

REVIEW

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# Application of fungi as biological control strategies for nematode management in horticultural crops

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## Abstract

Plant-parasitic nematodes are a major problem for horticultural production, causing significant economic losses. Chemical nematicides are a common nematode control strategy but can negatively impact the environment and human health. In this review, we provide an overview of the use of fungi for the biological control of plant-parasitic nematodes in horticultural crops. Fungal bio-control represents an alternative, environmentally friendly strategy for managing nematodes. The use of fungi for the bio-control of nematodes has gained increasing attention due to the potential benefits of selectivity, sustainability, and long-term control. Here, we discuss the different types of fungi used for nematode management, the mechanisms of their action, the advantages and limitations of using fungi for bio-control, and the factors affecting their efficacy. Additionally, we provide several case studies of fungal bio-control against root-knot, cyst, and lesion nematodes in horticultural crops. The review concludes with a discussion of future directions and research recommendations for implementing fungal bio-control in horticultural crops.

**Keywords** Fungi, Biological control, Nematode, Horticultural crops, Long-term control

## Background

Plant nematodes are the most common phytopathogens, comprising 80–90% of eukaryotic soil microbiota (Rueda-Ramírez et al. 2022; Khan 2023). They can, however, also seriously harm crops, causing large losses for the agricultural and horticulture sectors. Over 4100 plant-parasitic nematodes (PPN) species have been found. A few genera are major plant pathogens, whereas others affect a limited range of crops and significantly impact economically important crops. Plant nematodes are suspected of being responsible for a forecasted 12.3% (\$157 billion)

decrease in worldwide output. Crop roots are infected by plant-parasitic nematodes, which feed on the root tissues and interfere with the intake of nutrients and water (Sikder and Vestergård 2020). This may cause wilting, yellowing, stunted growth, and lower yields. The impact of nematode damage on crops is exacerbated by the fact that some nematode species are also plant virus vectors (Hoysted et al. 2017; Desmedt et al. 2020).

Numerous nematode management techniques have been developed for the long-standing recognition of nematodes' negative effects on crops and soil health. The potential viability of these tactics may be compromised due to their economic inefficiency, as well as the potential loss of resistance over time. This resistance is attributed to the significant diversity seen in the parasitism genes of nematodes, along with the ongoing challenge of identifying plant nematode resistance genes. The use of chemical nematicides, which have historically been utilized to control nematodes, is being questioned more and more

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because of worries about the effects on the environment and the emergence of resistance (Desaeger et al. 2020; Poveda et al. 2020; Sasanelli et al. 2021). The suppression of cyst nematode populations can be achieved by using many taxonomically varied antagonistic fungi widely distributed throughout the fungal kingdom. This accumulation of fungi can ensnare and parasitize nematodes (Nordbring-Hertz et al. 2001; Saxena 2018). A specific subset of these fungi, known as egg parasites, exhibits a parasitic relationship with stationary PPNs by targeting their eggs and female individuals. This sub-group infects the host using individual hyphae or specialized infection structures such as the appressoria (Ashrafi et al. 2017). The female individuals of cyst nematodes provide a viable target for possible assault by nematophagous fungi. During nematode development, an immature female destroys the roots, matures, lays eggs, and eventually dies as a cyst; this cyst can persist in the soil as an infective agent for several years without a host plant. This procedure results in an extended duration of female and cyst nematodes being subjected to various species of egg-parasitic fungi (Ashrafi et al. 2017; Haj Nuaima et al. 2021).

A number of these fungi have been shown to exhibit a multifunctional lifestyle in the context of interactions. Some fungi (*Lecanicillium lecanii*, *Pochonia chlamydosporia*, and *Purpureocillium lilacinum*) exist as endophytes of the host plant while also acting as pathogens for nematodes or insects (Schouten 2016). Some other species of fungi (*Exophiala pisciphila* and *Pyrenochaeta terrestris*) parasitize the nematode eggs (Chen and Chen 2002). Recent studies reported the endophytic fungi *Exophiala salmonis* and *Polydomus karssenii* from the roots of *Paris polyphylla* and *E. radices* from the roots of *Microthlaspi perfoliatum* (Wang et al. 2013; Maciá-Vicente et al. 2016; Ashrafi et al. 2023). Similarly, *Polyphilus frankenii* and *Polyphilus sieberi* have been used as nematode antagonistic fungi (Wennrich et al. 2023). Two new species under consideration are *Laburnicola nematophilus* and *L. radiciphila*, which show endophytic interactions with plant roots and parasitic interactions with nematode eggs (Knapp et al. 2022). Consequently, there is an increasing interest in developing ecologically acceptable and sustainable strategies for nematode control, such as bio-control employing fungi and other soil bacteria (Abd-Elgawad and Askary 2018; Bhat et al. 2023). In this review, we will examine the role of fungi in controlling nematodes in soil and crops, explore the mechanisms of nematocidal action, and discuss the advantages and limitations of using fungi for nematode management.

