

Review

Pythium oligandrum Is a Type of Biocontrol Oomycete with Great Potential

Kun Yang ^{1,*}, Rongbo Wang ^{2,†}, Liguang Liu ^{3,†}, Kang An ¹, Jitao Liu ¹, Li Wang ¹, Jianwei Shan ¹, Chengchen Li ¹, Liang Qi ¹, Li Zheng ³ and Xiaobo Li ^{1,*}

¹ Guangdong Provincial Key Laboratory of Crop Genetic Improvement, Crops Research Institute, Guangdong Academy of Agricultural Sciences, Guangzhou 510640, China; ankang@gdaas.cn (K.A.); liu-j-t@163.com (J.L.); wangli20090617@163.com (L.W.); chanyujianwei@126.com (J.S.); lccazdb@163.com (C.L.); qiliang@gdaas.cn (L.Q.)

² Fujian Key Laboratory for Monitoring and Integrated Management of Crop Pests, Institute of Plant Protection, Fujian Academy of Agricultural Sciences, Fuzhou 350013, China; wrb16128@163.com

³ Key Laboratory of Green Prevention and Control on Fruits and Vegetables in South China, Ministry of Agriculture and Rural Affairs, College of Agriculture and Biology, Zhongkai University of Agriculture and Engineering, Guangzhou 510225, China; llgwx156@163.com (L.L.); bluestar183@163.com (L.Z.)

* Correspondence: yangkun@gdaas.cn (K.Y.); lixiaobo@gdaas.cn (X.L.)

† These authors contributed equally to this paper.

Abstract

As a non-pathogenic oomycete, *Pythium oligandrum* possesses unique advantages, particularly in the context of being a biological control agent. With the increasing awareness of consumer consciousness, people are paying more attention to the use of environmentally friendly strategies in plant disease prevention and control. *Pythium oligandrum* is a type of biocontrol oomycete that can be developed as a biological control agent, and it does not have adverse effects on humans in the prevention and control of plant diseases. Consequently, there is increasing scientific interest in the beneficial plant–microbe interactions mediated by *P. oligandrum*. Currently, the main points of focus regarding the beneficial role of *P. oligandrum* in plant interactions are as follows: (i) *P. oligandrum* can activate plant defense responses and cause plants to produce resistance, thus protecting them from disease attacks; (ii) it is a strong mycoparasite that can coil around various oomycetes and fungi, directly killing pathogenic microorganisms; (iii) in addition, it can also promote plant growth. In this paper, we will discuss the aforementioned three main features in detail.

Keywords: eco-friendly control; non-pathogenic oomycetes; induced plant resistance



Academic Editor: Katrina Maria Ramonell

Received: 14 April 2026

Revised: 4 May 2026

Accepted: 4 May 2026

Published: 18 May 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and

conditions of the [Creative Commons Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

1. Introduction

Oomycetes are indeed microorganisms that can be found in diverse ecosystems, including tropical rainforests, oceans, deserts, and even extreme environments like Antarctica [1,2]. They have adapted to survive in a wide range of conditions and play important roles in these ecosystems. Currently, research on oomycetes has mostly focused on pathogenic species, while the study of non-pathogenic oomycetes such as *P. oligandrum* has been relatively limited. In 1930, *P. oligandrum* was first discovered in the root system of peas by Drechsler [2]. In 2020, Faure et al. reported the genome of *P. oligandrum* [3]. In soil, the interaction between *P. oligandrum* and plants is highly complex, and its exact role in these interactions has yet to be fully elucidated. *Pythium oligandrum*, as a biological control agent (BCA), not only activates plant defense responses but also kills pathogens through mycoparasitism, in addition to promoting plant growth. These effects make *P. oligandrum*

an effective tool for plant protection, encouraging its wide use in agricultural production and ecosystem management.

2. An Efficacious Biological Control Agent for Boosting Plant Resistance Mechanisms

Pythium oligandrum is a biocontrol oomycete that can protect plants from pathogen invasion by inducing plant resistance. Through its symbiotic relationship with *P. oligandrum*, plants are better able to resist attacks from pathogens and improve their overall resistance levels. The mechanism of induced resistance plays a pivotal role in plant defense and protection. At present, *P. oligandrum* employs four primary mechanisms to induce plant resistance: (i) *P. oligandrum* and oospores trigger plant resistance: The presence of *P. oligandrum* and oospore suspension initiates a plant response, leading to the development of resistance against pathogens; (ii) *P. oligandrum* utilizes cell wall protein fraction (CWP) to induce plant resistance: The cell wall protein fraction released by *P. oligandrum* activate the plant defense response, bolstering their resistance against pathogens; (iii) *P. oligandrum* secretes microbe-associated molecular patterns (MAMPs) to induce plant resistance: The secretion of MAMPs by *P. oligandrum* triggers an immune response in plants, heightening their resistance against pathogens; (iv) *P. oligandrum* induces ferroptosis-like cell death to suppress pathogen infection: *P. oligandrum* triggers ferroptosis-like cell death as a defense strategy to protect plants from pathogen invasion. Considerable research endeavors have been directed towards investigating the above-mentioned four strategies, which serve as the primary means by which *P. oligandrum* achieves the goal of eliciting plant resistance.

2.1. Induction of Plant Resistance by *P. oligandrum*

2.1.1. *P. oligandrum* Elicits Enhanced Resistance in Plants Against Pathogenic Oomycetes

