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ARTICLE

Oomycetes as biocontrol agents: unveiling their potential and mechanisms in plant disease control

Li Y[1*], Ahmadi F[2*], Wan S[1] and Kariman K[2]

[1] *College of Agricultural Resources and Environmental Science, Yunnan Agricultural University, Kunming 650201, China*
[2] *UWA School of Agriculture and Environment, The University of Western Australia, Perth, WA 6009, Australia*

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Abstract

Plant disease outbreaks represent significant global food security and environmental sustainability challenges, resulting in reduced primary productivity, biodiversity, and critical food/feed shortages worldwide. The indiscriminate use of synthetic fungicides has already caused substantial harm to human health and ecosystems. Certain human diseases, such as Alzheimer's and autism, have risen dramatically over the past decades, a trend partially attributed to the use/overuse of fungicides in modern agriculture and horticulture. Given these alarming signs, it should be time to reconsider plant disease management strategies. The use of certain beneficial microorganisms, referred to as biological control agents, holds promise as an eco-friendly approach to combating plant pathogens. Oomycetes are often cast as the bad guys in the plant world, causing chaos through destructive diseases like late blight, damping off, and dieback, which might have catastrophic consequences such as the Irish potato famine. However, not all oomycetes are harmful! Some are good guys in disguise, showing promising potential to help us fight plant diseases, acting as effective biological control agents. Understanding the mechanisms underlying the protective effects of biocontrol oomycetes is crucial for achieving desirable outcomes and developing innovative strategies. The biocontrol mechanisms of oomycetes can be categorized into five classes: i) mycoparasitism, ii) exudation of lytic enzymes, iii) competition with pathogens over nutrients and space, iv) induced systemic resistance (ISR), and v) production of injection cells (gun cells). This review elucidates the biocontrol mechanisms employed by oomycetes, highlighting their potential practical implications as well as their positive impact on plant growth. Edaphic and environmental factors influencing the efficacy of biocontrol oomycetes are also discussed, alongside diverse strategies aimed at enhancing their biocontrol efficiency or broadening the spectrum of target pathogens. Despite advancements in understanding biocontrol oomycetes, their commercial application faces challenges due to inconsistent field performance influenced by environmental conditions, soil types, inoculum viability, competing microorganisms. Enhancing biocontrol oomycetes efficacy through the development of stable formulations, genetic modification, synthetic biology, combining multiple strains, and integrating with other agronomic practices can help overcome these challenges and promote their adoption in sustainable agriculture. Performing comprehensive risk assessments to avoid non-target effects, and streamlining regulatory approval processes are also crucial. Understanding how biocontrol oomycetes counteract plant pathogens will improve our fundamental knowledge of interactions between beneficial and harmful microbes, enhance our ability to predict plant disease development dynamics influenced by

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***Corresponding Authors:** Yu Pin Li – e-mail – liyupin2021@163.com,
Fatemeh Ahmadi – e-mail – fatemeh.ahmadi@uwa.edu.au
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oomycetes-pathogen interactions, and facilitate the development of new tools for plant disease management with minimal environmental footprint.

Keyword – Biocontrol – induced systemic resistance – lytic enzymes – mycoparasitism – Oomycetes – sustainable agriculture

INTRODUCTION

Ecosystems comprise intricate networks of interactions between environmental elements and living organisms (Jiao et al. 2022). With the continuous growth of the global population, the need for food production has reached unprecedented levels. Agriculture, essential for human survival, faces increasing pressure to meet the dietary needs of a growing population (Vallance et al. 2012). Central to this challenge, lies the cultivation of plants, which serve as the primary source of sustenance for billions of people worldwide (Derevnina et al. 2016). However, as humanity heavily depends on agricultural yields for food, the looming threat of plant diseases presents a significant obstacle to achieving food security (Bělonožníková et al. 2020). The spread of plant pathogens poses a serious risk, reducing crop yields and hindering efforts to bridge the gap between food supply and demand (Paul et al. 2024). In the ongoing effort to support a constantly expanding global population, the threat of plant diseases emerges as a challenging adversary, jeopardizing the delicate balance necessary for ensuring food security (Manoharachary et al. 2014).

A variety of microorganisms, including fungi, bacteria, actinobacteria, protozoans, viruses, and oomycetes, can establish connections with plant tissues, utilizing plants for nutrition, habitat, or dispersal to new environments (Basit et al. 2021). The abundance and diversity of microorganisms across ecosystems suggest that they hold untapped potential in various ecological functions, including the biological management of plant diseases (Ghorbanpour et al. 2018, Paul et al. 2024). Oomycetes, belonging to the kingdom Stramenopila, represent one of the largest groups of microorganisms, sharing traits with fungi and algae (Gilbert & Parker 2023). Despite morphological similarities to fungi, oomycetes possess distinct characteristics. Unlike true fungi, oomycete cell walls primarily consist of cellulose rather than chitin (Wilson & McDowell 2022). However, oomycetes possess chitin synthases active during tip morphogenesis (Gavrin et al. 2020). In the vegetative mycelial phase, oomycetes are diploid, contrasting with fungi that typically form haploid thalli, although exceptions are known to occur (Pavić et al. 2022). Oomycete cells can be distinguished from true fungi by their mitochondria, characterized by tubular cristae rather than the flattened cristae typically observed in fungi (Veloso et al. 2014), and by their non-septate hyphae (Bozkurt et al. 2012). A defining characteristic of oomycetes is the production of asexual spores called ‘zoospores’ within sporangia (Babadoost 2016). In certain oomycetes, the ability to produce zoospores is absent, and sporangia have evolved into structures that directly germinate to form germ tubes (Kamoun 2015). Hence, sporangia can germinate directly to produce germ tubes or indirectly to form numerous zoospores, each of which can germinate and act as a propagule. This trait, i.e., direct or indirect germination of sporangia, is often influenced by temperature, with zoospores typically produced at cooler temperatures (Judelson & Ah-Fong 2019).

Oomycetes demonstrate diverse levels of specificity toward hosts, influencing their capacity to infect various organisms (Pandaranayaka et al. 2019). Some oomycetes exhibit notable specificity, targeting particular plant species under specific environmental conditions (Kamoun 2015). This specificity often results from the co-evolutionary dynamics between the oomycete pathogen and its host, leading to highly specialized interactions (Wilkinson et al. 2011). Table 1 provides a list of the most prevalent pathogenic oomycetes, along with their respective hosts and the diseases they cause. With mounting concerns regarding the environmental and health impacts of conventional disease control methods, the search for sustainable alternatives has become increasingly urgent (Nirwan et al. 2023). Traditional practices, such as the widespread use of synthetic fungicides, not only contribute to the emergence of fungicide-resistant strains of pathogens but also cause unintended harm to non-target organisms and ecosystems (Patil et al. 2023). *Pythium* spp. is one of the most extensively studied genera in biocontrol research due to its adaptability and extensive data availability (Le Floch et al. 2009). Its widespread presence in diverse ecosystems has led to a significant focus on its mechanisms as a biocontrol agent, especially in plant-pathogen interactions (Yacoub et al. 2023).