#### Lifecycle of nematodes and their damage to crops

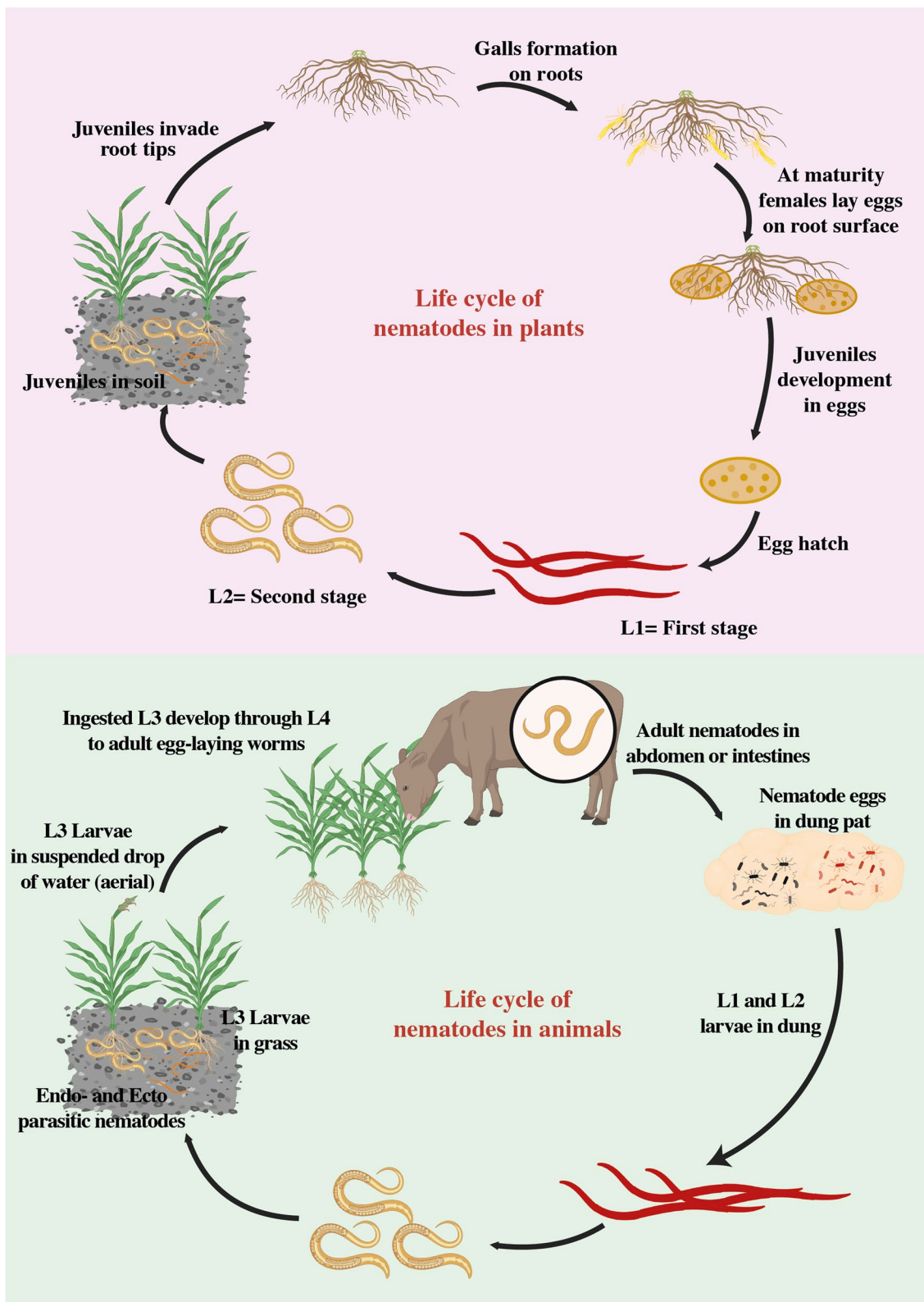
Nematodes are a highly diverse and abundant group of organisms that belong to the phylum Nematoda. The life

cycle of nematodes is a complex process that comprises several stages, including one embryonic stage, four to five larval phases, and an adult stage (Fig. 1). The body size of larvae grows with each molt, finally attaining sexually mature adult size. First is the egg stage, during which the adult nematode reproduces sexually or asexually, laying eggs that are either fertilized or unfertilized. The eggs of nematodes are typically small, oval-shaped, and covered in a protective layer (Mathison and Pritt 2018). Second is the larva stage, during which the eggs hatch into larvae, which emerge from the egg as small, worm-like organisms. The larvae have a body structure similar to that of the adult nematode but smaller in size. They may go through several molts before reaching the next stage (Poinar 2012). Third, as the larvae continue to grow, they eventually reach the juvenile stage. During this stage, the larvae mature into young adult nematodes. This stage is characterized by the development of reproductive structures and the ability to reproduce (Hand et al. 2016; Karp 2021). In the final stage of the life cycle, the adult nematode reproduces and lays eggs, starting the cycle again (Mkandawire et al. 2022). The adult nematode is responsible for perpetuating the species and maintaining the population. In addition to these stages, some species have additional life cycle stages, such as the infective stage. This stage occurs in parasitic nematodes and is characterized by the development of specialized structures (white cysts and crystal structure) that allow the nematode to infect its host and reproduce (Gang and Hallem 2016; Vlaar et al. 2021).