Pythium oligandrum serves as an efficacious biological control agent through the elicitation of heightened plant resistance mechanisms. Multiple research studies have yielded extensive evidence demonstrating the efficacy of applying *P. oligandrum* in mitigating plant diseases induced by oomycetes, fungi, and bacteria (Table 1). Leveraging the use of *P. oligandrum* as a means to combat oomycete diseases proves efficacious in mitigating the detrimental effects inflicted by these pathogens. As early as 1997, Abdelzaher et al. reported the isolation of *P. oligandrum* from Egyptian soil, demonstrating its remarkable efficacy in controlling damping-off disease caused by *Pythium ultimum* on wheat [4]. In 1999, Ali-Shtayeh and Saleh reported that *P. oligandrum* was also effective in controlling diseases caused by *P. ultimum* on cucumber [5]. *Pythium oligandrum* has also been demonstrated to effectively control diseases caused by *Pythium aphanidermatum*. For example, the study conducted by Sayed et al. demonstrated that three strains of *P. oligandrum*, namely MS15, MS19, and MS31, were effective in controlling diseases caused by *P. aphanidermatum* on soybean [6]. The *P. oligandrum* strain D11 is also effective in controlling soybean damping off caused by *P. aphanidermatum* and *Pythium myriotylum* [7]. The strain GAQ1 of *P. oligandrum* is capable of significantly inhibiting *Pythium* soft rot of ginger caused by *P. myriotylum* [8,9]. Cultural filtrate of *P. oligandrum* (JU0328 and JU0329) significantly inhibited mycelial growth and the production of zoospores and oospores of *P. aphanidermatum* and *Pythium diclinum* [10]. Polyversum (*P. oligandrum*) is also employed for controlling *P. aphanidermatum* on tomato and eggplant [11]. Three strains of *P. oligandrum*, namely LMSA 1.01.631, CBS 109981 and CBS 530.74, have also been identified as effective agents in the control of diseases caused by *Pythium dissotocum* on tomato [12]. Furthermore, *P. oligandrum* induces significant resistance in two grapevine cultivars against *Plasmopara viticola* [13]. Together, *P. oligandrum* is currently being applied in the control of various pathogenic oomycetes, including *P. ultimum*, *P. aphanidermatum*, *P. myriotylum*, *P. diclinum*, *P.*

dissotocum and *Pl. viticola*, in several plants including wheat, soybean, tomato, eggplant, and cucumber (Table 1).

Table 1. Summary of *P. oligandrum* as biological control agent.

Pathogen Type	Pathogen Species
Oomycete	<i>Pythium myriotylum</i> , <i>Pythium aphanidermatum</i> , <i>Pythium diclinum</i> , <i>Pythium dissotocum</i> , <i>Pythium ultimum</i> , <i>Plasmopara viticola</i>
Fungus	<i>Fusarium culmorum</i> , <i>Fusarium oxysporum</i> , <i>Fusarium graminearum</i> , <i>Phaeoconiella chlamydospora</i> , <i>Erysiphe necator</i> , <i>Aphanomyces cochlioides</i> , <i>Verticillium wilt</i> , <i>Verticillium dahlia</i> , <i>Rhizoctonia solani</i> , <i>Botrytis cinerea</i> , <i>Sphaerotheca macularis</i> , <i>Mycosphaerella fragariae</i> , <i>Neofusicoccum parvum</i> , <i>Sclerotinia sclerotiorum</i>
Bacteria	<i>Ralstonia solanacearum</i>
Nematode	<i>Meloidogyne incognita</i>

2.1.2. *P. oligandrum* Triggers an Elevation of Resistance Among Plants in the Battle Against Fungal Pathogens

Pythium oligandrum not only provides protection against oomycete-related diseases but also demonstrates efficacy in the control of fungal pathogens (Table 1). Of all the research conducted on *P. oligandrum*, it has been most extensively studied for its efficacy in the control of *Fusarium*. *Pythium oligandrum* has been utilized on wheat, barley and tomato to combat various *Fusarium* species, including *F. culmorum*, *F. oxysporum* and *F. graminearum* [14–17]. Yacoub et al. found that the *P. oligandrum* strains Po1, Po2, Po3 and Po37 could be applied for the control of both pathogenic species *Phaeoconiella chlamydospora* and *Neofusicoccum parvum* on grapevine [18–20]. Gerbore et al. discovered that *P. oligandrum* culture filtrate or Oligandrin can be used to effectively control *Erysiphe necator* on grapevine [21]. *Pythium oligandrum* applied to peppers can effectively control *Verticillium dahliae* and *V. Wilt* [22,23]. After treating sugar beet with *P. oligandrum*, it can effectively control seedling and taproot diseases caused by *Aphanomyces cochlioides* [24]. In addition, *P. oligandrum* can also prevent and control a variety of other fungal pathogens, including: *Sclerotinia sclerotiorum*, *Rhizoctonia solani*, *Botrytis cinerea*, *Sphaerotheca macularis* and *Mycosphaerella fragariae* [13,25–29] (Table 1).

2.1.3. *P. oligandrum* Can Also Induce Resistance in Plants Against Bacterial and Root-Knot Nematode Diseases

We have already discussed that *P. oligandrum* plays a remarkable role in inducing plant defense mechanisms against pathogenic oomycetes and fungi. Furthermore, it exhibits the ability to stimulate plant defenses against bacterial pathogens as well. Implementing treatment of tomato plants with *P. oligandrum* demonstrates a significant potential to impede the onset of the bacterial pathogen, *Ralstonia solanacearum*, a causative agent of wilt disease [30–33]. Moreover, *P. oligandrum* is also used to control and prevent several root diseases. Písarčík et al. found that Polyversum, also known as *P. oligandrum*, can effectively control root diseases in lucerne [34]. Polyversum 1 and Polyversum 3 are also effective in controlling root diseases in red clover [35]. *Pythium oligandrum* can also control root-knot nematode diseases on tomatoes [36]. *Pythium oligandrum* can also be used to prevent and treat some unknown pathogens in rapeseed and tomato [37,38]. Together, the use of *P. oligandrum* to induce plant resistance can prevent and treat various types of diseases, including those caused by oomycetes, fungi, bacteria, as well as pathogens that are yet to be identified (Table 1).

2.2. *P. oligandrum* Produces Numerous Molecules to Induce Plant Resistance

Pathogens secrete several substances that allow them to colonize and utilize the target host. Some of these substances, such as microbe-associated molecular patterns (MAMPs), are recognized by plants and initiate defense reactions [39]. *Pythium oligandrum* also produces an extensive array of molecules that exert influence on plants; these include Oligandrin, CWPs, MAMPs and RXLR effectors. These molecules can induce plant defense responses to varying degrees.