In the sphere of plant disease management, biological control agents (BCAs) are pivotal in mitigating the adverse effects of pathogens, acting either directly through antagonistic measures or indirectly by modulating plant physiology and structure (Lecomte et al. 2016). The effectiveness of BCAs, comprising beneficial microorganisms, varies depending on specific strains and environmental factors (Glick 2015). The primary advantages of BCAs for associated plants include establishing a competitive microbial community in the rhizosphere, suppressing pathogens, enhancing plant vigor, stimulating growth, improving nutrient availability and uptake, and bolstering resilience against both biotic and abiotic stresses (Harman et al. 2004). Increased nutrient availability may impact the progression of certain diseases. For example, elevated nitrogen (N) levels could decrease the host plant’s susceptibility to facultative pathogens like *Alternaria solani* (Blachinski et al. 1996), while enhanced manganese (Mn) concentrations might alleviate the severity of diseases such as powdery mildew, downy mildew, and take-all (Haber & Harder 1992, Elad et al. 2021). However, the favorable outcome in disease management is not solely reliant on elevated nutrient levels in plants and varies depending on the specific nutrient and the implicated pathogen; for instance, high N levels might exacerbate diseases caused by obligate pathogens such as *Puccinia graminis* (Pinto 1992). Fungi and bacteria are the primary types of biocontrol agents used in managing plant pathogens. Extensive research has explored the potential of bacterial and fungal biocontrol agents and their underlying mechanisms (Latz et al. 2018, Ghorbanpour et al. 2018). While the majority of oomycetes are recognized for their ability to cause plant diseases, it is important to acknowledge the beneficial oomycete species that do not exhibit pathogenic behavior (Chen et al. 2022). Unlike their pathogenic counterparts, these non-pathogenic oomycetes, referred to as biocontrol oomycetes, play unique and often underestimated roles in various ecosystems (Bhowmick & Tripathy 2014). Diverse interactions between oomycetes and plants underscore the complexity of their roles in different ecological settings (Sharpee & Dean 2016). For example, *Pythium oligandrum* not only provides direct protection to plants from fungal pathogens but also triggers plant defense mechanisms against other pathogens while simultaneously enhancing plant growth and vigor (Bělonožníková et al. 2022). Operating as a potent mycoparasite, *Pythium oligandrum* envelops the hyphae of various fungi and oomycetes, including *Fusarium oxysporum*, *Phytophthora parasitica*, *Verticilium dahliae*, *Botrytis cinerea*, *Aphanomyces cochlioides*, and other *Pythium* species (Benhamou et al. 2012). Moreover, *Pythium oligandrum* can stimulate plant defense responses, thus serving as an effective biocontrol agent (Gerbore et al. 2014). In another instance, inoculation of *Brassica juncea* plants with an incompatible *Albugo candida* strain (non-pathogenic) induced both local and systemic protection of cotyledons and true leaves against the pathogenic *Albugo candida* strain (Singh et al. 1999). Though several studies highlight the promising applications for biocontrol oomycetes as biocontrol agents, a crucial gap remains in our understanding of the magnitude of their potential and how they function. Here, we probe the mechanisms behind how oomycete controls plant diseases, seeking diverse strategies to boost their effectiveness and pave the way for sustainable solutions.

Biocontrol mechanisms of biocontrol oomycetes

Diverse interactions occur between biocontrol oomycetes and plant pathogens, some of which have been simulated in laboratory settings by exposing two microorganisms to each other in Petri dishes, while others have been revealed through molecular and biochemical analyses of plants subjected to pathogens *in vivo* (Glick 2015). Here, we investigate the five classes of biocontrol mechanisms utilized by biocontrol oomycetes, thoroughly analyzing their capacity and exploring the potential methods to enhance their effectiveness.

Mycoparasitism

In fungal interactions, when one fungus obtains nutrients from another by directly parasitizing it, it is termed “mycoparasitism”, a concept introduced by Viterbo & Horwitz (2010). At one end of the spectrum, the host fungus remains viable, and the mycoparasitic fungus derives nutrients from within the host mycelium, resulting in a stable and balanced relationship known as biotrophic mycoparasitism (van West et al. 2003). Conversely, necrotrophic mycoparasitism leads to the demise of the host fungus, after which the mycoparasite utilizes the deceased host remains as a source of nutrients (Mukherjee et al. 2022). Although nutrient transfer through the mycoparasitic interface may not always be demonstrated, parasitism is inferred from morphological alterations or physiological observations (Pal & Gardener 2006). In essence, a fungus should be considered mycoparasitic if it derives some or all of its nutrients from another fungus, thereby causing harm to the latter (Brozova 2002). Although oomycetes primarily feed on living plants as pathogens, some species exhibit mycoparasitic behavior (as a kind of trophy habit), serving as a form of biocontrol agent (van West et al. 2003). Mycoparasitism could play a crucial role in regulating the populations of pathogenic fungi and oomycetes (Glick 2015). For instance, *Pythium oligandrum* has been recognized as a mycoparasite, with an established capacity to parasitize oomycetes and fungi including other *Pythium* species, *Fusarium oxysporum*, *Phytophthora parasitica*, *Verticilium dahliae*, *Botrytis cinerea*, and *Aphanomyces cochlioides* (Benhamou et al. 2012, Gerbore et al. 2014). Previous investigations conducted by Hasan et al. (2022) revealed the involvement of hydrolytic enzymes, including cellulases, in the process of mycoparasitism. For example, Picard et al. (2000) noted that *Pythium oligandrum* secretes cellulolytic enzymes when encountering *Phytophthora megasperma*. Horner et al. (2012) explored the molecular aspects of mycoparasitism in *Pythium oligandrum*, identifying various proteins involved in the process. While these proteins likely contribute to mycoparasitism, further research is needed to understand their specific roles (Wilkinson et al. 2011). Butler (1957) investigated the mycoparasitism of *Rhizoctonia solani* on different fungal hosts and found that factors like temperature, nutrition, and light influence its growth; suggesting that mycoparasitism in oomycetes could also be influenced by soil/environmental factors. Table 1 underscores the main mycoparasitic *Pythium* species that have potential as BCAs, among which *P. oligandrum* is acknowledged as one of the most ubiquitous *Pythium* species worldwide, with a significant portion of research on *Pythium* species mycoparasitic activities centered around this species (Brozova 2002, Gerbore et al. 2014).

Table 1 Main morphological characteristics of mycoparasitic *Pythium* species.