Many nematodes can cause significant damage to horticultural crops, such as vegetables, fruits, and ornamental plants (Table 1). Numerous ways exist for nematodes to destroy crops. Some nematode species are plant parasites that feed on crop roots, damaging the root system and impairing the plant's capacity to absorb water and nutrients, leading to the plant's eventual death (Pulavarty et al. 2021). Some other nematode species can result in the establishment of galls, which are swollen, deformed growths that appear on the roots or stems of crops. Galls prevent plants from absorbing water and nutrients, which causes stunted growth and decreases yields (Bernard et al. 2017). Additionally, some species of nematodes act as vectors, transmitting plant pathogens from one plant to another and causing soil-borne diseases that reduce crop yields and lead to plant death (Gamalero and Glick 2020; Wielkopolan et al. 2021).

#### Fungi as biological control agents

Bio-control is a strategy used to manage pests and diseases in agriculture and horticulture by utilizing natural predators and pathogens to control pest populations. In the context of managing nematodes, bio-control refers to



**Fig. 1** The general life cycle of nematodes under various environments

**Table 1** Prevalence and diversity of nematode-induced diseases in horticultural crops

Nematode disease	Scientific name	Affected crops	Symptoms	References
Root knot nematode	<i>Meloidogyne</i> spp.	Tomato, pepper, cucumber, eggplant, beans, melons, squash, and many other crops	Stunted growth, yellowing of leaves, wilting, root galls	(Philbrick et al. 2020; Sikandar et al. 2020; Hajji-Hedfi et al. 2022)
Citrus nematode	<i>Tylenchulus semipenetrans</i>	Citrus trees	Stunted growth, yellowing leaves, root damage, fruit drop	(Verdejo-Lucas and McKenry 2004; Nasir et al. 2021)
Northern root knot nematode	<i>Meloidogyne hapla</i>	Carrots, beets, parsnips, lettuce, spinach, onions, and other crops	Stunted growth, reduced yield, root galls	(Hussain and Zouhar 2017)
Columbia lance nematode	<i>Hoplolaimus columbus</i>	Turfgrass, ornamentals, vegetables	Stunted growth, chlorosis, root damage	(Garcia et al. 2022)
Sting nematode	<i>Belonolaimus longicaudatus</i>	Sweet potato, turfgrass, strawberry	Root damage, plants become stunted, wilt, and with a severe infestation, die.	(Grabau et al. 2022)

the use of nematode-trapping fungi, bacteria, and other nematode-parasitic organisms (Table 2). Nematodes are preyed upon by these natural predators, which lower their population and limit crop damage (Nyaku et al. 2017; Liang et al. 2019; Zhang et al. 2020). Incorporation of fungi into cropping systems can be an effective way to reduce nematode populations and improve plant health (Collange et al. 2011). Fungi have adopted several different mechanisms against nematodes.

#### Direct mechanisms employed by fungi to combat nematodes

There are reportedly over 100,000 species of fungi, and there are undoubtedly many more that have yet to be found and identified. Among them, a small group of microfungi that can capture, kill, and digest nematodes are called nematophagous fungi (NF) (Nordbring-Hertz et al. 2001). They live on the exterior or interior of the host organism, exploiting it for nutrition. Nematophagous fungi are crucial agents that balance the nematode population by parasitizing, capturing, and poisoning in the natural world. They use particular traps for catching, conidia for adhering, and hyphae tips for parasitizing females and eggs or generating toxins to attack nematodes (Fig. 2). On this basis, the NFs have been traditionally categorized into four groups: (1) predatory fungi use specialized structures, (2) egg parasitic fungi invade nematode eggs or females with their hyphal tips, (3) endoparasitic fungi use their spores, and (4) toxin-producing fungi immobilize nematodes before invasion (Liu et al. 2009; Abd-Elgawad and Askary 2018; Rahman et al. 2023). G protein-coupled receptors are the most common conserved signaling pathway involved in trap formation in response to several environmental stimuli. The

G protein  $\beta$  subunit *gpb1* mutant in *C. elegans* exhibits impaired functionality, particularly affecting trap formation (Li et al. 2007; Yang et al. 2020). G protein receptors coordinate with mitogen-activated protein kinases (MAPK) in trap formation. One of MAPK cascade SLT2 was found to be involved in trap formation in filamentous fungi *A. oligospora* (Zhen et al. 2018). The cAMP-dependent protein kinase A signaling pathway is also involved in trap formation. The downstream genes of the cAMP/PKA pathway were downregulated in *ras2* and *rheb* mutants (Yang et al. 2021).