2.2.1. Oligandrin, a Molecule Produced by the *P. oligandrum* Induces Resistance to Pathogens

A low-molecular protein, termed as Oligandrin, was meticulously extracted in its pure form from the cultural filtrate of *P. oligandrum*. Upon application to tomato plants, this protein exhibited the capacity to instigate plant defense mechanisms, thereby playing a pivotal role in confining the invasion of stem cells by the deleterious oomycete, *Ph. parasitica* [40]. Oligandrin demonstrates tangible effectiveness in instigating plant defenses against the onslaught of fungal pathogens. The application of Oligandrin triggered the expression of various defense-associated transcripts and, via diverse mechanisms, amplified resistance against powdery mildew in an otherwise susceptible tomato genotype [41]. Oligandrin also possesses the capacity to manage gray mold, and it may hold significant influence on the stimulation of resistance against *B. cinerea* [42–44]. Oligandrin initiates a systemic resistance to Fusarium crown and root rot within tomato plants [45]. Moreover, Oligandrin enhances tomato resistance to the postharvest pathogen *Alternaria nees* by activating both the salicylic acid- and jasmonic acid-mediated defense signaling pathways [46] (Table 2).

Table 2. Summary of Oligandrin, CWPs, MAMPs and RXLR effectors of *P. oligandrum*.

CWP/MAMPs Type	Pathogen Type	Pathogen Species
Oligandrin	Fungus	<i>Oidium neolycopersici</i> , <i>Botrytis cinerea</i> , <i>Fusarium oxysporum</i> , <i>Alternaria nees</i>
	Oomycete	<i>Phytophthora parasitica</i>
CWPs	Bacteria	<i>Burkholderia glumae</i> , <i>Ralstonia solanacearum</i>
	Fungus	<i>Rhizoctonia solani</i>
POD-1, POD-2	Fungus	<i>Aphanomyces cochlioides</i>
Oli-D1, Oli-D2	Fungus	<i>Botrytis cinerea</i>
PoEli8	Oomycete	<i>Phytophthora capsici</i>
PyoINLP5, PyoINLP7	Oomycete	<i>Phytophthora capsici</i>
PyoRXLR32	Oomycete	<i>Phytophthora capsici</i>

2.2.2. The CWPs of *P. oligandrum* Possess the Ability to Induce Plant Resistance

The elicitor activity of *P. oligandrum* CWPs effectively contributes to the induction of defense responses in plants. CWPs exhibit a potent capacity to induce resistance in *Arabidopsis* and tomato plants against the bacterial pathogen *R. solanacearum*, effectively mitigating disease development [31,33,47]. CWPs enhance the resistance of rice against the bacterial pathogen *B. glumae* by elevating the gene expression involved in the jasmonic acid (JA) signaling pathway, thereby bolstering the plant's defense capabilities against the disease [24]. In addition, CWP remarkably bolsters the defense capacity of potato tubers, amplifying their resistance towards the fungal disease known as black scurf [26]. Together, the aforementioned research reports highlight the importance of Oligandrin and CWPs, derived from *P. oligandrum*, in driving plant resistance induction (Table 2).

2.2.3. *P. oligandrum* MAMPs and RXLR Effector Induce Plant Resistance

As it is widely known, the innate immune system of plants indeed consists of two distinct phases. Firstly, PTI (Pattern-Triggered Immunity), also known as the immunity induced by microbe-associated molecular patterns, serves as the primary line of defense in plants. In simple terms, plants can recognize and counteract invaders through their highly conserved pattern recognition receptors (PRRs). The PTI response primarily addresses a wide range of potential pathogens. Secondly, ETI (Effector-Triggered Immunity) is considered the second line of defense in plants. In this stage, plants are capable of recognizing and combating effector molecules of specific pathogens. This response is typically stronger and more effective, as it can lead to a hypersensitive cell death response (HR) and prevent further spread of the pathogenic microorganisms [39]. Currently, some MAMPs and effectors that can induce plant resistance have been identified from *P. oligandrum* (Table 2).

MAMPs can trigger plant defense responses, and Elicitin is a typical class of MAMPs. The CWPs from *P. oligandrum* can trigger plant defense responses. Further studies have discovered two novel Elicitin-like proteins, POD-1 and POD-2, isolated from *P. oligandrum* CWP. These proteins are capable of inducing defense-related gene expression in both sugar beet and tomato, and also enhance sugar beet's resistance against the fungus *Aphanomyces cochlioides* [48,49]. *Pythium oligandrum* and its Elicitin-like proteins, known as Oligandrins, have been demonstrated to induce disease resistance across a variety of plants. Further research has unveiled that two variants of Oligandrin, Elicitin-like proteins Oli-D1 and Oli-D2, are capable of inducing immune responses in tobacco and tomato [50]. Moreover, our team has identified a novel Elicitin protein, PoEli8, from *P. oligandrum*, which has the ability to confer resistance to *Ph. capsici* in Solanaceae plants. Further research has revealed that a cell surface receptor-like protein (RLP), RELi, is capable of perceiving the immune response of PoEli8 [51].

Necrosis- and ethylene-inducing peptide 1 (Nep1)-like proteins (NLPs) represent another category of MAMPs that are pervasively distributed among both eukaryotic and prokaryotic microorganisms. PyoNLP5 and PyoNLP7, derived from *P. oligandrum*, have significantly reduced disease severity and suppressed the in planta growth of *Ph. capsici* in solanaceous plants, including tobacco (*N. benthamiana*), tomato (*S. lycopersicum*) and pepper (*C. annuum*) [52]. NLPs have been postulated to exert bifunctional effects in plant-microorganism interactions, serving simultaneously as elicitors of immune reactions and as virulence factors akin to toxins [53]. A more in-depth investigation elucidated that the plant disease resistance conferred by PyoNLP5 is independent of its necrosis-inducing capabilities and the generation of reactive oxygen species (ROS) [54]. Taken together, the primary research on MAMPs inducing plant resistance in *P. oligandrum* mainly focuses on two types: Elicitin and NLPs (Table 2).

In the interaction between oomycetes and plants, oomycetes secrete a plethora of intracellular effectors to modulate plant defense responses. Of these, RXLR serves as a paradigmatic example of such intracellular effectors. PyoRXLR32, a novel RXLR effector derived from *P. oligandrum*, has been identified by our studies to trigger cell death and the accumulation of reactive oxygen species in tobacco (*N. benthamiana*). Furthermore, it has been proven to possess the capability to enhance the resistance of *N. benthamiana* against *Ph. capsici* [55]. Our discovery represents evidence for the first identification of RXLR effectors in *P. oligandrum* (Table 2).

