



REVIEW ARTICLE

The mechanistic pathways of *Pochonia chlamydosporia*: A biology perspective on Nematode suppression and plant promotion

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Abstract

Pochonia chlamydosporia is a promising nematophagous fungus known for its multifaceted role in the biological suppression of plant parasitic nematodes and the enhancement of plant health. This review provides a mechanistic perspective on its functional biology, systematically dissecting the pathways through which *P. chlamydosporia* establishes in the rhizosphere, parasitizes nematode eggs, produces bioactive metabolites and triggers systemic defense responses in host plants. The fungus exhibits robust colonization strategies both in soil and plant roots, driven by factors like inoculum density and environmental conditions. It secretes enzymes and forms specialized structures for nematode egg parasitism, while also synthesizing metabolites with nematocidal and plant-growth-promoting properties. Moreover, its endophytic interaction with host plants modulates signaling pathways, triggering systemic defense gene expression. Through its diverse mechanistic actions, *P. chlamydosporia* emerges as a powerful bioagent contributing to both nematode management and improved plant growth.

Keywords: biocontrol efficacy; endophytic nature; plant defense mechanism; Plant growth promotion; *Pochonia chlamydosporia*; secondary metabolite

Abbreviations

PPN - Plant parasitic nematodes; PCN - Potato cyst nematode; BCA - Biocontrol agents; spp. - Species; ETL - Economic threshold level; PGP - Plant growth promotion; HPR - Host plant resistance; C - Celsius; cm - Centimetre; PCC - Presumed carrying capacity PCR- Competitive polymerase chain reaction; LOX - Lipoxygenase; PIN II - Proteinase inhibitor II; PAL - Phenylalanine ammonia-lyase; PR1- Pathogenesis related protein

Introduction

Plant parasitic nematodes (PPNs) are a major concern in agriculture, leading to significant economic losses worldwide due to their detrimental effects on plant health. Their widespread distribution and ability to infest numerous crops make them a silent but formidable adversary. Estimates suggest annual losses ranging from \$80 billion to \$157 billion due to PPNs (1). Many different phytoparasitic nematodes represent a danger to a variety of vegetables and field crops across the world, but the most significant ones are sedentary endoparasitic nematodes from the genera *Meloidogyne*, *Globodera* and *Heterodera* (2-5). In comparison to other PPN, the root-knot nematodes (*Meloidogyne* spp.) and the cyst nematodes (*Heterodera* spp. & *Globodera* spp.) were thought to be covert foes for crops. Due to their rapid reproduction, short life cycle,

broad host range and endoparasitic nature, these soil pathogens are challenging to handle (6, 7).

Various management approaches, including cultural, physical, chemical and biological treatments, are used to control the nematode infestation at the economic threshold level (ETL). To achieve long-term nematode control, a variety of techniques were used (8). Chemical and biological control strategies were mostly preferred. Growers have therefore focused primarily on the use of chemicals for managing nematodes, which causes several issues, such as pesticide resistance, adverse impacts on human health, depletion of beneficial microorganisms, entry of lingering harmful substances in the food chain and reduced diversity of macro and microorganisms (9, 10). In response to several issues, more work is being done to create environmentally benign microbe-based pesticides or bio

pesticides that employ biocontrol agent (BCA) functions in a distinct manner as an active component than conventional chemical nematicides (10, 11).

The term biocontrol is defined as a decrease in nematode populations achieved by the action of living species other than the nematode-resistant host plant, which happens naturally or through the modification of the environment or the introduction of antagonists (12). In order to manage PPNs, a few nematophagous bacteria and fungi are commercially available (13). Among biocontrol agents, fungi have sophisticated techniques for entangling nematodes in both constricting and non-constricting rings, adhesive branches and can also kill them by secreting poisonous chemicals and digest their bodies by colonizing their female reproductive processes (14). The genera, such as *Paecilomyces*, *Verticillium*, *Purpureocillium*, *Arthrobotrys*, *Acremonium*, *Clonostachys*, *Chaetomium*, *Fusarium*, *Isaria*, *Penicillium*, *Phyllosticta* and *Trichoderma*, were reported to be nematophagous and hostile to nematodes (15, 16).

