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 Phythium- 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 Phythium, Phytophthora, Aphanomyces and Rhizoctonia, etc. are known to cause damping-off disease (Agrios 2011). Albugo candida causes white rust on Erysimum crassicaule (Mirzae 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 bishoria* (raspberry, rose, and strawberry diseases) (Abad *et al*. 2008), *Pastula* sp. (sunflower white rust) (Rost & Thines 2012), *Phytophthora echinoagynum* (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 *Phytophthora 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 Phytophthora blight on pepper plant with characteristic wilting due to *Phytophthora 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 scarring 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

<table>
<thead>
<tr>
<th>Pathogen</th>
<th>Disease caused</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>Phytophthora</td>
<td>Root rot pathogen of soybean</td>
<td>Tyler 2007, Souli <em>et al.</em> 2011, Sang <em>et al.</em> 2013</td>
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<tr>
<td>Phytophthora</td>
<td>Root and crown necrosis of bean</td>
<td>Abad <em>et al.</em> 2008</td>
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<td>Phytophthora</td>
<td>Damping off disease</td>
<td>Agrios 2011</td>
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<tr>
<td>Phytophthora</td>
<td>Root rot on ginseng</td>
<td>Sang <em>et al.</em> 2006</td>
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<tr>
<td>Pythium species</td>
<td>damping-off pathogen” to tomato and cucumber seedlings</td>
<td>Van West <em>et al.</em> 2003, Schmitthenner 1985, Cohen 1981a</td>
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<tr>
<td>Pythium species</td>
<td>Root rot disease of legumes</td>
<td>Balghouthi <em>et al.</em> 2013</td>
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<td>Peronospora Bremia, Plasmopara</td>
<td>Various downy mildews</td>
<td>Souli <em>et al.</em> 2011</td>
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<td>Albugo species</td>
<td>White blister</td>
<td>Agrios 2011</td>
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<tr>
<td>Albugo species</td>
<td>Sunflower white rust</td>
<td>Abbasi &amp; Mohammadi, 2009</td>
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<td>Aphanomyces</td>
<td>Damping off disease</td>
<td>Rost &amp; Thines, 2012</td>
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<td>Aphanomyces</td>
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<td>Agrios 2011, Gaulin <em>et al.</em> 2007</td>
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</table>
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, Enterobacter*, 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