2.3. *P. oligandrum* Induces Ferroptosis to Enhance Plant Resistance

Ferroptosis, a recently unearthed modality of cellular demise, is characterized by an assemblage of iron and lipid peroxidation. It is remarkable in that it can be elicited within plant cells as a response to both biotic and abiotic stresses, thus broadening the spectrum

of its potential impact in the scientific field [56–58]. Our research team has pioneered in discovering the capability of *P. oligandrum* to trigger ferroptosis-like cell death, further demonstrating its potential to suppress the attack of *Ph. sojae* within soybean plants [59]. This is a groundbreaking piece of evidence in the realm of scientific breakthroughs.

3. *P. oligandrum* Has the Ability to Suppress and Kill Pathogens Through Its Mycoparasitic Interactions

Pythium oligandrum not only mitigates pathogens by inducing plant resistance, but it also suppresses, and potentially kills, pathogens through its potent mycoparasitic functions. Exhibiting formidable mycoparasitic properties, *P. oligandrum* has been demonstrated to entwine its hyphae around those of various oomycetes and fungi, including *Pythium*, *Phytophthora*, *Fusarium*, etc. (Table 3). For example, the hyphae of *P. oligandrum* possess the ability to coil around and penetrate the hyphal structures of *Pythium myriotylum* [7,9], and the volatile organic compounds (VOCs) emitted by *P. oligandrum* significantly contribute to its parasitic interaction as well [60]. *Pythium oligandrum* decreased the mycelial growth of the pathogenic *P. aphanidermatum* through mycoparasitism on plates [6,7]. Additionally, *P. oligandrum* exhibits parasitic behavior towards several oomycete pathogens, including *Phytophthora infestans*, *Phytophthora megasperma*, *Pythium ultimum*, *Pythium debaryanum* and *Aphanomyces laevis* [4,5,61–63]. *Pythium oligandrum* also has a mycoparasitic effect on various fungal pathogens. Amongst these, *P. oligandrum* manifests parasitism predominantly on the *Fusarium*, incorporating species such as *F. graminearum*, *F. verticillioides*, and *F. oxysporum* [16,62,64,65]. The *Microsporium* genus, inclusive of *M. canis* and *M. gypseum*, comes next [66,67]. Besides these, it also exhibits parasitic behaviors towards various fungi including *Trichophyton mentagrophytes*, *Rhizoctonia solani*, *Botrytis cinerea*, *Sclerotinia minor*, and *Verticillium dahliae*, among others [22,26,67,68] (Table 3).

Table 3. Summary of mycoparasite of *P. oligandrum*.

Pathogen Type	Pathogen Species
Oomycete	<i>Pythium myriotylum</i> , <i>Pythium aphanidermatum</i> , <i>Phytophthora infestans</i> , <i>Pythium ultimum</i> , <i>Phytophthora megasperma</i> , <i>Pythium debaryanum</i> , <i>Aphanomyces laevis</i>
Fungus	<i>Fusarium graminearum</i> , <i>Fusarium verticillioides</i> , <i>Fusarium oxysporum</i> , <i>Microsporium canis</i> , <i>Microsporium gypseum</i> , <i>Trichophyton mentagrophytes</i> , <i>Rhizoctonia solani</i> , <i>Botrytis cinerea</i> , <i>Sclerotinia minor</i> , <i>Verticillium dahlia</i>

4. *P. oligandrum* Possesses the Potential to Stimulate and Augment Plant Growth

The phenomenon of growth enhancement by beneficial microorganisms has been extensively documented and is frequently linked to the production of microbial phytohormones and secondary metabolites. *Pythium oligandrum* improves plant fitness by augmenting the root system with tryptamine, a precursor of the phytohormone auxin [2,69]. In recent years, there have been numerous research reports documenting the ability of *P. oligandrum* to stimulate plant growth. *Pythium oligandrum* VOCs have been noted to enhance the growth of ginger, specifically in aspects such as root volume, the quantity of root tips, cumulative root length, and the mean root diameter [8]. The *P. oligandrum* strains MS15, MS19, and MS31 have been found to significantly augment the shoot length and root length of soybeans [6]. Furthermore, *P. oligandrum* not only encourages growth parameters in tomatoes and eggplants such as plant height, fresh weight, and dry weight [11], but

it also enhances attributes of the red clover like tap-root diameter, root branching, stand height, and forage yield [35] (Table 4).

Table 4. *P. oligandrum* promotes plant growth.

Plant Species	Growth-Promoting Characteristics
Ginger (<i>Zingiber officinale</i> Roscoe)	Root volume, number of root tips, total root length, and average root diameter
Soybean (<i>Glycine max</i> L.)	Shoot length, Root length
Tomato (<i>Solanum lycopersicum</i> L.), Eggplant (<i>Solanum melongena</i> L.)	Plant height, Fresh weight, Dry weight
Red clover (<i>Trifolium pratense</i> L.)	Tap-root diameter, Root branching, Stand height, Forage yield

5. Conclusions

Pythium oligandrum has been increasingly recognized by the scientific community for its dual biocontrol mechanisms: mycoparasitism against fungal pathogens and the induction of systemic resistance in host plants. Furthermore, *P. oligandrum* elevates plant growth through the provision of tryptamine to the root system. Consequently, *P. oligandrum* has the potential to exert multifaceted effects on the plant. We have encapsulated the present-day perspective on molecules, such as Oligandrin, CWPs, MAMPs, and RXLR effectors, that foster plant resistance. However, the scale of extant research on these facets remains constrained. Therefore, a pronounced understanding of the molecular mechanisms underpinning these molecules’ modus operandi is essential to harness the formidable capabilities of *Pythium oligandrum* optimally.