Nematophagous fungi, widely studied as natural enemies of nematodes, occur naturally in soil and function as either saprophytic or parasitic agents (17, 18). The potential of nematophagous fungi to control PPNs has been documented by several authors (19-21). Nevertheless, there are only a limited number of commercial products accessible for managing *Meloidogyne* spp. (19, 22-24). Among these nematophagous fungi, *P. chlamydosporia* is a promising candidate as a biocontrol agent (25-27) from the Clavicipitaceae family within the order Hypocreales. The genus *Verticillium chlamydosporium* was revised as *P. chlamydosporia* by (28). This fungus was reported to parasitize eggs and females of important species of PPNs like root-knot nematode, *Meloidogyne* spp. and cyst nematode like *Globodera* spp. and *Heterodera* spp. (29, 30). The mechanism of action of *P. chlamydosporia* was explored by Swarnakumari and Kalaivasan (31). Complex tri-tropic interaction between plant-fungus-nematode was investigated for efficient application of *P. chlamydosporia* as a biopesticide within an integrated pest control strategy (32).

Pochonia chlamydosporia has been utilized for nematode management in essential crops for food security (Table 1). *Pochonia chlamydosporia* is used in the biological control of animal parasitic nematodes (33) and has demonstrated infectivity towards laboratory insect hemiptera (34).

Table 1. *Pochonia chlamydosporia* for control of nematodes in key crop species

Crop	Reference
Rice	(86)
Tomato	(87)
Potato	(88)
Cucumber	(63)
Banana	(89)
Soybean	(90)
Root beet	(91)

Entry and Establishment in the Rhizosphere

Colonization in soil

Research indicates that colonization and growth of *P. chlamydosporia* in soil (35-38). Abundant growth was observed when *P. chlamydosporia* was inoculated in the soil as only hyphal fragments and chlamydospores without any food base, then applied as colonized sand bran (Fig. 1). The population of *M. arenaria* was reduced >80 % due to *P. chlamydosporia* on tomato under glasshouse (35). Some isolates proliferated and survived for at least 3 months in significant numbers in soil. When the fungus was applied in the soil before planting, it resulted in long-term survival of the fungus as well as control of nematodes (27). The growth of *P. chlamydosporia* was more in peaty soil than in the loamy sand and sandy soil. The control of *M. incognita* on tomato was more in peaty sand (59 %) than in loamy sand (51 %) and sandy soil (39 %). The fungus survived in potted tomato plants for about 8 weeks (39). Efficient percolation and proliferation of *P. chlamydosporia* in both sandy and clayey soil up to 50 cm depth when it was applied through seed dressing against *M. incognita* population (40).

The saprophytic proliferation of *P. chlamydosporia* was abundant in the sterilized (γ -radiated) soil than in the field soil because of less competition from other soil microorganisms. At least 3 weeks are required for the fungus to reach the presumed carrying capacity (PCC) in soil. The increased growth of fungus in the potato cyst nematode (PCN) infested plant rhizosphere was found through competitive PCR (CPCR) after 14 weeks (41). *Pochonia chlamydosporia* growth in soil was less and the chlamydospore was the most important survival stage for the establishment of *P. chlamydosporia* in soil, has been emphasized by (42). Increased application of chlamydospores as inoculum

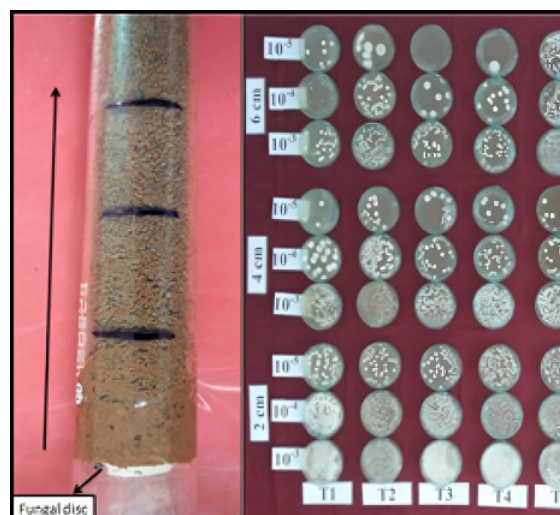


Fig. 1. Colonization of *P. chlamydosporia* in soil.

resulted in 10-fold increased density of *P. chlamydosporia* in the soil and there was no relationship between density of the fungus and parasitized eggs (43).