#### Predatory fungi

Predatory fungi use specialized hyphal structures as traps to capture nematodes (Fig. 3). The nematode's cuticle is damaged by the traps produced by the mycelium of the fungi. The hyphae spread throughout the interior of the worm body and create a penetration peg. Eventually, the hyphae develop over the exterior of the colonized nematodes (Nordbring-Hertz et al. 2001). Adhesive branches, adhesive networks, adhesive knobs, constricting rings, and non-constricting rings are all structures (Fig. 3) used by the trapping fungi to entrap nematodes (Jiang et al. 2017). Compared to regular hyphae, adhesive traps have a longer lifespan (Bedeckovic and Brand 2022). These structures (traps) are used by over two hundred species of fungi (spread among the Zygomycota, Basidiomycota, and Ascomycota) to catch free-living nematodes in soil (Liu et al. 2009). More than 80% of the nematode-trapping fungi in the Ascomycota belong to the Orbiliaceae family; however, due to relatively inadequate isolation and culture methods, nematode-trapping fungi within Zygomycota have not been well studied (Saikawa 2011).

**Table 2** Fungi as bio-control agents against nematodes in horticultural crops

Fungi Name	Horticultural Crops	Affective against Nematodes	Mode of Action	References
<i>Acremonium strictum</i> , <i>Trichoderma harzianum</i> , <i>P. lilacinus</i> , <i>P. marquandii</i> , <i>Dactylaria brochopaga</i> (NDDb-15), <i>Drechslerella dactyloides</i> (NDAd-05), <i>Duddingtonia flagrans</i>	Tomato ( <i>Solanum lycopersicum</i> )	<i>Meloidogyne incognita</i> , <i>M. paranaensis</i>	Possessed both egg parasitic or opportunistic and toxic properties, Use of predatory trapping and volatile organic compounds (VOCs), Activation of the phenylpropanoid pathway in the root apoplast, which is involved in defense	(Sexton and Howlett 2006; Goswami et al. 2008; Singh et al. 2019; Mei et al. 2021)
<i>Exophiala</i> spp., <i>P. chlamydosporia</i> , <i>Pyrenochaeta</i> spp. <i>T. harzianum</i>	Sugar beet ( <i>Beta vulgaris</i> )	<i>Heterodera schachtii</i>	Efficient in parasitizing the eggs of the nematode	(Haj Nuaima et al. 2021)
<i>Trichoderma viride</i> <i>P. lilacinus</i>	Turnip ( <i>Brassica rapa</i> ) Turmeric ( <i>Curcuma longa</i> )	<i>M. incognita</i> <i>M. incognita</i>	Enhanced resistance level and development in turnip Parasitized the nematode eggs and juveniles	(Ibrahim et al. 2012) (Niranjana Prabhu et al. 2018)
<i>Arthrobotrys dactyloides</i> , <i>A. oligospora</i> <i>P. lilacinum</i> , <i>P. chlamydosporia</i>	Ginger ( <i>Zingiber officinale</i> ) Cardamom ( <i>Elettaria cardamomum</i> )	<i>M. incognita</i> <i>Meloidogyne</i> Spp.	Nematode-trapping Reduction in root-knot formation and promoted the highest yield of cardamom	(Peiris et al. 2018) (Sathyan et al. 2021)
<i>Verticillium chlamydosporium</i> strains (Vc-10 and Vc-2 M) <i>P. chlamydosporia</i>	Celery ( <i>Apium graveolens</i> ) Potato ( <i>Solanum tuberosum</i> )	<i>M. incognita</i> <i>M. incognita</i> , <i>Heterodera</i> spp., <i>Globodera</i> spp. <i>M. incognita</i>	Egg parasite Reduction in eggs and juveniles of nematodes Parasitized the egg masses	(Nyongesa 2002) (Muthulakshmi et al. 2012) (Mittal et al. 1995)
<i>Trichoderma</i> isolates (Tvc1, Tvc2 and Thc) <i>T. harzianum</i>	Eggplant ( <i>Solanum melongena</i> ) Cabbage ( <i>Brassica oleracea</i> var. <i>capitata</i> ) Pea ( <i>Pisum sativum</i> )	<i>M. incognita</i> <i>M. incognita</i> <i>M. incognita</i>	Effective in inhibition of egg hatching ability of root-knot nematode, egg parasite Effective in reducing the number of galls, egg masses, and final nematode population in soil	(Loganathan et al. 2010; Liang et al. 2020) (Brahma and Borah 2016)
<i>P. lilacinus</i> , <i>Paecilomyces</i> spp.	Cucumber ( <i>Cucumis sativus</i> ) Lettuce ( <i>Lactuca sativa</i> )	<i>M. incognita</i> <i>M. hapla</i> ,	Highest inhibition to gall formation and production of compounds affecting motility of the second stage Reduced root gallings and increased lettuce head weight	(Yan et al. 2011; Nesha and Siddiqui 2017) (Chen et al. 2000)
<i>P. marquandii</i> , <i>Streptomyces costaricanus</i> <i>P. lilacinus</i> , <i>Aspergillus niger</i> , <i>Pochonia chlamydosporia</i> var. Pc-10 (Pc-10)	Carrot ( <i>Daucus carota</i> )	<i>M. javanica</i> , <i>M. incognita</i>	Maximum reduction in gallings and nematode multiplication in carrot and improves carrot quality and yield	(Bontempo et al. 2014; Nesha and Siddiqui 2017)