Author Contributions: Overarching conceptualization, K.Y., R.W., L.Z. and X.L.; data curation, K.Y.; funding acquisition, K.Y.; writing—original draft, K.Y.; writing—review and editing, R.W.; Literature survey, L.L.; Academic writing guidance, K.A., J.L., L.W., J.S., C.L., L.Q., L.Z. and X.L. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Guangdong Basic and Applied Basic Research Foundation (2023A1515110331 and 2025A1515011232), National Natural Science Foundation of China (32402461) and Program of Fujian Key Laboratory for Monitoring and Integrated Management of Crop Pests (MIMCP-202401).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Thines, M. Oomycetes. *Curr. Biol.* **2018**, *28*, R812–R813. [\[CrossRef\]](#) [\[PubMed\]](#)

2. Bělonožníková, K.; Hýsková, V.; Chmelík, J.; Kavan, D.; Čeřovská, N.; Ryšlavá, H. *Pythium oligandrum* in plant protection and growth promotion: Secretion of hydrolytic enzymes, elicitors and tryptamine as auxin precursor. *Microbiol. Res.* **2022**, *258*, 126976. [\[CrossRef\]](#)

3. Faure, C.; Veyssière, M.; Boëlle, B.; San, C.H.; Bouchez, O.; Lopez-Roques, C.; Chaubet, A.; Martinez, Y.; Bezouška, K.; Suchánek, M.; et al. Long-Read Genome Sequence of the Sugar Beet Rhizosphere Mycoparasite *Pythium oligandrum*. *G3 Genes Genomes Genet.* **2020**, *10*, 431–436. [\[CrossRef\]](#)

4. Abdelzaher, H.M.A.; Elnaghy, M.A.; Fadl-Allah, E.M. Isolation of *Pythium oligandrum* from Egyptian soil and its mycoparasitic effect on *Pythium ultimum* var. *ultimum* the damping-off organism of wheat. *Mycopathologia* **1997**, *139*, 97–106. [\[CrossRef\]](#)

5. Ali-Shtayeh, M.S.; Saleh, A.S.F. Isolation of *Pythium acanthicum*, *P. oligandrum*, and *P. periplocum* from soil and evaluation of their mycoparasitic activity and biocontrol efficacy against selected phytopathogenic *Pythium* species. *Mycopathologia* **1999**, *145*, 143–153. [\[CrossRef\]](#)
6. Sayed, S.R.M.; Abdelmohsen, S.A.M.; Abdelzaher, H.M.A.; Elnaghy, M.A.; Mostafa, A.A.; Al-Harbi, F.F.; Abdelbacki, A.M.M. Myco-Suppression Analysis of Soybean (*Glycine max*) Damping-Off Caused by *Pythium aphanidermatum*. *Plants* **2021**, *10*, 788. [\[CrossRef\]](#)
7. You, X.; Barraud, J.; Tojo, M. Suppressive Effects of *Pythium oligandrum* on Soybean Damping off Caused by *P. aphanidermatum* and *P. myriotylum*. *Ann. Rept. Kansai Pl. Prot. Soc.* **2019**, *61*, 9–13. [\[CrossRef\]](#)
8. Sheikh, T.M.M.; Zhou, D.; Ali, H.; Hussain, S.; Wang, N.; Chen, S.; Zhao, Y.; Wen, X.; Wang, X.; Zhang, J.; et al. Volatile Organic Compounds Emitted by the Biocontrol Agent *Pythium oligandrum* Contribute to Ginger Plant Growth and Disease Resistance. *Microbiol. Spectr.* **2023**, *11*, e0151023. [\[CrossRef\]](#)
9. Daly, P.; Chen, S.; Xue, T.; Li, J.; Sheikh, T.M.M.; Zhang, Q.; Wang, X.; Zhang, J.; Fitzpatrick, D.A.; McGowan, J.; et al. Dual-Transcriptomic, Microscopic, and Biocontrol Analyses of the Interaction Between the Bioeffector *Pythium oligandrum* and the *Pythium* Soft-Rot of Ginger Pathogen *Pythium myriotylum*. *Front. Microbiol.* **2021**, *12*, 765872. [\[CrossRef\]](#)
10. Moustafa, S.M.N. Influence of *Pythium oligandrum* on Mycelia and Production of Zoo-and Oo-spores of Two Phytopathogenic *Pythium* spp. *J. Pure Appl. Microbiol.* **2019**, *13*, 233–240. [\[CrossRef\]](#)
11. Habib, W.; Saab, C.; Gerges, E.; Kareh, C.A.; Gerges, R. Evaluation of Different Control Measures against Damping off in Greenhouse *Solanaceous* Crops. *Res. J. Plant Pathol.* **2021**, *4*, 1–9.
12. Vallance, J.; Floch, G.L.; Dénier, F.; Barbier, G.; Lévesque, C.A.; Rey, P. Influence of *Pythium oligandrum* Biocontrol on Fungal and Oomycete Population Dynamics in the Rhizosphere. *Appl. Environ. Microbiol.* **2009**, *75*, 4790–4800. [\[CrossRef\]](#) [\[PubMed\]](#)