Pochonia chlamydosporia was able to establish within the first 2-3 weeks in the soil, increased in the number of colonies seen in the next 6-7 weeks, whereas 8-10 weeks after, growth marginally reduced and consistent growth was observed at the 12th week (44). Mountain soil, red laterite and alluvial soil are conducive environments for the growth and establishment of *P. chlamydosporia*. Mountain soil was better in terms of parasitisation of egg mass and multiplication of spores due to the prevalence of lower pH and high organic carbon in that soil for the proliferation of the fungus. Incorporation of *P. chlamydosporia* into the soil reduced the reproduction factor compared to the surface application in carrot beds, which also improved its quality and yield (36).

Colonization in the roots

The root colonization of *P. chlamydosporia* was recorded, in which the cell wall modification was induced in the epidermis, but it did not affect the growth of plants. Hyphae of the fungus penetrated and proliferated into the roots by means of appresoria formation and a hyphal network was formed in the epidermis and cortical cells of the root, which was documented through Scanning Electron Microscope (46). The colonization of *P. chlamydosporia* was minimal near the root cap but gradually intensified as the distance from the cap increased, resulting in the development of a sporadic network of hyphae. *Pochonia chlamydosporia* promotes the growth of tomato and lettuce and produces the maximum number of chlamydospores within 15 days.

The ability to colonize the root of both native and introduced isolates was similar and there is no significant difference in *P. chlamydosporia*. Colony-forming unit formed by the introduced isolate on tomato and cabbage under the growth chamber was higher in cm⁻² of root surface (Table 2) (47, 48). But in the native isolate, colonization and recovery from the soil were higher under the tunnel house on tomato (49). *Pochonia chlamydosporia* was able to colonize weeds as well as cultivated crops (50). *Pochonia chlamydosporia* root colonization caused the metabolic changes in *M. javanica* roots, with a particular emphasis on the production of phenolic compounds and flavonoids and altered the expression of genes related to the defense system (51).

Colonization pattern rhizosphere

Impact of varying levels of *P. chlamydosporia* inoculum density on colonization in soil, root and nematode control was analysed that the growth of the fungus partially depended on initial inoculum density, had maximum influence over root colonization and nematode parasitism (52). Density of *P. chlamydosporia* colonization was greater in the rhizosphere compared to the surrounding soil (53, 54). In sterile conditions,

there was a weak positive correlation between the fungal density on plant roots and the extent of hyphal growth on tomato through direct observation. *Pochonia chlamydosporia* fungal spores population in the soil and rhizosphere was higher in all the plants screened except velvet beans after 30 days of planting (55). The fungal spores were found significantly higher in the maize rhizosphere compared to others on 90 days after planting.

The fungus proliferated in the tomato rhizosphere even though rhizosphere colonization does not cause lesions on roots and does not affect plant growth. The rhizosphere colonization of the fungus *P. chlamydosporia* differed with various plant species. The extensive rhizosphere colonization was found in the Brassicaceae family crops, especially kale and cabbage (56). *Pochonia chlamydosporia* has a high ability to colonize the rhizosphere and the persistence was about 10 weeks in the tomato rhizosphere. Single or individual isolate treatment of *P. chlamydosporia* in soil resulted in improved *M. javanica* control on tomato (38, 57). The application of fungus before planting in the rhizosphere resulted in 50 % of infected eggs, 25 % reduction of multiplication and root galling by root knot nematode (58).