***Pythium* species**	**Sporangia**	**Oogonia**	**Antheridia**	**Oospores**
P. acanthophoron	Not observed	15–25 µm with 1–3 µm conical projections	Monoclinous	Plerotic 13–20 µm
P. amasculinum	Contiguous	Mostly terminal, 19–29 µm with 3–7 µm, acute mammiform projections	No antheridia	Plerotic, 18–26 µm
P. lycopersicum	Hyphal swellings of various shapes	Terminal or intercalary 18–30 µm with acute mammiform projections of 4–6 µm long	Rare, monoclinous	Plerotic, 16–27 µm
P. oligandrum	Complex hyphal swellings	Terminal, 19–28 µm, with 3–9 µm long conical projections	Rare, monoclinous	Aplerotic, 17–22 µm
P. paroecandrum	Spherical, zoospore discharge observed	Smooth-walled, intercalary, 20–25 µm	Monoclinous or hypogynous	Aplerotic, 18–21 µm
P. periplocum	Toruloid, zoospor discharge observed	Terminal or intercalary, 21–30 µm, with 2.6–3.7 µm, conical or blunt projections	Diclinous, lobed, branched	Aplerotic, 19–25 µm

Note: The data are based on Brozova (2002), Ağaner et al. (2021), Paul et al. (2024).

Exudation of lytic enzymes

In recent years, there has been considerable focus on studying various aspects of interaction specificity and defense mechanisms employed by biocontrol oomycetes against plant pathogens (Gilbert & Parker 2023). Fungal cell walls are comprised of a complex network of intertwined polysaccharides and proteins (Geoghegan et al. 2017). While fungal cell walls differ in structure across species, cell types, developmental stages, and isolates, the fundamental architecture and synthesis of the primary cell wall remain consistent (Bowman & Free 2006, Geoghegan et al. 2017). Among the arsenal of compounds that microorganisms release to disrupt microbial growth and activities, lytic enzymes play a significant role (Downer et al. 2001). These enzymes primarily target the breakdown of polymers like proteins and polysaccharides such as cellulose, while also interfering with DNA biosynthesis. Oomycetes are capable of producing lytic enzymes, which facilitate the degradation of cell walls in competing microorganisms, thereby allowing them to access nutrients and suppress the growth of pathogens (Downer et al. 2001).

As osmotrophic organisms, oomycetes release enzymes to obtain nutrients from living or dead cells of fungal hosts (McGowan & Fitzpatrick 2017). For instance, interactions between *Pythium oligandrum* hyphae and cells of fungal pathogens can disrupt cellular integrity, leading to the loss of protoplasm in the target fungus (Bělonožníková et al. 2022). Enzymes potentially involved in cell wall breakdown have been extensively studied (Rafiei et al. 2021). Genomic sequencing of oomycetes has unveiled genes encoding hydrolytic enzymes capable of degrading cell wall components like polysaccharides, proteins, and glycoproteins (Berger et al. 2016, Faure et al. 2020, Kushwaha et al. 2017). Leveraging this genomic data, McGowan & Fitzpatrick (2017) identified genes for various enzymes and proteins, including glycosidases, proteases, and effectors in 37 oomycete species, including *Pythium oligandrum*. This species, well known for its mycoparasitic behavior, secretes cell wall-degrading enzymes and putative effectors during the colonization of pathogens like *Phytophthora infestans in vitro* (Horner et al. 2012, Liang et al. 2020). Comparative genomics research suggests *Pythium oligandrum* may have gained its mycoparasitic abilities through gene duplication and horizontal gene transfer of specific carbohydrate-active enzymes (CAZy) from fungal and bacterial species, allowing it to exploit fungal and oomycete species for nutrition (Liang et al. 2020). Cellulases and β-1,3-glucanases have been found in *Pythium oligandrum* secretions, indicating their role in degrading shorter oligosaccharide chains through exoglycosidases (Bělonožníková et al. 2022, 2020). Among the exoglycosidases studied, β-glucosidase exhibited the highest level of activity (Bělonožníková et al. 2020). Prior investigations conducted by Rey et al. (2008) also reported that *Pythium oligandrum* produces β-glucosidase, cellulase, and cellulose β-1,4-cellobiosidase *in vitro*. Notably, α-glucosidase displayed significantly lower activity compared to β-glucosidase (Bělonožníková et al. 2020). Additionally, the amylase activity of *Pythium* species was detected by Geethu et al. (2013).

Proteolytic function is essential for breaking down cell wall proteins. *Pythium oligandrum* forms thin filaments that likely infiltrate host species hyphae, absorbing their decomposed contents, including proteins (Wilkinson et al. 2011). The targeted mycelium of the pathogen may ultimately be completely degraded (Brimner & Boland 2003). Faure et al. (2020) estimated 156 genes encoding secreted proteases in the *Pythium oligandrum* genome. McGowan & Fitzpatrick (2017) categorized these proteases into various types, including subtilases, trypsin-like proteins, cysteine proteases, and aspartyl proteases. Bělonožníková et al. (2020) observed differing proteolytic activity in *Pythium oligandrum* secretions among strains. Cell wall proteins are typically glycosylated, resulting in varied oligosaccharide structures, with *Pythium oligandrum* secretions containing exoglycosidases like α-mannosidase and β-galactosidase, potentially involved in glycoprotein degradation (Bělonožníková et al. 2020). Additionally, many cell wall glycoproteins are anchored by a glycosylphosphatidylinositol (GPI) anchor (Bowman & Free 2006). The above-mentioned studies demonstrate a diverse array of lytic enzymes that may serve as a biocontrol strategy against pathogenic fungi/oomycetes in non-pathogenic oomycetes. By considering the target cell wall properties of the pathogen, some of these enzymes within the biocontrol genome of oomycete can be selectively genetically modified to overexpress, thereby enhancing its biocontrol efficiency.

Competition with pathogens over nutrients and space

The rhizospheric microbial community plays a pivotal role in ecosystem functioning and represents one of the most intricate and diverse communities in the natural world (Andersen et al. 2006). The diversity of microorganisms within the rhizosphere is strongly associated with the type of plant species present, largely driven by the dynamic interactions between root exudates and soil microorganisms, which are influenced by co-evolutionary factors (Jain et al. 2020). Recent research has been dedicated to investigating how biocontrol agents impact the structure and functions of the rhizosphere microbiome (Kozdrój et al. 2004, Vallance et al. 2012). Below are several mechanisms through which biocontrol agents, such as biocontrol oomycetes, exert their influence in the rhizosphere via their competitive advantages.