13. Yacoub, A.; Haidar, R.; Mesguida, O.; Gerbore, J.; Hachicha, M.; Attard, E.; Guyoneaud, R.; Rey, P. Deciphering Plant-Induced Responses toward *Botrytis cinerea* and *Plasmopara viticola* Attacks in Two Grapevine Cultivars Colonized by the Root Biocontrol Oomycete, *Pythium oligandrum*. *J. Fungi.* **2023**, *9*, 511. [\[CrossRef\]](#)
14. Postulkova, M.; Rezanina, J.; Fiala, J.; Ruzicka, M.C.; Dostalek, P.; Branyik, T. Suppression of fungal contamination by *Pythium oligandrum* during malting of barley. *J. Inst. Brew.* **2018**, *124*, 336–340. [\[CrossRef\]](#)
15. Cwalina-Ambroziak, B.; Nowak, M. The effects of biological and chemical controls on fungal communities colonising tomato (*Lycopersicon esculentum* Mill.) plants and soil. *Folia Hort.* **2012**, *24*, 13–20. [\[CrossRef\]](#)
16. Benhamou, N.; Rey, P.; Chérif, M.; Hockenhull, J.; Tirilly, Y. Treatment with the Mycoparasite *Pythium oligandrum* Triggers Induction of Defense-Related Reactions in Tomato Roots When Challenged with *Fusarium oxysporum* f. sp. *radicis-lycopersici*. *Phytopathology* **1997**, *87*, 108–122. [\[CrossRef\]](#)
17. Ng, C.A.; Pernica, M.; Yap, J.; Belakova, S.; Vaculova, K.; Branyik, T. Biocontrol effect of *Pythium oligandrum* on artificial *Fusarium culmorum* infection during malting of wheat. *J. Cereal Sci.* **2021**, *100*, 103258. [\[CrossRef\]](#)
18. Yacoub, A.; Magnin, N.; Gerbore, J.; Haidar, R.; Bruez, E.; Compant, S.; Guyoneaud, R.; Rey, P. The Biocontrol Root-Oomycete, *Pythium Oligandrum*, Triggers Grapevine Resistance and Shifts in the Transcriptome of the Trunk Pathogenic Fungus, *Phaeoconiella Chlamydospora*. *Int. J. Mol. Sci.* **2020**, *21*, 6876. [\[CrossRef\]](#) [\[PubMed\]](#)
19. Yacoub, A.; Haidar, R.; Gerbore, J.; Masson, C.; Dufour, M.; Guyoneaud, R.; Rey, P. *Pythium oligandrum* induces grapevine defence mechanisms against the trunk pathogen *Neofusicoccum parvum*. *Phytopathol. Mediterr.* **2020**, *59*, 565–580.
20. Yacoub, A.; Gerbore, J.; Magnin, N.; Chambon, P.; Dufour, M.-C.; Corio-Costet, M.-F.; Guyoneaud, R.; Rey, P. Ability of *Pythium oligandrum* strains to protect *Vitis vinifera* L., by inducing plant resistance against *Phaeoconiella chlamydospora*, a pathogen involved in Esca, a grapevine trunk disease. *Biol. Control* **2016**, *92*, 7–16. [\[CrossRef\]](#)
21. Gerbore, J.; Vallance, J.; Yacoub, A.; Delmotte, F.; Grizard, D.; Regnault-Roger, C.; Rey, P. Characterization of *Pythium oligandrum* populations that colonize the rhizosphere of vines from the Bordeaux region. *FEMS Microbiol. Ecol.* **2014**, *90*, 153–167. [\[CrossRef\]](#)
22. Al-Rawahi, A.K.; Hancock, J.G. Parasitism and Biological Control of *Verticillium dahliae* by *Pythium oligandrum*. *Plant Dis.* **1998**, *82*, 1100–1106. [\[CrossRef\]](#)
23. Rekanovic, E.; Milijasevic, S.; Todorovic, B.; Potocnik, I. Possibilities of Biological and Chemical Control of *Verticillium* Wilt in Pepper. *Phytoparasitica* **2007**, *35*, 436–441. [\[CrossRef\]](#)
24. Takenaka, S.; Ishikawa, S. Biocontrol of Sugar Beet Seedling and Taproot Diseases Caused by *Aphanomyces cochlioides* by *Pythium oligandrum* Treatments before Transplanting. *Jpn. Agric. Res. Q. JARQ* **2013**, *47*, 75–83. [\[CrossRef\]](#)
25. Baturo-Cieśniewska, A.; Łukanowski, A.; Koczwara, K.; Lenc, L. Development of *Sclerotinia sclerotiorum* (Lib.) de Bary on stored carrot treated with *Pythium oligandrum* Drechsler determined by qPCR assay. *Acta Sci. Pol. Hortorum Cultus* **2018**, *17*, 111–121. [\[CrossRef\]](#)
26. Ikeda, S.; Shimizu, A.; Shimizu, M.; Takahashi, H.; Takenaka, S. Biocontrol of black scurf on potato by seed tuber treatment with *Pythium oligandrum*. *Biol. Control* **2012**, *60*, 297–304. [\[CrossRef\]](#)
27. Meszka, B.; Bielenin, A. A new biological product against strawberry grey mould. *Phytopathologia* **2010**, *58*, 13–19.