Factors Responsible for Colonization by *P. chlamydosporia*

The abiotic factors like temperature, pH and C:N ratio influence colonization of *P. chlamydosporia*. The colony-forming units of *P. chlamydosporia* are influenced by soil temperature, particularly when the temperature exceeds 30 °C colony counts were less (37). Optimum temperature for the growth and development of *P. chlamydosporia* was 24 °C and 25 °C and it produced about 3.5 and 5.2×10^6 chlamydospores per gram of colonized substrate (59). Optimum temperature and pH required for spore production of *P. chlamydosporia* were standardized by (60). Increased water content resulted in increased mycelial growth duration, time taken for sporulation and production cycle. There exists an inverse correlation between the production of spores and the initial moisture content. The optimum proportion of water added to the substrate was a 1:1 (v/w) ratio. The growth and sporulation of *P. chlamydosporia* are significantly influenced by the C:N ratio and pH level. At pH 3.7 and the C:N ratio 10:1 yielded the maximum yield, while at pH 6.8 and the C:N ratio 40:1 yielded the highest biomass (61). Highest egg parasitization observed with *P. chlamydosporia* was 30.99 % infestation at a C:N ratio of 5:100, while the lowest rate was 12.03 % at a C:N ratio of 10, 5 which was recorded by (62) in the yeast extract medium against the root knot nematode. The nitrogen was increased (0.5-100 mM) with the carbon at 10 mM, resulting in increased parasitisation of eggs. Organic amendments decomposed at different temperatures affect the colony-forming units of *P. chlamydosporia* and the cfu was higher in decomposed material than the non-decomposed material. Fungal spores were higher in the sawdust, which was composted at 15 °C and 20 °C compared to other composts (62).

Table 2. Classification of the host based on fungus growth and development

Fungal colonization (CFU/cm ²) in the root	Quality of the host	Crops
Less than 100	Poor host	Beans, cabbage, crotalaria, kale, pigeon pea, potato, pumpkin and tomato
100 - 200	Moderate host	Chilli, sweet potato, cowpea, rye, tobacco and cotton
More than 200	Good host	Aubergine, okra, soybean, sorghum and wheat

Nematode Egg Parasitism Cascade

Research indicates the mode of action of *P. chlamydosporia* (31). Hyphae of fungus attached to the egg surface on the first day of inoculation of spores, appressoria were produced on the second day and eventually the observation of complete colonization of the eggs was recorded on the fourth day (63). The eggs have become condensed and growth was arrested at the gastrula stage (Table 3) (31).

An *in vitro* study was performed to assess the parasitic activity of 10 strains of *P. chlamydosporia* on eggs of the PCN, *Globodera pallida*. The observed levels of pathogenicity varied between 34 % and 49 %. Impulsive hatching occurs when isolates of *P. chlamydosporia* exhibit a strong tendency to parasitize immature eggs rather than those containing second-stage juveniles (64). The effectiveness of utilizing *P. chlamydosporia* in seed treatment against root knot nematode *Meloidogyne hapla* led to a significant reduction in *M. hapla* eggs observed during a greenhouse experiment by up to 95.6 % (65). Moreover, the subsequently grown tomato plant had a lower gall index (66). *Pochonia chlamydosporia* reduced the number of egg masses, juveniles and galls nearly 50 % on tomato roots when the inoculum was applied as chlamydospores in the soil under greenhouse conditions (67). The population density of *M. hapla* on tomato and *G. pallida* on potato was reduced by more than 50 % when the chlamydospores were applied in the soil under greenhouse conditions (68). The most effective concentration of *P. chlamydosporia* inoculum for effective management of root knot nematode was 5000 chlamydospores per gram of soil (69).

Secondary Metabolite Production Pathway

Two compounds, namely Phomalactone and Monorden from *P. chlamydosporia* have nematocidal activity and various biological activities. *Meloidogyne incognita* control was less through Phomalactone in comparison with Aldicarb (70). The new compounds, which were present in the culture broth of *P. chlamydosporia* var. *spinulospora*, were Pochoniolides A and B, which exhibited capabilities in scavenging hydroxyl radicals and quenching singlet oxygen (Table 4) (71-73). A secondary metabolite, 3,4,7-trimethyl-6,8-dioxo-7,8-dihydro-6H-isochromen-7-yl ester, synthesized by *P. chlamydosporia* was named as Chlamyphilone, which had significant insecticidal activity and also this azaphilone compound caused mortality of aphids within 3 days of exposure (74). *Pochonia chlamydosporia* was grown in potato dextrose broth and kept under incubation at a temperature of 28 °C. After incubation, the extract was separated from the fungal mycelial mass. Nuclear magnetic resonance spectroscopy was used to identify the ketamine component from the extract. When ketamine is applied *in vivo* and *in vitro*, it validates its efficacy as a nematocide in *P. chlamydosporia* (34).