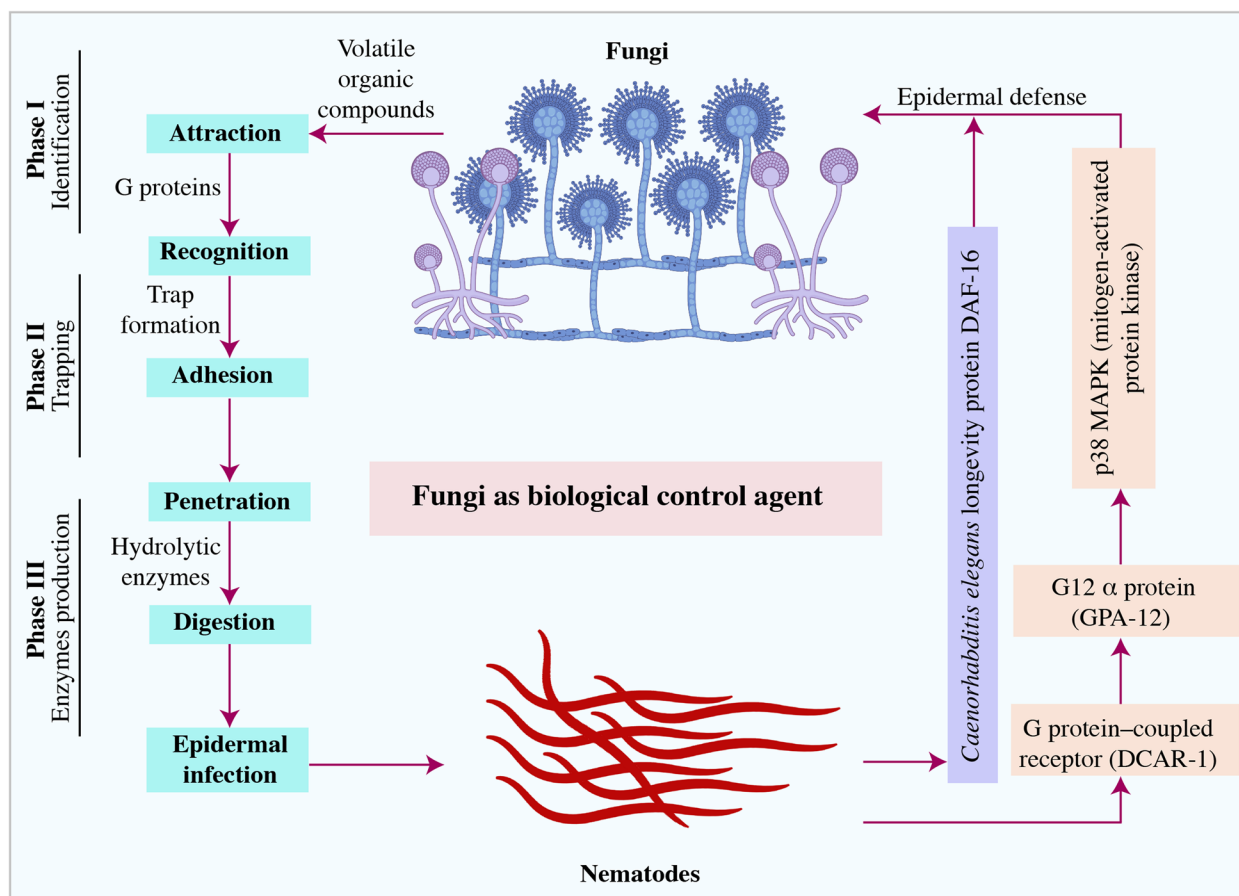


**Table 2** (continued)

Fungi Name	Horticultural Crops	Affective against Nematodes	Mode of Action	References
<i>Arbuscular mycorrhizal fungi</i> (AMF, Septoglomus deserticola, Funneliformis mosseae), Vesicular Arbuscular Mycorrhizae, Pochonia hallamydosporea	Pepper ( <i>Piper nigrum</i> )	<i>Glomus fasciculatum</i> , <i>Pratylenchus coffea</i> , <i>M. incognita</i>	Inhibiting nematode infection, enhancing growth and fruit yield of pepper genotypes, inhibiting egg hatching of root-knot nematodes (RKN) in spice crops	(Nair et al. 2022; Saad et al. 2022; Udo et al. 2023)
<i>P. chlamydosporia</i>	Okra ( <i>Abelmoschus esculentus</i> )	<i>M. incognita</i>	Suppressed the galling, egg production, and soil population	(Dhawan and Satyendra 2009)
<i>Trichoderma viride</i>	Gotukola ( <i>Centella asiatica</i> )	<i>Meloidogyne</i> spp.	Reduction of RKN gall formation	(Shamalie et al. 2011)
<i>Pichia gliuilliermondii</i> Moh 10, <i>Pachytrichospora transvaalensis</i> Y-1240, <i>Candida albicans</i> Moh Y-5, <i>Geotichum terrestre</i> Y 2162, <i>Glomus versiforme</i> .	Grapes ( <i>Vitis vinifera</i> )	<i>M. incognita</i>	The induction of a defense response, including the up-regulation of the class III chitinase gene <i>VCH3</i> , significantly reduced the number of juveniles and disease under greenhouse conditions, similarly reduced populations	(Li et al. 2006; Hashem et al. 2008)
<i>Fusarium oxysporum</i> strain 162 (Fo162)	Melon ( <i>Cucumis melo</i> )	<i>M. incognita</i>	Reduced early root penetration of parasitic nematode	(Menjivar et al. 2011)
<i>Acaulospora longula</i> , <i>Claroideoglomus claroideum</i>	Apple ( <i>Malus pumila</i> )	<i>Pratylenchus penetrans</i>	Colonization of the roots of apple seedlings by AMF species and nematode reduction in the soil of the seedlings	(Ceustermans et al. 2018; Kanfra et al. 2022)
<i>P. lilacinus</i> , <i>Hirsutella rhossiliensis</i> , <i>Glomus mosseae</i>	Cherry ( <i>Prunus avium</i> )	<i>M. javanica</i> , <i>Meloidogyne</i> spp.	The highest reduction percentage in nematode population achieved and significantly suppressed the number of galls and egg masses	(Abo-Korah 2017)
<i>P. lilacinus</i> , <i>Pseudomonas fluorescens</i>	Papaya ( <i>Carica papaya</i> L.)	<i>R. reniformis</i> , <i>M. incognita</i>	Reduced the root population	(Rao 2008)
<i>T. harzianum</i>	Guava ( <i>Psidium guajava</i> )	<i>M. enterolobii</i>	Reduced the number of <i>M. enterolobii</i> in both soil and roots	(Jindapunnapat et al. 2013)
<i>P. chlamydosporia</i> , <i>P. lilacinum</i> , <i>T. harzianum</i> , <i>T. viride</i> , <i>Glomus intraradices</i> , <i>G. mosseae</i> , <i>Glomus etunicatum</i>	Peach ( <i>Prunus persica</i> )	<i>M. javanica</i>	Suppression of root-knot nematode reproduction, exhibited effectiveness by significantly reducing the number of egg masses, eggs per egg mass, and reproductive factors	(Calvet et al. 2001; Saeed et al. 2023)