28. Le Floch, G.; Rey, P.; Déniel, F.; Benhamou, N.; Picard, K.; Tirilly, Y. Enhancement of development and induction of resistance in tomato plants by the antagonist, *Pythium oligandrum*. *Agronomie* **2003**, *23*, 455–460. [\[CrossRef\]](#)
29. Altieri, V.; Rossi, V.; Fedele, G. Efficacy of preharvest application of biocontrol agents against gray mold in grapevine. *Front. Plant Sci.* **2023**, *14*, 1154370. [\[CrossRef\]](#)
30. Takenaka, S.; Sekiguchi, H.; Nakaho, K.; Tojo, M.; Masunaka, A.; Takahashi, H. Colonization of *Pythium oligandrum* in the Tomato Rhizosphere for Biological Control of Bacterial Wilt Disease Analyzed by Real-Time PCR and Confocal Laser-Scanning Microscopy. *Phytopathology* **2008**, *98*, 187–195. [\[CrossRef\]](#)
31. Masunaka, A.; Nakaho, K.; Sakai, M.; Takahashi, H.; Takenaka, S. Visualization of *Ralstonia solanacearum* cells during biocontrol of bacterial wilt disease in tomato with *Pythium oligandrum*. *J. Gen. Plant Pathol.* **2009**, *75*, 281–287. [\[CrossRef\]](#)
32. Takenaka, S. Studies on biological control mechanisms of *Pythium oligandrum*. *J. Gen. Plant Pathol.* **2015**, *81*, 466–469. [\[CrossRef\]](#)
33. Hase, S.; Shimizu, A.; Nakaho, K.; Takenaka, S.; Takahashi, H. Induction of transient ethylene and reduction in severity of tomato bacterial wilt by *Pythium oligandrum*. *Plant Pathol.* **2006**, *55*, 537–543. [\[CrossRef\]](#)
34. Pisarčík, M.; Hakl, J.; Menšík, L.; Szábo, O.; Nerušil, P. Biological control in lucerne crops can negatively affect the development of root morphology, forage yield and quality. *Plant Soil Environ.* **2019**, *65*, 477–482. [\[CrossRef\]](#)
35. Pisarčík, M.; Hakl, J.; Hrevušová, Z. Effect of *Pythium oligandrum* and poly-beta-hydroxy butyric acid application on root growth, forage yield and root diseases of red clover under field conditions. *Crop Prot.* **2020**, *127*, 104968. [\[CrossRef\]](#)
36. Xue, Y.; Li, W.; Li, M.; Ru, N.; Chen, S.; Jiu, M.; Feng, H.; Wei, L.; Daly, P.; Zhou, D. Biological Control of a Root-Knot Nematode *Meloidogyne incognita* Infection of Tomato (*Solanum lycopersicum* L.) by the Oomycete Biocontrol Agent *Pythium oligandrum*. *J. Fungi* **2024**, *10*, 265. [\[CrossRef\]](#)
37. Le Floch, G.; Vallance, J.; Benhamou, N.; Rey, P. Combining the oomycete *Pythium oligandrum* with two other antagonistic fungi: Root relationships and tomato grey mold biocontrol. *Biol. Control* **2009**, *50*, 288–298. [\[CrossRef\]](#)
38. Bělonožníková, K.; Vaverová, K.; Vaněk, T.; Kolařík, M.; Hýšková, V.; Vaňková, R.; Dobrev, P.; Křížek, T.; Hodek, O.; Čokrtová, K.; et al. Novel Insights into the Effect of *Pythium* Strains on Rapeseed Metabolism. *Microorganisms* **2020**, *8*, 1472. [\[CrossRef\]](#) [\[PubMed\]](#)
39. Jones, J.D.; Dangl, J.L. The plant immune system. *Nature* **2006**, *444*, 323–329. [\[CrossRef\]](#)
40. Picard, K.; Ponchet, M.; Blein, J.P.; Rey, P.; Tirilly, Y.; Benhamou, N. Oligandrin. A Proteinaceous Molecule Produced by the Mycoparasite *Pythium oligandrum* Induces Resistance to *Phytophthora parasitica* Infection in Tomato Plants. *Plant Physiol.* **2000**, *124*, 379–395. [\[CrossRef\]](#)
41. Satková, P.; Starý, T.; Plešková, V.; Zapletalová, M.; Kašparovský, T.; Činčalová-Kubienová, L.; Luhová, L.; Mieslerová, B.; Mikulík, J.; Lochman, J.; et al. Diverse responses of wild and cultivated tomato to BABA, oligandrin and *Oidium neolyopersici* infection. *Ann. Bot.* **2017**, *119*, 829–840.
42. Wang, A.; Lou, B.; Xu, T.; Lin, C. Defense responses in tomato fruit induced by oligandrin against *Botrytis cinerea*. *Afr. J. Biotechnol.* **2011**, *10*, 4596–4601.
43. Lou, B.; Wang, A.; Lin, C.; Xu, T.; Zheng, X. Enhancement of defense responses by oligandrin against *Botrytis cinerea* in tomatoes. *Afr. J. Biotechnol.* **2011**, *10*, 11442–11449.
44. Mohamed, N.; Lherminier, J.; Farmer, M.-J.; Fromentin, J.; Béno, N.; Houot, V.; Milat, M.-L.; Blein, J.-P. Defense Responses in Grapevine Leaves Against *Botrytis cinerea* Induced by Application of a *Pythium oligandrum* Strain or Its Elicitin, Oligandrin, to Roots. *Phytopathology* **2007**, *97*, 611–620. [\[CrossRef\]](#)
45. Benhamou, N.; Bélanger, R.R.; Rey, P.; Tirilly, Y. Oligandrin, the elicitin-like protein produced by the mycoparasite *Pythium oligandrum*, induces systemic resistance to *Fusarium* crown and root rot in tomato plants. *Plant Physiol. Biochem.* **2001**, *39*, 681–698. [\[CrossRef\]](#)
46. Sun, J.; Xu, J.; Kang, C.; Cheng, L.; Gao, Y.; Hu, F.; Liang, J.; Guo, L.; Ma, X. Role of oligandrin in enhancing post-harvest disease resistance in cherry tomato through salicylic acid and jasmonic acid signaling pathways. *Appl. Environ. Microbiol.* **2025**, *91*, e0042125. [\[CrossRef\]](#)
47. Kawamura, Y.; Takenaka, S.; Hase, S.; Kubota, M.; Ichinose, Y.; Kanayama, Y.; Nakaho, K.; Klessig, D.; Takahashi, H. Enhanced Defense Responses in Arabidopsis Induced by the Cell Wall Protein Fractions from *Pythium oligandrum* Require *SGT1*, *RAR1*, *NPR1* and *JAR1*. *Plant Cell Physiol.* **2009**, *50*, 924–934. [\[CrossRef\]](#) [\[PubMed\]](#)
48. Takenaka, S.; Yamaguchi, K.; Masunaka, A.; Hase, S.; Inoue, T.; Takahashi, H. Implications of oligomeric forms of POD-1 and POD-2 proteins isolated from cell walls of the biocontrol agent *Pythium oligandrum* in relation to their ability to induce defense reactions in tomato. *J. Plant Physiol.* **2011**, *168*, 1972–1979. [\[CrossRef\]](#)
49. Takenaka, S.; Nakamura, Y.; Kono, T.; Sekiguchi, H.; Masunaka, A.; Takahashi, H. Novel elicitin-like proteins isolated from the cell wall of the biocontrol agent *Pythium oligandrum* induce defence-related genes in sugar beet. *Mol. Plant Pathol.* **2006**, *7*, 325–339. [\[CrossRef\]](#) [\[PubMed\]](#)