As outlined by Alabouvette et al. (2006), this idea of competition involves the control of microbial population dynamics within a shared ecological niche when resources are scarce. Biocontrol oomycetes can engage in competition with plant pathogens for essential nutrients and space, thereby restraining the proliferation of harmful microorganisms and fostering plant well-being (Kamoun et al. 2015). A notable example is the mycoparasitic oomycete *Pythium oligandrum*, which was proposed to possess high capabilities for competition with co-occurring microorganisms over nutrients and space (Gerbore et al. 2014). This biocontrol mechanism can be influenced by edaphic or environmental factors. Martin & Hancock (1986) noted that increased chloride levels led to higher densities of *Pythium oligandrum* propagules, enabling successful competition with the oomycete pathogen *P. ultimum*, resulting in the soil capability to suppress the pre-emergence damping off in cotton. Increased chloride levels might induce metabolic adaptations in *Pythium oligandrum*, leading to increased efficiency in nutrient uptake or utilization (Benhamou et al. 2012). This could allow *Pythium oligandrum* to outcompete other pathogens for limited resources in the soil, ultimately leading to suppressiveness against harmful pathogens (Martin & Hancock 1986). Higher chloride levels might also indirectly affect host plants, such as altering root exudate composition or stimulating plant defenses. These changes could influence the rhizosphere microbial community, favouring the growth and activity of *Pythium oligandrum* and contributing to soil suppressiveness against damping-off diseases (Martin & Hancock 1986).

Competition over resources, as a biocontrol mechanism, is a widespread phenomenon and has been reported in other biocontrol agents including *Trichoderma harzianum* and *Fusarium oxysporum* (Kareem & Al-Araji 2017, Ghorbanpour et al. 2018). Although this approach is frequently seen in microbial antagonism to manage post-harvest decay pathogens in vegetables (Sharma et al. 2009), its efficacy as a sole method for biocontrol, particularly against soilborne pathogens within the intricate soil microbiome, is deemed challenging (Alabouvette et al. 2006). Consequently, "competition with pathogens over nutrients and space" is likely a secondary strategy utilized by biocontrol oomycetes such as *Pythium oligandrum* that may lead to reduced populations of co-occurring pathogens.

Induced systemic resistance (ISR)

Plants can detect a range of chemical signals in their surroundings, including cues from beneficial microorganisms like biocontrol oomycetes. These signals stimulate biochemical responses aimed at strengthening defenses against pathogen attacks (Mohamed et al. 2007). An intriguing aspect of plant-biocontrol oomycetes interactions is induced resistance, where plants activate defense mechanisms upon encountering specific triggers, such as pathogen attack or exposure to certain compounds, protecting plants against subsequent infections (Van Damme et al. 2005). Understanding how biocontrol oomycete induces resistance in plants holds significant promise for innovative strategies in plant disease management and crop protection (Rey et al. 2008). Moreover, the induction of systemic resistance by biocontrol oomycete highlights the complexity of plant-microbe interactions and the potential for leveraging beneficial microbial agents in agriculture (Manoharachary et al. 2014). Studies have shown that oomycetes can induce systemic resistance not only against their infections but also against other pathogens, including fungi and bacteria. For instance, *Pythium* spp. (Picard et al. 2000) and *Albugo* spp. (Ploch & Thines 2011) have been explored for their ability to enhance plant defense against a wide range of plant pathogens. Deciphering the molecular mechanisms behind induced resistance caused by biocontrol oomycete and understanding the factors influencing its effectiveness are critical steps toward harnessing these interactions for sustainable and environmentally friendly disease management strategies.

Certain *Peronospora* species, like *Peronospora tabacina*, are known to trigger systemic resistance in plants. Similarly, certain *Albugo* species, such as *Albugo candida*, have been studied for their ability to induce systemic resistance in plants, particularly against the white rust disease (Singh et al. 1999, Nirwan et al. 2023, Miyaji et al. 2023). By activating the resistance mechanisms in plants, these microorganisms can enhance the defense ability of a plant against themselves and other plant pathogens (Wang et al. 2019). Biocontrol oomycetes produce a variety of elicitors, molecular signals essential for initiating plant immune responses against pathogens (Mohamed et al. 2007). These elicitors act as triggers, initiating a series of molecular events within plants that activate defense mechanisms to combat pathogen invasion, thereby ensuring plant health and survival (Patel et al. 2020). *Pythium oligandrum* produces two main types of elicitors, 1) oligandrin, an extracellular protein identified by Picard et al. (2000), and 2) specific cell wall polysaccharides (CWPs), discovered by Masunaka et al. (2010). Oligandrin, a 10 kDa elicitin-like protein, induces systemic resistance in various plants without triggering a hypersensitive reaction (Picard et al. 2000). It has been effective against *phytoplasma* infection in tobacco, and against pathogens like *Phytophthora parasitica*, *Botrytis cinerea*, and *Fusarium oxysporum f.* sp. *radicis-lycopersici* in tomato (Benhamou et al. 2001, Lou et al. 2011, Picard et al. 2000). Mohamed et al. (2007) demonstrated its efficacy in grapevine against *Botrytis cinerea*, proposing induced systemic resistance (ISR) as a significant biocontrol mechanism. The second type of elicitor, known as elicitin-like proteins POD-1 and POD-2, can induce resistance in various plants against bacterial and fungal pathogens (Kawamura et al. 2009). These elicitors exhibited similar disease protection against *Aphanomyces cochlioides* in sugar beet but varied in the number of defense-related genes they induced (Takenaka et al. 2011). This suggests that these elicitors may elicit distinct defense responses, although they might achieve the same level of protection. Combining both cell wall proteins and oligandrin could potentially activate more defense genes and enhance plant protection against pathogens (Picard et al. 2000). Furthermore, it is noteworthy that neither type of elicitor is specific to plant species, consistent with findings observed with the actual *Pythium oligandrum* inoculum (Bělonožníková et al. 2022), suggesting a potentially broad range of plants that could benefit from oomycete-derived elicitors or inoculums.

Production of injection cells (gun cells)

Spores of many fungal pathogens, including airborne species, possess specialized structures like sticky appendages, spines, and mucilages that aid in their attachment to surfaces (Beakes & Glockling 1998). Similarly, spores of biocontrol oomycetes *i.e. Haptoglossa* are equipped with specialized cells that facilitate infection. Upon attachment to a suitable host, spores often germinate and form specialized structures, such as appressoria, to penetrate host tissues. In the biflagellate oomycete *Haptoglossa*, the most remarkable infection structure is the gun or attack cell, which produces an invaginated injection tube containing a harpoon-shaped missile. When expelled, the tube inverts, launching the projectile through the host cuticle and acting as a conduit for injecting the parasite’s cytoplasm into the host. This unique mechanism has been observed in biocontrol oomycetes against phytopathogenic nematodes, such as *Meloidogyne* spp. (root-knot nematodes) and *Heterodera* spp. (cyst nematodes), showcasing its versatility across different nematode species. Beakes & Glockling (1998) proposed that the reflexed beak of the gun cell is coated with a fibrillar material resembling adhesives found in fungal spores, which may prevent premature firing. The gun cell tip adheres to the nematode cuticle upon contact, triggering the firing mechanism.

Research by Beakes & Glockling (1998) demonstrated the effectiveness of this mechanism against the root lesion nematode *Pratylenchus* spp., further highlighting its biocontrol potential.

