or bacteria-bacteria are also effective to control oomycetes (Dunne *et al*. 1998, Muthukumar *et al*. 2011).

Future perspectives

Development of anti-oomycetic BCAs is very important and utmost necessity for managing oomycetic diseases as it is considered as an alternative or a supplemental way of reducing the use of chemicals in agriculture (De weger *et al*. 1995, Gerhardson 2002). More researches should be carried out to elucidate the mechanism involved in the microorganism-pathogen interaction and to identify the novel efficient BCAs in future to establish sustainable BCAs against oomycetous diseases. Finally, we can conclude that different biological control approaches summarized in this review can shed light on future directions in developing and choosing different biological control agents against oomycetes.

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