<table>
<thead>
<tr>
<th>Name of BCAs</th>
<th>Target disease(s)/pathogen(s)</th>
<th>Product name (if available)</th>
<th>Mode of action</th>
<th>Reference</th>
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<tbody>
<tr>
<td><strong>Bacteria</strong></td>
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<td><em>Bacillus licheniformis</em></td>
<td>Turfgrass diseases</td>
<td>Ecogurad™</td>
<td>Radiation</td>
<td>Nelson 2004</td>
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<td><em>Bacillus lentiformis</em></td>
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<td><em>Bacillus pumilus</em></td>
<td>Pythium root rot Soybean seed, and root rots (<em>Pythium</em>)</td>
<td>GB34™</td>
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<td>Lee et al. 2003</td>
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<tr>
<td><em>Bacillus subtilis</em></td>
<td>Various foilar, and root diseases</td>
<td>Kodiak™, Avogreen™, Deny™</td>
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<td>Nelson 2004</td>
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<td><em>Bacillus amyloliquefaciens</em> and <em>Pseudomonas aeruginosa</em></td>
<td>Seed, seedlings, and root rots (<em>Pythium</em>)</td>
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<td>Nelson 2004</td>
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<tr>
<td><em>Enterobacter cloacae</em> and <em>Erwinia herbicola</em></td>
<td>Pythium seed rot, and pre-emergence damping-off of cotton</td>
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<td><em>Flavobacterium johnsoniae</em> strain GSE09</td>
<td><em>Phytophthora capsici</em></td>
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<td>Fluorescent <em>Pseudomonad</em> spp</td>
<td><em>Pythium ultimum</em>, Damping off, <em>Peronosporomyces, Aphanomyces cochlioides</em></td>
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<td><em>Lysobacter sp strain SB-K88</em></td>
<td><em>Phytophthora blight of pepper</em></td>
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<td>Islam et al. 2005</td>
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<td><em>Lysobacter antibioticus</em> HS124</td>
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<td>Ko et al. 2009</td>
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<tr>
<td>Organism</td>
<td>Colonization effect</td>
<td>Notes</td>
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<td>Lysobacter enzymogenes 3.1 T8</td>
<td>Pythium root rot in cucumber, <em>Pythium aphanidermatum</em></td>
<td>Colonization; root of cucumber plant. Production of organic acids such as propionic or lactic acid, and decrease in pH, accumulation of H₂O₂. Antimicrobial compounds. Effective selection procedure, colonization, and inhibition of mycelial growth. Folman 2003.</td>
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<td>Lactic acid bacterial strains</td>
<td><em>Pythium ultimum</em></td>
<td>Lutz et al. 2012</td>
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<td>Pseudomonas corrugate (CCR80), and Chryseobacterium indologenes ISE14</td>
<td>Phytophthora blight of pepper, <em>Phytophthora capsici</em></td>
<td>Antagonism; inhibition of mycelial growth; Induce systemic resistance. Muthukumar et al. 2011</td>
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<tr>
<td>Pseudomonas fluorescens EBL 20-PF</td>
<td><em>Pythium aphanidermatum</em></td>
<td>Seed colonization 2,4-diacetylphloroglucinol; a natural phenol renders antiphytopathogenic action. Dunne et al. 1998</td>
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<td>Pseudomonas cepacia</td>
<td><em>Pythium ultimum</em> damping-off of sugar beet</td>
<td>Antibiosis due to siderophere mediated compound. Maleki et al. 2010, Maleki et al. 2011</td>
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<tr>
<td>Pseudomonas fluorescens F113</td>
<td>Cucumber root, and crown rot by <em>Phytophthora dreschleri</em></td>
<td>Inhibition of mycelial growth. Gravel et al. 2005</td>
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<tr>
<td>Pseudomonas fluorescens CV69 and V11</td>
<td><em>Pythium ultimum</em> or <em>Pythium aphanidermatum</em></td>
<td>Antibiosis due to siderophere mediated compound. Buyens et al. 1996.</td>
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<tr>
<td>Pseudomonas marginalis Pseudomonas chlororaphis</td>
<td>Turfgrass diseases</td>
<td>Antibiosis due to siderophere mediated compound. Williams &amp; Asher 1996</td>
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<td>Pseudomonas sp</td>
<td>Rhizoctonia, and <em>Pythium root of wheat</em></td>
<td>Biofilm formation, and niche exclusion. Timmusk et al. 2009</td>
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<td>Paenibacillus polymyxa GBR-462</td>
<td><em>Phytophthora capsici</em> <em>Phytophthora palmivora,</em> and <em>Pythium aphanidermatum</em></td>
<td>Production of antifungal metabolites. Lee et al. 2008</td>
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<td>Paenibacillus polymyxa</td>
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<td>Paenibacillus lentimorbus WJ15</td>
<td><em>Phytophthora capsici,</em> and <em>Pythium ultimum</em></td>
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<td><strong>Fungi</strong></td>
<td><strong>Actinomycetes</strong></td>
<td><strong>Rhizobacteria</strong></td>
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<td>Chaetomium cupreum/C. globosum</td>
<td>Chaetomium globosum</td>
<td>Rhizobium leguminosarum Jordan bv. Viceae</td>
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<td>Clonostachys rosea</td>
<td>Fusarium oxysporum EF119</td>
<td>Rhizobacteria</td>
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<tr>
<td>Clonostachys rosea</td>
<td>Fusarium oxysporum Strain Fo47</td>
<td>Rhizobacteria</td>
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<tr>
<td>Glicocladium virens</td>
<td>Glicocladium virens</td>
<td>Rhizobacteria</td>
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<tr>
<td>Ganoderma appalantum</td>
<td>Phoma nov.sp</td>
<td>Rhizobacteria</td>
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<tr>
<td>Phoma nov.sp</td>
<td>Trichoderma viride (TVA)</td>
<td>Serratia plymuthica A21-4</td>
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<td>Trichoderma viride (TVA)</td>
<td>Trichoderma</td>
<td>Rhizobacteria</td>
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<td>Trichoderma</td>
<td>Actinoplanes spp, Micromonospora chalcea, and Streptomycyes spiralis</td>
<td>Rhizobacteria</td>
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<tr>
<td>Actinoplanes spp, Micromonospora chalcea, and Streptomycyes spiralis</td>
<td>Actinoplanes spp</td>
<td>Rhizobacteria</td>
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**Paenibacillus sp**
- Damping off (*Pythium*)
- *Pythium ultimum*, and *Aphanomyces cochlioides* on sugar-beet seedlings

**Rhizobacteria**
- *Rhizobium leguminosarum* Jordan bv. *Viceae*
- Serratia plymuthica A21-4
- Senterophomomas *maltophilia* W81

**Fungi**
- Chaetomium cupreum/C. globosum
- Clonostachys rosea
- Fusarium oxysporum EF119
- Fusarium oxysporum Strain Fo47
- Glicocladium virens
- Ganoderma appalantum
- Phoma nov.sp
- Trichoderma viride (TVA)
- Trichoderma

**Actinomycetes**
- Actinoplanes spp
- Actinoplanes spp, Micromonospora chalcea, and Streptomycyes spiralis
- Actinoplanes spp, Micromonospora chalcea, and Streptomycyes spiralis
- Actinoplanes spp
- Streptomycyes

**Indirect; Inducing plant systemic resistance by plant growth promotion**
- Li et al. 2007
- Mavrodi et al. 2012
- Bardin et al. 2004
- Shen et al. 2002
- Dunne et al. 1997, Dunne et al. 1998

**Colonization, and antifungal metabolites**
- Mavrodi et al. 2012
- Bardin et al. 2004
- Shen et al. 2002
- Dunne et al. 1997, Dunne et al. 1998

**Colonization**
- Bardin et al. 2004
- Shen et al. 2002
- Dunne et al. 1997, Dunne et al. 1998

**Induction of defense-related enzymes, and phenolic compound**
- Muthukumar et al. 2011
- Yang et al. 2004

**Production of extracellular protease**
- Dunne et al. 1997, Dunne et al. 1998

**Inhibition of sporangia, zoospore release, and zoospore motility**
- Sadisha & Shetty 2009
- French patent application (FR 1051767)

**Antibiosis; cell wall degrading enzymes, and inducing systemic resistance in cucumber plant**
- Filonow & Lockwood 1985
- Nelson 2004

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 oomycotic 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 oomycetic 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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