<i>P. lilacinum</i> (strain AUMC 10.620), <i>G. mosseae</i>	Citrus ( <i>Citrus</i> spp.)	<i>Tylenchulus semipenetrans</i> , <i>Tylenchulus semipenetrans</i>	Highest reduction percentage against citrus nematode, effectively reduced larval activity and egg hatching	(Sweelam et al. 2019; El-Marzoky et al. 2023)

**Table 2** (continued)

Fungi Name	Horticultural Crops	Affective against Nematodes	Mode of Action	References
<i>P. marquandii</i> , <i>P. lilacinus</i>	Banana ( <i>Musa acuminata</i> )	<i>Radopholus similis</i> , <i>Helicotylenchus multicinctus</i> ,	As an effective biocontrol agent, the suppression of <i>R. similis</i> was observed in banana and promoted banana height, leaf numbers, healthy root weight, and reduced the number of nematodes	(Esnard et al. 1998; Mendoza et al. 2007)
<i>P. chlamydosporia</i> strains (Pcc10, Pcc60C and Pcc20)	Pistachio ( <i>Pistacia vera</i> )	<i>M. javanica</i>	All strains infected and parasitized nematode eggs on the roots of pistachio plants to varying degrees	(Ebadi et al. 2018)
<i>F. verticilliods</i>	Pomegranate ( <i>Punica granatum</i> )	<i>M. javanica</i>	Culture filtrate showed the highest mortality percentage of <i>M. javanica</i>	(El-Qurashi et al. 2019)
<i>P. lilacinus</i> , <i>P. chlamydosporia</i>	Gerbera ( <i>Gerbera jamesonii</i> )	<i>M. incognita</i>	Significantly reduced populations of <i>M. incognita</i> , suppressed infection and mortality of plants	(Nagesh and Reddy 2005)
<i>Penicillium citrinum</i>	Rose ( <i>Rosa hybrida</i> )	<i>M. javanica</i>	Significantly decreased the viable juveniles, eggs count and increased hatching inhibition, indicating that sufficient production (unknown) happened in potato dextrosebroth	(Baazeem et al. 2022)
<i>P. lilacinum</i> , <i>H. rhossiliensis</i>	Gladiolus <i>grandiflorus</i>	<i>M. incognita</i>	<i>P. lilacinum</i> parasite on <i>M. incognita</i> eggs and <i>H. rhossiliensis</i> on second-stage juvenile of nematode in <i>G. grandiflorus</i>	(Abokora 2021)
<i>P. chlamydosporia</i> , <i>T. harzianum</i>	Tuberose ( <i>Polygonum tuberosum</i> )	<i>M. incognita</i>	significantly decreased the incidence of root-knot nematode and increased the number of florets/spikes and spikes/plot in Tuberose ( <i>Polygonum tuberosum</i> )	(Rao et al. 2003)
<i>A. niger</i> F22	Watermelon ( <i>Citrullus lanatus</i> )	<i>M. incognita</i>	The culture filtrate exhibited high activity against <i>M. incognita</i> , resulting in significant mortality of second-stage juveniles (J2s) and inhibition of egg hatching due to production of oxalic acid	(Jang et al. 2016)
<i>A. oligospora</i>	Spinach ( <i>Spinacea oleracea</i> ).	<i>M. incognita</i>	Reduced the number of root-knot nematode	