Signal Transduction in Plant Defense

Roots fortified by *P. chlamydosporia* colonization wield a shield against invaders (75-78). Molecular research indicates that *P. chlamydosporia* could induce phenotypes related to plant defense, which include anatomical alterations and the synthesis of distinct metabolites (45). In the presence of biotic stress factors, the interaction between host plants and *P. chlamydosporia* leads to colonization of plant roots, triggering a systemic activation of defense genes (Fig. 2). This process is intricate yet functional (78, 79). The following genes related to defense were tracked in terms of expression: lipoxygenase (LOX), proteinase inhibitor II (PINII), phenylalanine ammonia-lyase (PAL) and pathogenesis-related protein 1 (PR1). This was done after inoculating roots with *P. chlamydosporia* and subjecting plants to various sources of biotic stress. These genes were chosen because of their differential expression in tomato roots colonized by *P. chlamydosporia* (76). *Pochonia chlamydosporia* aided in boosting the plant defense response, which resulted in decreased nematode parasitism and increased phenolic compound levels. Indeed, there were also changes in the quantity of some particular phenolic chemicals. During fungal colonization, roots showed higher amounts of chlorogenic acid, correlating with diminished root parasitism (80). Research indicates that the phenomenon mirrors observations in soybean genotypes resistant to root knot nematode (81, 82). *Pochonia chlamydosporia* increased the expression of PI1, an inhibitor of serine protease belonging to the family of PR proteins (80). These proteins play a crucial role in enhancing plant defense mechanisms against *M. incognita* (83). Applying both *P. chlamydosporia* to the soil and plant defense activators like Benzothiadiazole/cis-jasmone as foliar sprays resulted in a reduced number of eggs per egg masses in *M. chitwoodi* than potato plants treated with cis-jasmone alone on potato. Rhizosphere colonization of *P. chlamydosporia* was poor. However, they are efficient parasites of nematode eggs (84, 85).

Conclusion

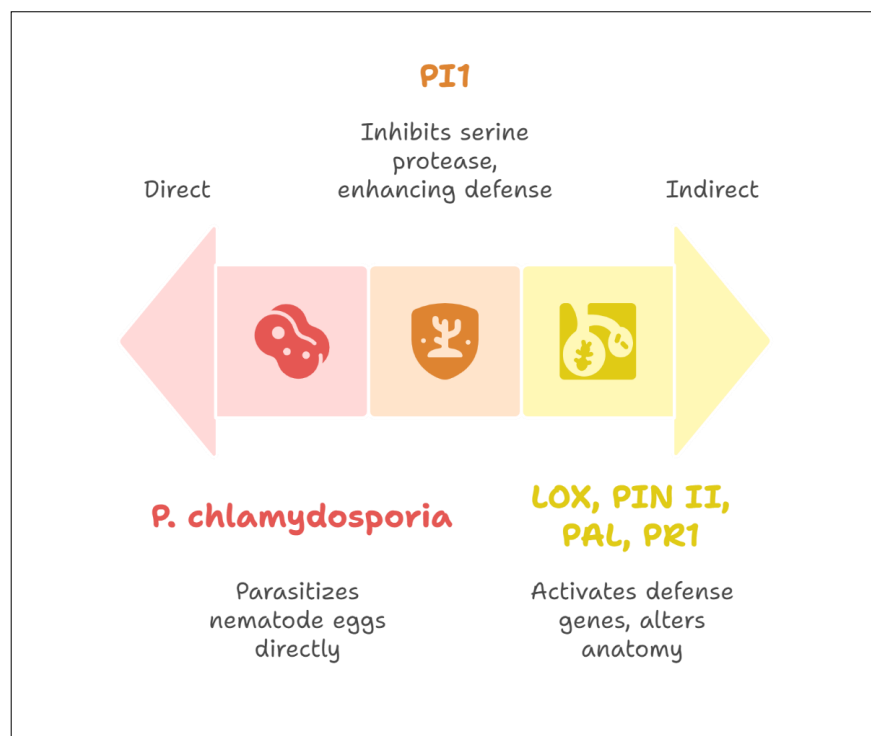
In the quest for sustainable nematode management strategies, *P. chlamydosporia* stands out as a promising ally. Through its adept colonization patterns and potent biocontrol efficacy against various plant-parasitic nematodes, this nematophagous fungus holds immense potential. Not only does it suppress nematode populations effectively, but its secretion of antinematic metabolites and stimulation of plant defence mechanisms further enhance its value. As we navigate the complexities of agricultural sustainability, harnessing the power of *P. chlamydosporia* could prove instrumental. With its multifaceted benefits, including endophytic capabilities, production of