50. Ouyang, Z.; Li, X.; Huang, L.; Hong, Y.; Zhang, Y.; Zhang, H.; Li, D.; Song, F. Elicitin-like proteins Oli-D1 and Oli-D2 from *Pythium oligandrum* trigger hypersensitive response in *Nicotiana benthamiana* and induce resistance against *Botrytis cinerea* in tomato. *Mol. Plant Pathol.* **2015**, *16*, 238–250. [\[CrossRef\]](#) [\[PubMed\]](#)
51. Yang, K.; Wang, Y.; Zhao, H.; Shen, D.; Dou, D.; Jing, M. Novel Elicitin from *Pythium oligandrum* Confers Disease Resistance against *Phytophthora capsici* in Solanaceae Plants. *J. Agric. Food Chem.* **2022**, *70*, 16135–16145. [\[CrossRef\]](#)
52. Yang, K.; Dong, X.; Li, J.; Wang, Y.; Cheng, Y.; Zhai, Y.; Li, X.; Wei, L.; Jing, M.; Dou, D. Type 2 Nep1-Like Proteins from the Biocontrol Oomycete *Pythium oligandrum* Suppress *Phytophthora capsici* Infection in Solanaceous Plants. *J. Fungi* **2021**, *7*, 496. [\[CrossRef\]](#)
53. Ottmann, C.; Luberaeki, B.; Kufner, I.; Koch, W.; Brunner, F.; Weyand, M.; Mattinen, L.; Pirhonen, M.; Anderluh, G.; Seitz, H.U.; et al. A common toxin fold mediates microbial attack and plant defense. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 10359–10364. [\[CrossRef\]](#)
54. Yang, K.; Chen, C.; Wang, Y.; Li, J.; Dong, X.; Cheng, Y.; Zhang, H.; Zhai, Y.; Ai, G.; Song, Q.; et al. Nep1-Like Proteins From the Biocontrol Agent *Pythium oligandrum* Enhance Plant Disease Resistance Independent of Cell Death and Reactive Oxygen Species. *Front. Plant Sci.* **2022**, *13*, 830636. [\[CrossRef\]](#)
55. Ai, G.; Yang, K.; Ye, W.; Tian, Y.; Du, Y.; Zhu, H.; Li, T.; Xia, Q.; Shen, D.; Peng, H.; et al. Prediction and Characterization of RXLR Effectors in *Pythium* Species. *Mol. Plant-Microbe Interact.* **2020**, *33*, 1046–1058. [\[CrossRef\]](#)
56. Conlon, M.; Dixon, S.J. Ferroptosis-like death in plant cells. *Mol. Cell. Oncol.* **2017**, *4*, e1302906. [\[CrossRef\]](#) [\[PubMed\]](#)
57. Cao, J.Y.; Dixon, S.J. Mechanisms of ferroptosis. *Cell. Mol. Life Sci.* **2016**, *73*, 2195–2209. [\[CrossRef\]](#)
58. Dixon, S.J.; Lemberg, K.M.; Lamprecht, M.R.; Skouta, R.; Zaitsev, E.M.; Gleason, C.E.; Patel, D.N.; Bauer, A.J.; Cantley, A.M.; Yang, W.S.; et al. Ferroptosis: An Iron-Dependent Form of Nonapoptotic Cell Death. *Cell* **2012**, *149*, 1060–1072. [\[CrossRef\]](#)
59. Cheng, Y.; Zhang, H.; Zhu, W.; Li, Q.; Meng, R.; Yang, K.; Guo, Z.; Zhai, Y.; Zhang, H.; Ji, R.; et al. Ferroptosis induced by the biocontrol agent *Pythium oligandrum* enhances soybean resistance to *Phytophthora sojae*. *Environ. Microbiol.* **2022**, *24*, 6267–6278. [\[CrossRef\]](#) [\[PubMed\]](#)
60. Sheikh, T.M.M.; Zhou, D.; Haider, M.; Hussain, S.; Wang, N.; Chen, S.; Zhao, Y.; Wen, X.; Feng, H.; Wang, X.; et al. Volatile Organic Compounds from *Pythium oligandrum* Play a Role in Its Parasitism on Plant-Pathogenic *Pythium myriotylum*. *Appl. Environ. Microbiol.* **2023**, *89*, e0203622. [\[CrossRef\]](#)
61. Horner, N.R.; Grenville-Briggs, L.J.; van West, P. The oomycete *Pythium oligandrum* expresses putative effectors during mycoparasitism of *Phytophthora infestans* and is amenable to transformation. *Fungal Biol.* **2012**, *116*, 24–41. [\[CrossRef\]](#) [\[PubMed\]](#)
62. Benhamou, N.; Rey, P.; Picard, K.; Yves, T. Ultrastructural and Cytochemical Aspects of the Interaction Between the Mycoparasite *Pythium oligandrum* and Soilborne Plant Pathogens. *Phytopathology* **1999**, *89*, 506–517. [\[CrossRef\]](#) [\[PubMed\]](#)
63. Veselý, D. Parasitic Relationships between *Pythium oligandrum* Drechsler and Some Other Species of the Oomycetes Class. *Zbl. Bakt.* **1978**, *133*, 341–349. [\[CrossRef\]](#)
64. Pellan, L.; Durand, N.; Martinez, V.; Fontana, A.; Schorr-Galindo, S.; Strub, C. Commercial Biocontrol Agents Reveal Contrasting Compartments Against Two Mycotoxigenic Fungi in Cereals: *Fusarium Graminearum* and *Fusarium Verticillioides*. *Toxins* **2020**, *12*, 152. [\[CrossRef\]](#)
65. Benhamou, N.; le Floch, G.; Vallance, J.; Gerbore, J.; Grizard, D.; Rey, P. *Pythium oligandrum*: An example of opportunistic success. *Microbiology* **2012**, *158*, 2679–2694. [\[CrossRef\]](#)
66. Gabrielova, A.; Mencl, K.; Suchanek, M.; Klimes, R.; Hubka, V.; Kolarik, M. The Oomycete *Pythium oligandrum* Can Suppress and Kill the Causative Agents of Dermatophytoses. *Mycopathologia* **2018**, *183*, 751–764. [\[CrossRef\]](#)
67. Načeradská, M.; Fridrichová, M.; Kellnerová, D.; Peková, S.; Lány, P. Antifungal effects of the biological agent *Pythium oligandrum* observed in vitro. *J. Feline Med. Surg.* **2016**, *19*, 817–823. [\[CrossRef\]](#)
68. Rey, P.; Le Floch, G.; Benhamou, N.; Salerno, M.; Thuillier, E.; Tirilly, Y. Interactions between the mycoparasite *Pythium oligandrum* and two types of sclerotia of plant-pathogenic fungi. *Mycol. Res.* **2005**, *109*, 779–788. [\[CrossRef\]](#)
69. Gerbore, J.; Benhamou, N.; Vallance, J.; Le Floch, G.; Grizard, D.; Regnault-Roger, C.; Rey, P. Biological control of plant pathogens: Advantages and limitations seen through the case study of *Pythium oligandrum*. *Environ. Sci. Pollut. Res.* **2014**, *21*, 4847–4860. [\[CrossRef\]](#) [\[PubMed\]](#)

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.