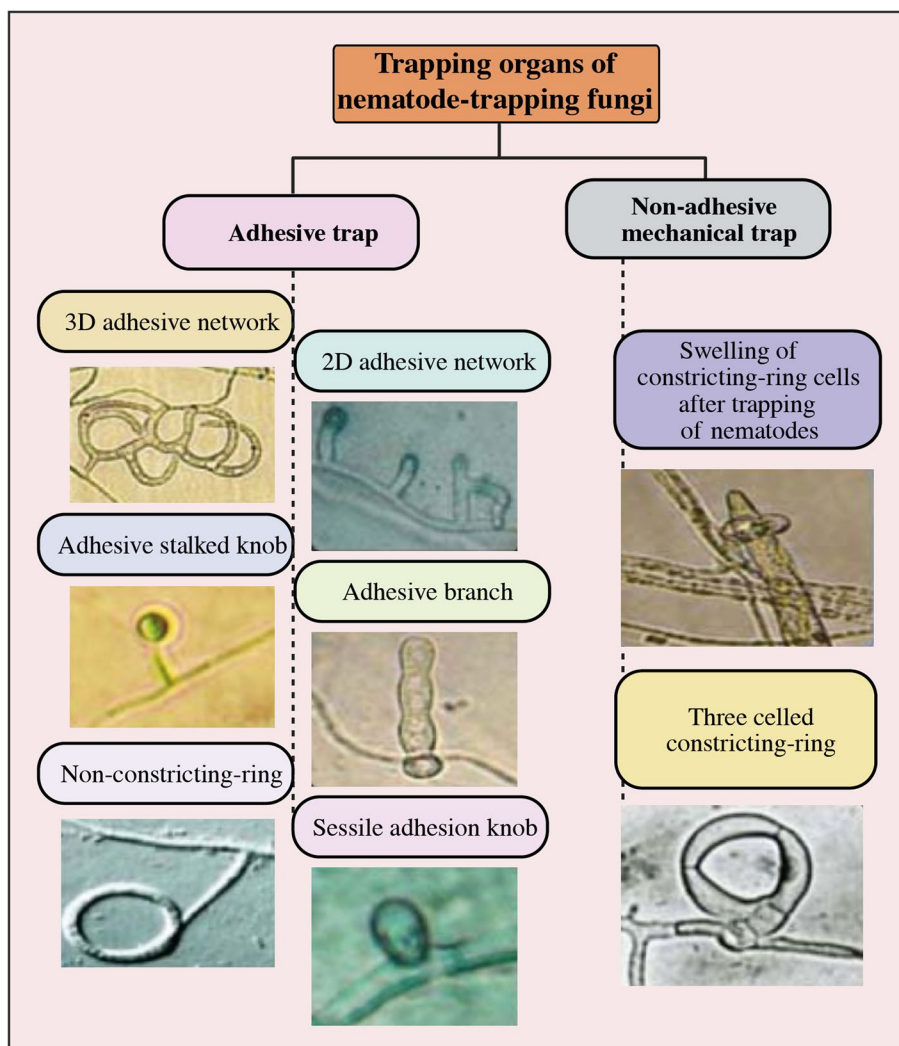
**Fig. 2** Mechanism of fungi as a bio-control against nematodes. Dendritic cell activating receptor (DCAR1), a part of the defense mechanism, is a G protein-coupled receptor that binds to endogenous ligand 4-hydroxyphenyl lactic acid (HPLA), which activates G12 α protein. This protein undergoes activation via the conserved p38 mitogen-activated protein kinase (MAPK) pathway to produce antimicrobial peptides released in the epidermis of the nematode (Zugasti et al. 2014)