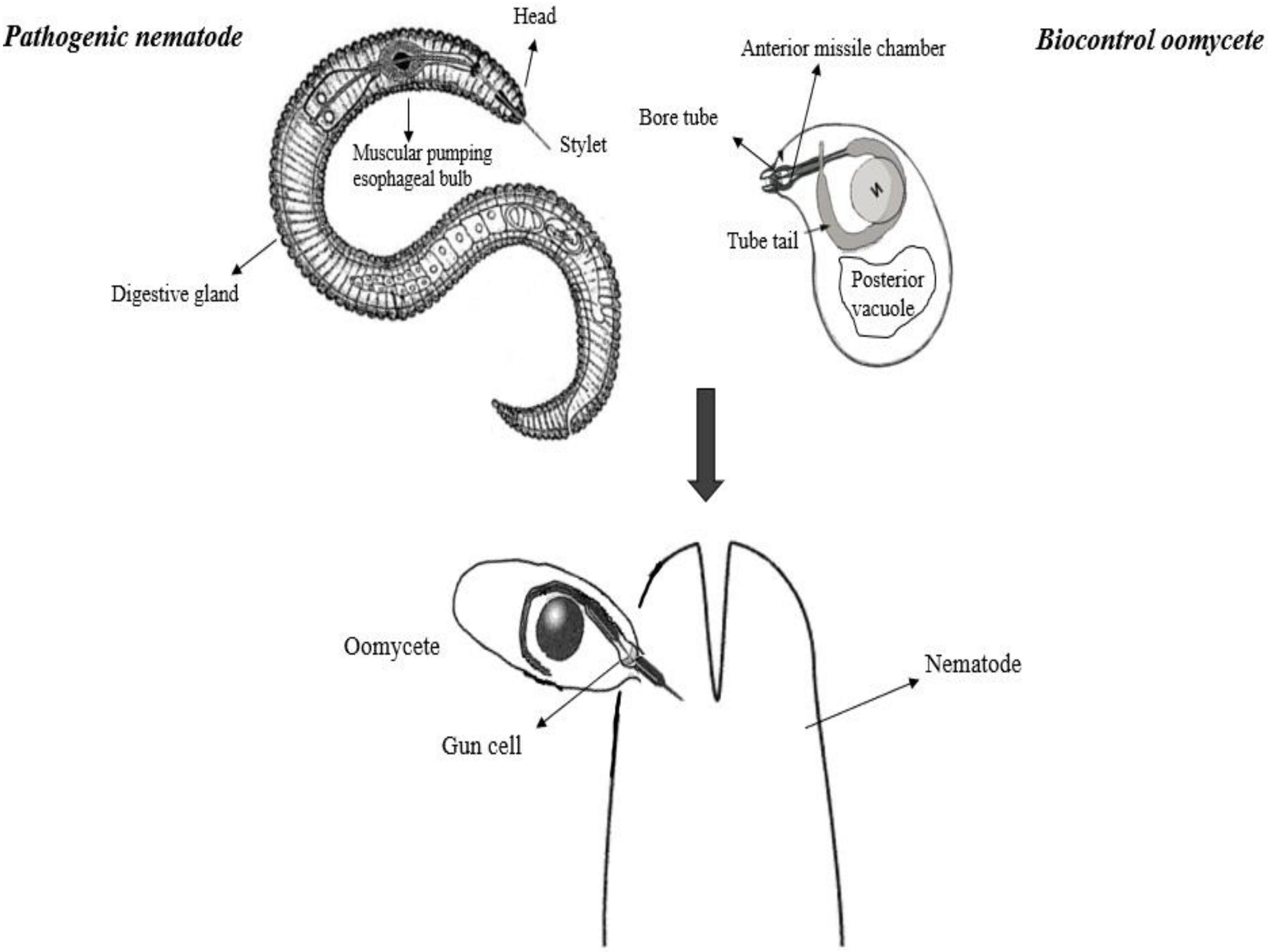

Figure 1 – Structure of gun cells produced by the biocontrol oomycete *Haptoglossa* against plant pathogenic nematodes (adopted from Beakes & Glockling 1998).

Factors affecting the activities of biocontrol oomycetes

Soil characteristics, environmental conditions, biological factors, and agronomic practices can influence the activity and survival of biocontrol oomycetes, impacting their ability to suppress fungal pathogens (Bonanomi et al. 2007, Chowdhury et al. 2015). Understanding these factors is crucial for optimizing biocontrol strategies and mitigating the impact of phytopathogens on crop yields.

Soil characteristics such as temperature, moisture, nutrient composition, and pH can influence the growth and function of biocontrol oomycete (Abbas et al. 2022). For instance, heavy metals like copper (Cu), manganese (Mn), molybdenum (Mo), iron (Fe), and zinc (Zn) are essential for plant growth and physiological functions (Singh et al. 2016). However, excessive concentrations of these metals can harm living microorganisms such as biocontrol oomycetes, by deactivating essential molecules like proteins and enzymes (Gajewska et al. 2022). Studies have shown that non-pathogenic oomycetes in soil may experience significant growth inhibition and undergo morphological and physiological changes in response to excess heavy metals (Gajewska et al. 2022). McQuilken (1990) examined how various soil/environmental factors affect the activity of *Pythium oligandrum*. The study showed that *Pythium oligandrum* exhibited growth and oospore germination within a pH range of 4.5 to 9.0, with reduced activity at pH extremes, suggesting that *P. oligandrum* may not be effective in soils with extreme acidity or alkalinity. However, farmers can potentially manipulate soil pH to enhance the biocontrol activity of *Pythium oligandrum* in agricultural and horticultural systems.

Environmental conditions such as temperature and moisture levels as well as seasonal changes can significantly affect the abundance and function of biocontrol oomycetes in soil ecosystems (Gahagan et al. 2023). For example, some species thrive in warmer conditions, while others prefer cooler environments (Huey et al. 2012). *Pythium oligandrum* is a typical example of a biocontrol oomycete that displays seasonal variations in its abundance and activity, often reaching peak levels during periods of higher soil moisture and moderate temperatures (Drake & Jones 2017). Changes in moisture availability during the seasons can impact the distribution and survival of oomycetes in soil, as these microorganisms rely on adequate moisture levels for growth and dispersal (Drake & Jones 2017). The ability of biocontrol oomycetes to control diseases may fluctuate with the seasons, peaking during times of intensified pathogen pressure or when environmental conditions are favourable for the proliferation of biocontrol oomycetes (Sullam & Musa 2021).