Table 3. Infection process of *Pochonia chlamydosporia* on root knot nematode eggs

Days after inoculation (DAI)	Fungal infection process	Embryonic development
DAI 1	On the surface of egg attachment of fungal hyphae	Gastrula stage
DAI 2	Formation of peg	Gastrula stage
DAI 3	Egg cell penetration and mycelial growth	Condensation of egg contents
DAI 5	Complete colonization	An empty space formed between the egg wall and the internal content
DAI 7	Colonization of internal contents	Disintegration of the egg wall
DAI 10	Thick-walled chlamydospore formation	Dissolution of egg

Table 4. Secondary metabolites produced by *Pochonia chlamydosporia*

Metabolite name	Metabolite class	References
13-Chloro-5,6,9,14,16-pentahydroxy-3-methyl-3,4,5,6,9,10-hexahydro-1H-2-benzoxacyclotetradecine-1,11(12H)-dione		(92)
6,13-Dichloro-5,9,14,16-tetrahydroxy-3-methyl-3,4,5,6,9,10-hexahydro-1H-2-benzoxacyclotetradecine-1,11(12H)-dione		(92)
Hexahydromonorden		(92)
Radicicol or Monorden		(70, 92-94)
Monorden analogue-1		(94)
Monorden E		(94)
Pochoniolides A		(71)
Pochoniolides B		(71)
Pochonin A		(92)
Pochonin B		(92)
Pochonin C		(92)
Pochonin D		(92)
Pochonin E	Resorcylic acid lactones	(92, 94)
Pochonin F		(92, 94)
Pochonin G		(93)
Pochonin H		(93)
Pochonin I		(93)
Pochonin J		(93)
Pochonin K		(94)
Pochonin L		(94)
Pochonin M		(94)
Pochonin N		(94)
Pochonin O	Alkaloid Azaphilone Cyclohexanone	(94)
Pochonin P		(94)
Monocillin I		(94)
Monocillin II glycoside		(92, 94)
Monocillin II		(92, 94)
Monocillin III		(92, 94)
Monocillin I		(94)
Pseurotin A		(95)
Chamydophilone		(74)
Ketamine		(34)
Aurovertin D	Pyranones	(96, 97)
Aurovertin F		(96, 97)
Aurovertin E		(96, 97)
Aurovertin I		(96, 97)
Phomalactone		(70)

**Fig. 2.** Direct and indirect parasitism of *P. chlamydosporia*.

secondary metabolites and promotion of plant growth, *P. chlamydosporia* emerges as a beacon of hope in the fight against nematode-induced crop losses. Let's cultivate this alliance and pave the way for a greener, more resilient agricultural future.

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Authors' contributions

SB conceptualized the review structure, collected and reviewed the literature and wrote the initial draft of the manuscript. SN¹ supervised the overall development of the review, provided critical revisions and coordinated the final manuscript submission. AB contributed to the framing of the biological mechanisms and critically reviewed the content related to nematode suppression. TG contributed insights on fungal biology and reviewed the plant-pathogen interaction sections. SA reviewed entomological aspects and contributed to the biocontrol mechanism sections. SN² contributed to the molecular pathway insights and critically revised the bioinformatics and gene expression-related content. All authors read and approved the final manuscript. [SN¹ stands for Swarnakumari Narayanan and SN² stands for Saranya Nallusamy].

Compliance with ethical standards

Conflict of interest: The Authors do not have any conflict of interest to declare.

Ethical issues: None.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Grammarly in order to improve the language and readability. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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