Biological factors, such as the genetic diversity within populations of biocontrol oomycetes, are crucial for determining their efficiency against plant pathogens (Ploch & Thines 2011). Moreover, genetic diversity can lead to the development of new traits or mechanisms that enhance the biocontrol oomycete's ability to control pathogens (Grünwald & Flier 2005). This might involve the creation of novel antimicrobial compounds, better competition against pathogens, or improved compatibility with host plants (Heydari & Pessarakli 2010). The optimal conditions for biocontrol oomycetes may not align with those preferred by the target pathogens. Hence, it is vital to isolate and employ indigenous biocontrol oomycete strains to combat plant pathogens, ensuring their high level of adaptation to soil and environmental factors (Glick 2015). Vallance et al. (2009) investigated the colonization of tomato plant roots by three strains of the biocontrol oomycetes *Pythium oligandrum*. Interestingly, the strain that most effectively colonized the rhizosphere produced the fewest oospores (*in vitro*) among the strains tested. This finding highlights the varying potential of different strains for root colonization and also demonstrates that a strain’s *in vitro* oospore production capacity is not directly linked to its ability to colonize the rhizosphere. Furthermore, inoculation with the well-adapted and most abundant strain (CBS 530.74) did not significantly alter the indigenous fungal populations, except for a reduction in the population of the pathogenic oomycete *Pythium dissotocum*.

Agronomic practices such as tillage, irrigation, fertilization, and pesticide application may influence the presence and function of biocontrol oomycetes in agricultural settings (Slippers et al. 2005). Excessive tillage disrupts soil structure and microbial communities, potentially reducing the biocontrol oomycetes populations. Conversely, conservation tillage methods enhance soil health and microbial diversity, creating a more conducive environment for biocontrol oomycetes (Njira & Nabwami 2013). Integrated pest management strategies promote biological control methods, enhancing the effectiveness of biocontrol oomycetes in disease suppression (Nega 2014). The use of synthetic fertilizers or broad-spectrum pesticides may harm biocontrol oomycetes by upsetting microbial balance or directly inhibiting their growth (Soonvald et al. 2019). Stridh et al. (2022) observed promising effects of the biocontrol oomycete *Pythium oligandrum* on potato early blight in greenhouse experiments. However, these effects diminished in field trials. This decline in efficacy between controlled and field environments was attributed to different factors including variations in the plant microbiome as well as the application of late blight fungicides that might have been toxic to the employed biocontrol oomycetes.

Strategies to enhance the biocontrol efficiency of biocontrol oomycetes

As discussed, biocontrol oomycete offers promising avenues for biocontrol strategies against various plant pathogens. However, to maximize their efficiency, several approaches can be employed, including genetic engineering (Chen et al. 2022), strain combination (Abdeljalil et al. 2021), and combined applications of biocontrol oomycetes inoculum with elicitors or chemical/physical additives (Astha & Sangha 2019), along with compatible agronomic practices

(Njira & Nabwami 2013, Nega 2014). One strategy to enhance the biocontrol efficiency of biocontrol oomycetes involves genetic engineering techniques. Through genetic modification, researchers can introduce specific lytic genes into the genome of oomycetes, thus boosting their proficiency in breaking down the cell walls of targeted pathogens (Hashemi et al. 2022). The manipulation of regulatory elements within the oomycete genome can result in the constitutive expression of biocontrol-related genes, ensuring a sustained and heightened defense response against invading pathogens (Piombo et al. 2023). Moreover, advancements in synthetic biology have enabled the design and construction of customized lytic enzymes with enhanced catalytic properties, which can provide biocontrol oomycetes with tailored weapons for combating specific plant pathogens (Sae-Chew et al. 2020).

Another approach to improve the biocontrol efficiency of biocontrol oomycetes is combining multiple strains of biocontrol oomycetes (Abdeljalil et al. 2021). This strategy aims to enhance the collective ability of different biocontrol oomycete strains to survive in harsh environmental conditions and compete effectively with pathogens (Sullam & Musa 2021). By selecting strains with complementary traits, such as different modes of action or broader host ranges, researchers can create consortia that exhibit synergistic effects in disease suppression. For example, the combination of different biocontrol agent strains producing distinct sets of antimicrobial compounds has been shown to result in enhanced efficacy against plant pathogens (Volynchikova & Kim 2022). Furthermore, combining strains with different ecological niches can enhance the overall stability and resilience of biocontrol communities such as biocontrol oomycetes. Research conducted by Rojas et al. (2017) has highlighted the importance of ecological diversity in maintaining the long-term effectiveness of biocontrol strategies, as niche differentiation among coexisting oomycete strains can reduce competition and promote coexistence within plant-associated microbial communities. The combination of multiple biocontrol oomycete strains represents a promising approach for maximizing biocontrol efficiency and ensuring sustainable disease management in agricultural systems (Vallance et al. 2009, Abdeljalil et al. 2021).

Furthermore, the combined application of biocontrol oomycete inoculums with elicitors represents a promising approach to maximize biocontrol efficacy (Volynchikova & Kim 2022). Elicitors are compounds that trigger plant defense responses, priming them for enhanced resistance against pathogens. For instance, studies by Astha & Sangha (2019) have demonstrated the effectiveness of various elicitors, such as salicylic acid and jasmonic acid, in activating plant defense pathways and strengthening resistance against fungal and oomycete pathogens. By co-applying biocontrol oomycete inoculum with elicitors, researchers can aim to potentiate the biocontrol activity of beneficial oomycetes while simultaneously boosting plant defenses against invading pathogens (Morcillo et al. 2020). This integrated approach leverages both the direct antagonistic activity of biocontrol oomycete and the indirect induction of plant immunity, resulting in a more robust defense system against plant diseases (Lerksuthirat et al. 2015). Findings by Astha & Sangha (2019) have highlighted the potential synergistic effects of combining specific biocontrol oomycete strains with elicitors targeting key defense pathways, leading to enhanced disease suppression and crop protection. By exploiting the crosstalk between oomycete-mediated biocontrol and plant immune responses, this approach offers a promising strategy for sustainable crop disease management. Using both a biocontrol oomycete inoculum and a synthetic fungicide or additives together, either at the same time or alternately, is likely to lead to increased disease suppression, assuming that the biocontrol oomycete is compatible with the fungicide/additive being used (Liu et al. 2022). Tian et al. (2005) examined how the combined biocontrol actions of *Cryptococcus laurentii* and *Rhodotorula glutinis*, along with silicon (Si), synergistically combat *Alternaria alternata* and *Penicillium expansum* moulds in jujube fruit stored. Their results showed that utilizing a combination of these two biocontrol agents with 2% Si proved most efficient in managing diseases in jujube fruit.

Agronomic practices including soil modification and amendments can be employed to enhance the efficiency of biocontrol oomycetes in a given farming system. For instance, in soils with extreme pH, lime or sulfur can be applied to adjust the pH, potentially leading to enhanced efficiency of the biocontrol oomycete *Pythium oligandrum* (McQuilken 1990). Organic amendments, including biochar and compost, can potentially enhance the effectiveness of biocontrol agents, benefiting plant growth and disease control (Siddiqui et al. 2008, Fu et al. 2017, Bonanomi et al. 2018). This synergy reduces chemical inputs and tackles soilborne pathogens by promoting the introduced/indigenous beneficial soil microbiota. Arshad et al. (2021) investigated the effects of combining rice husk biochar with two biocontrol agents (*Trichoderma harzianum* and *Bacillus subtilis*) in combatting the root-knot nematode *Meloidogyne incognita* in tomato plants. Their results indicated that the application of 3% biochar with biocontrol agents effectively controlled the pathogenic nematode, boosted plant biomass, and stimulated the expression of defense-related genes in tomatoes.

Plant growth-promoting properties of biocontrol oomycetes

Oomycetes, predominantly acknowledged for their adverse effects as plant pathogens, are increasingly being identified as pivotal contributors to enhancing plant growth and overall plant vitality. Recent investigations have unveiled a plethora of advantageous interactions between specific oomycete species and host plants, resulting in improved nutrient assimilation, enhanced resilience to stress, and enriched growth characteristics (Oubaha et al. 2020). Despite their historical association with plant diseases, the revelation of oomycetes' capacity to enhance plant growth underscores the intricacy of their ecological roles and emphasizes their potential as invaluable partners in sustainable agriculture and ecosystem stewardship.

Pythium oligandrum supports plant growth by providing tryptamine to the roots and aiding in auxin production. Auxin promotes root growth, although excessive amounts can inhibit it (Le Floch et al. 2009). Plants produce auxins using various pathways, some of which involve tryptophan (Zhao 2012). *Pythium oligandrum* helps convert tryptophan to tryptamine, boosting root growth (Rey et al. 2008). Although tryptophan is scarce in soil, *Pythium* strains produce abundant tryptamine, which significantly affects auxin levels in plants (Bělonožníková et al. 2020). Research suggests that treating seeds with *Pythium oligandrum* leads to changes in auxin levels, influencing plant growth (Bělonožníková et al. 2020). Initially, plants may grow slowly due to metabolic changes but later experience accelerated growth (Wolters & Jürgens 2009). Additionally, *Pythium oligandrum*-treated plants may exhibit increased phosphorus uptake (Rey et al. 2008). The presence of *Pythium oligandrum* alters the rhizosphere microbial community, which may lead to improved plant nutrition and metabolism (Andersen et al. 2024). However, the application of *Pythium oligandrum* might not necessarily be accompanied by significant changes in the soil microbiome. Andersen et al. (2024) demonstrated that the biocontrol oomycete *Pythium oligandrum* promoted the growth of starch potato plants under field conditions, with the effects varying depending on the genotype, indicating a cultivar-dependent growth-promoting effect. However, despite these genotype-dependent effects, *Pythium oligandrum* had only minor impacts on the diversity and structure of the rhizosphere microbiome.

Current status and challenges

Despite the advancements in understanding the mechanisms of biocontrol oomycetes, their commercial application faces several challenges. Inconsistent field performance due to varying environmental conditions such as temperature, humidity, soil pH (Chen et al. 2020), and the presence of competing microorganisms can influence the survival, proliferation, and biocontrol efficacy of oomycetes (Sullam & Musa 2021). Different soil types and climatic conditions can significantly affect the activity of biocontrol oomycetes, making it challenging to standardize their use across diverse agricultural settings (Domínguez-Begines et al. 2021). Maintaining the viability of biocontrol oomycetes during storage and transportation is a major challenge, as many oomycete formulations have limited shelf-life, reducing their effectiveness by the time they are applied (Amoako-Attah et al. 2021).

Developing stable and effective formulations that protect biocontrol oomycetes during storage and ensure their viability upon application is crucial, with techniques such as encapsulation, freeze-drying, and liquid formulations being explored but requiring further optimization (Del Castillo-González et al. 2024). While biocontrol oomycetes are generally considered safe, there is a potential for non-target effects on beneficial soil microorganisms, insects, and plants, necessitating comprehensive risk assessments to ensure that biocontrol oomycetes do not disrupt

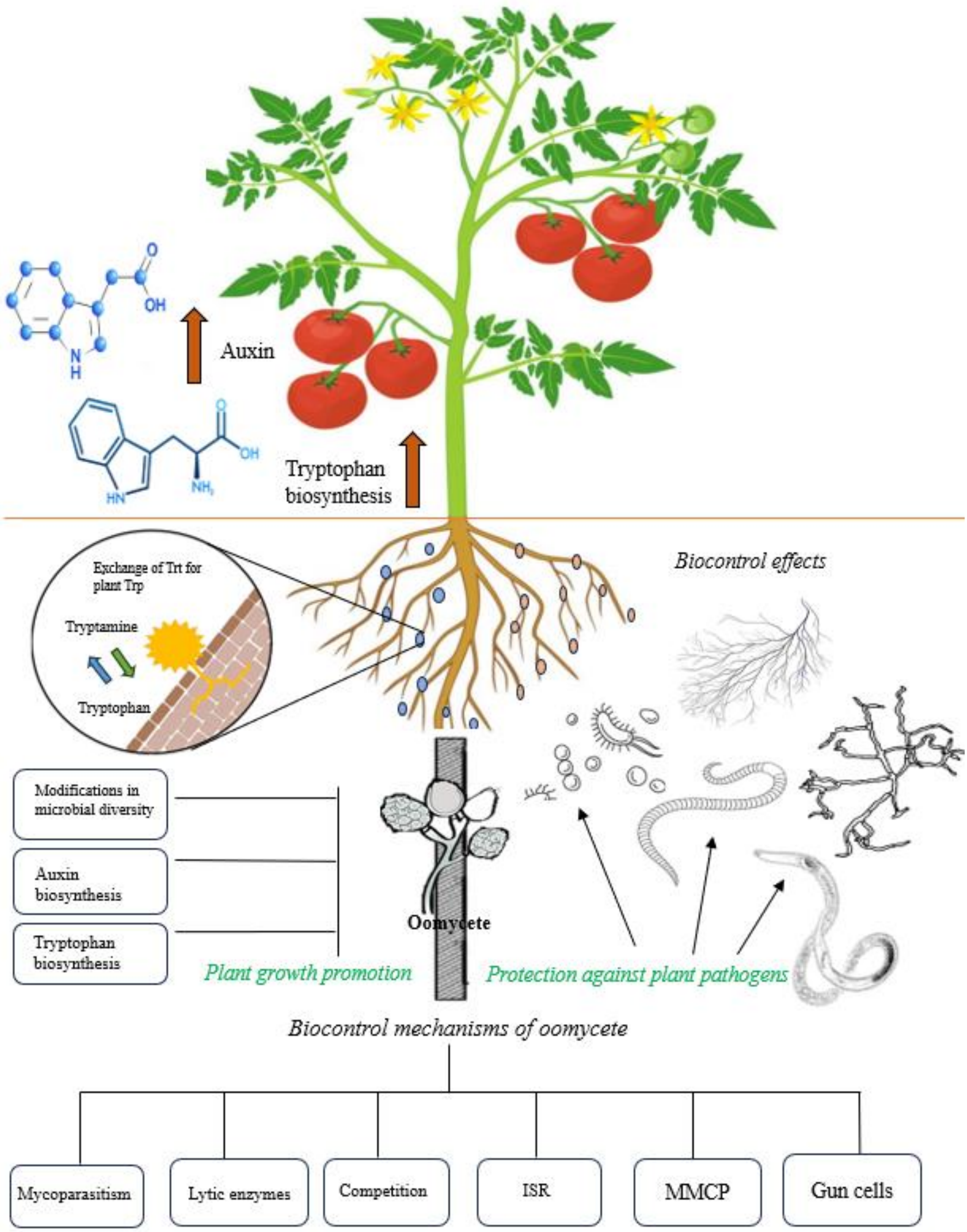

Figure 2 – Schematic diagram indicating the biocontrol mechanisms and growth-promoting interactions of biocontrol oomycetes.

local ecosystems. Ensuring that biocontrol oomycetes target only the intended pathogens without affecting non-target species is essential for their safe and effective use (Corredor-Moreno & Saunders 2020). The regulatory approval process for biocontrol agents can be lengthy and complex, involving rigorous testing for efficacy, safety, and environmental impact. Streamlining regulatory pathways can help in the faster deployment of biocontrol oomycetes (Judelson 2017). Farmers and agricultural stakeholders may be hesitant to adopt new biocontrol technologies due to a lack of awareness, perceived risks, or initial higher costs compared to traditional chemical pesticides. Educational programs and demonstration projects can help increase the acceptance and adoption of biocontrol oomycetes (Lahlali et al. 2022).

To overcome these challenges and enhance the efficiency of biocontrol oomycetes, several approaches can be employed. Genetic modification can be used to enhance desirable traits in biocontrol oomycetes, such as increased production of lytic enzymes, improved resistance to environmental stressors, and enhanced pathogen-targeting abilities (McGowan & Fitzpatrick 2020). Advancements in synthetic biology allow for the design and construction of custom biocontrol agents with specific functionalities tailored to combat particular pathogens effectively (Ghimire et al. 2022). Combining multiple strains of biocontrol oomycetes with complementary traits can enhance overall biocontrol efficacy, improving resilience against environmental stresses and broadening the spectrum of targeted pathogens (Köhl et al. 2019). Developing consortia of different biocontrol oomycete strains can create a more stable and robust biocontrol system, leveraging the strengths of each strain (Niu et al. 2020). Co-applying biocontrol oomycete inoculum with plant defense elicitors or chemical/physical additives can potentiate their biocontrol activity (Janků et al. 2020). Elicitors such as salicylic acid and jasmonic acid can enhance plant immune responses, while additives like biochar can improve soil health and microbial activity (Li et al. 2020). Combining biocontrol oomycetes with other biocontrol methods and compatible agronomic practices, such as crop rotation, soil amendments, and conservation tillage, can enhance their effectiveness and sustainability (Fernández et al. 2022). By addressing these challenges and employing strategic approaches, the potential of biocontrol oomycetes as effective and sustainable biocontrol agents can be fully realized, contributing to safer and more environmentally friendly agricultural practices.

Conclusions and future perspective

This review underscores the importance of oomycete-mediated biocontrol in addressing plant pathogens, revealing a diverse range of mechanisms and metabolites utilized by the biocontrol oomycetes. Understanding these biocontrol mechanisms is essential for optimizing their effectiveness in specific scenarios, enabling the development of tailored biocontrol strategies. Similar to fungal biocontrol agents, biocontrol oomycetes can serve as sources of beneficial genes, e.g., those encoding lytic enzymes and elicitors, to directly combat phytopathogens or enhance plant resistance against pathogens. Additionally, utilizing biotechnological tools and omics methodologies can further enhance the biocontrol capacity of biocontrol oomycete strains. Metabolites produced by biocontrol oomycetes offer promising avenues for disease management, functioning either as direct biofungicides or as triggers of plant defense mechanisms. Furthermore, mycovirus-mediated cross-protection (MMCP) has been well-documented as a promising biocontrol strategy in beneficial fungi. However, this mechanism has not yet been explored in biocontrol oomycetes, though it may hold potential, e.g., through the incorporation of mycoviruses associated with reduced virulence into the biocontrol oomycete with the aim of horizontal virus translocation from the biocontrol oomycete into the compatible/related pathogenic oomycetes. However, the potential practical applications of MMCP require further exploration, including screening natural populations of pathogenic oomycetes across different habitats to discover hypovirulence-associated viruses, along with exploring the biocontrol oomycete-infecting viruses and their potential role, and transmission to pathogenic oomycetes.

To maximize the efficiency of biocontrol oomycetes, several approaches can be employed, including genetic engineering, strain combination, combined applications of biocontrol oomycete inoculum with elicitors or chemical/physical additives, along with compatible agronomic practices such as soil amendments and pH adjustments. Biocontrol agents must establish themselves in the given soil habitat and effectively compete with other microorganisms and endure in the environment to be effective. Simultaneous use of multiple species or strains of biocontrol oomycetes originating from habitats with diverse environmental/edaphic conditions could yield synergistic advantages, enhanced chance of survival under harsh conditions, expanding the array of targeted pathogens, and strengthening plant defense mechanisms. Comprehending the intricate relationships among plants, pathogens, and biocontrol oomycetes is essential for effectively utilizing biocontrol oomycete-mediated ISR against plant diseases. By harnessing the innate capabilities of biocontrol oomycetes and state-of-the-art biotechnological methods, more efficient and sustainable approaches can be developed for managing plant pathogens in farming systems. However, the ecological dynamics of multispecies interactions in agricultural ecosystems and their implications for biocontrol effectiveness are not fully understood, underscoring the importance of interdisciplinary research approaches integrating ecology, microbiology, and agronomy. Furthermore, careful consideration and thorough risk assessment are required to understand the potential ecological impacts of genetically modified biocontrol oomycetes and the long-term consequences of their release into the environment.

The predominance of *Pythium* spp. in this manuscript is due to its extensive documentation in the literature, reflecting the significant amount of research conducted on this genus as a biocontrol agent. This is likely because *Pythium* species are not only widespread but also highly adaptable to various environmental conditions, making them ideal candidates for extensive experimentation. Additionally, the data availability and successful biocontrol applications of *Pythium* spp. in numerous studies suggest that this genus has a higher probability of being effectively utilized as a biocontrol agent in various agricultural contexts. While other oomycete species also show potential, the depth of research on *Pythium* spp. gives it a distinct advantage, making it a valuable organism in the development of sustainable biocontrol strategies. However, future research should consider exploring the potential of other less-studied oomycetes, such as *Albugo* and *Haptoglossa*, which may offer additional or complementary biocontrol strategies.

Despite significant advancements in uncovering the biological control mechanisms of biocontrol oomycetes, many inquiries remain unanswered. Future research should concentrate on clarifying the genetic, metabolic, and ecological intricacies of biocontrol oomycetes, aiming to develop eco-friendly and sustainable solutions for managing crop diseases.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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