**Adhesive branches** Adhesive branches, also known as adhesive columns, are the simplest trapping organs in terms of morphology. These branches consist of one to three cells that simply join to form adhesive rings or networks with two dimensions that look like crochet or lines. The nematodes are trapped if they come into contact at any point with the thin adhesive layer that completely envelops these branches. As these branches are often close together, a nematode will quickly become attached to other branches during the struggle to break free. These are typical trapping mechanisms of *Monacrosporium cionopagum* and *Monacrosporium gephyrophagum* (Saxena 2018). *Dactylella cionopaga* is the most commonly isolated species from temperate soils with sticky branches (Poinar 2012). *M. cionopagum* produces sticky branches that trap and immobilize the sugar beet cyst nematode *Heterodera schachtii* (Anderson et al. 2014). Similarly, *Gamsylella gephyropaga*

produces adhesive branches to trap nematodes (Zhang et al. 2014).

**Adhesive hyphal network** An adhesive network is a highly dispersed trap formed by a vertical lateral branch that consists of three-dimensional complex networks and develops and grows 20–25 μm from the primary hypha (Niu and Zhang 2011). Adhesive networks are formed by bending a single lateral branch and can fuse with parental hyphae. More lateral hyphae are produced from the parental hyphae, or the loop is formed to produce more loops. Nematodes are attracted to the surface of the network, which is covered with a fine layer of adhesive. *A. oligospora* is the most common species of fungi found to form this type of trapping structure worldwide (Wang et al. 2023).





**Fig. 3** Predatory fungi employ different morphological structures to capture nematodes. Two types of traps (adhesive and non-adhesive) are usually used by fungi

**Adhesive knobs** Adhesive or sticky knobs are morphologically unique cells covered with an adhesive film. When the nematode comes into contact with the adhesive mass, which has formed a thick pad, the fungus takes over, significantly increasing the attachment area and ensuring that the captured nematode is firmly bound. The penetration of fungus into the nematode body is a combination of enzymatic and physical activity. For example, the synthesis of collagenase may help the fungus to penetrate the nematode’s cuticle, but the added strength and hardness of attachment provided by the thick sticky pad is necessary if the penetrating hyphae are to reach the cuticle (Poinar 2012). Assimilative hyphae then emerge from the newly formed globular infection bulb to consume the nematode’s internal organs

(Bahadur 2021). *Dactylellina arcuata*, *D. copepodii*, *Dactylella asthenopaga*, and *D. ellipospora* produce adhesive knobs to capture nematodes (Jiang et al. 2017). Similarly, All Basidiomycota-trapping fungi use spores and adhesive knobs (Thorn et al. 2000).

**Non-constricting rings** Non-constricting rings are three-celled rings that grow on a slender support stem from prostrate septate hyphae. They are passive in the process of nematode predation. The point of contact between the stalk and the ring was found to be weakened during the nematode’s struggle to escape, and the ring often breaks off, suggesting that the fungus wants the captured nematode to escape with the non-constricting ring, which is tightly wrapped around the prey body.

This appears to be a preferred method of achieving wide dispersal in the soil (Poveda et al. 2020). Fungi that produce non-constricting rings, such as *Dactylaria candida* and *Dactylella lysipaga*, often form sticky knobs and capture nematodes through non-constricting rings (Wu et al. 2012). A similar pattern has been observed with *Drechslerella daliensis* (Su et al. 2008).

**Constricting rings** Constricting rings are circular hyphal branches, usually consisting of three cells. They are the most sophisticated traps and actively capture prey. When a nematode enters the ring, the three cells quickly triple their volume, seal the ring, and hold the nematode in place. Hyphae then enter the body and consume the nematode (Liu et al. 2012). The volume of the cells forming the ring is likely to increase as a result of rapid water uptake (Feng et al. 2016). The mega-traps of *D. brochopaga* mutants are rings eight times the size of normal traps, and it was found that each cell releases drops of fluid at the expense of cell volume (Liu et al. 2012). Water from the atmosphere can easily move in and out of these cells by changing the relative humidity of the environment. There is also a relationship between the ambient humidity and the frequency of ring closures. It has been investigated that the water source is mainly exogenous, although it is initiated by stem cells or mycelium (Liu et al. 2022). This view is supported by the discovery that rings can continue to spread effectively even after being detached from the initial source (stem) over which they first developed (Barron and Thorn 1987). Moreover, there was no visible movement of intracellular components after stalk cell closure, suggesting that water is reserved for the atmosphere. This hypothesis is reasonable, as live worms are typically covered by a thin layer of water, which may provide sufficient fluid for ring closure. In addition to physical methods of inflation, chemical induction of ring closure has also been observed in *D. brochopaga* (Dowsett et al. 1977), whose traps expanded within 10 to 15 seconds when cultures of this fungus were exposed to solutions containing methanol, ethanol, propanol, butanol, or chlorobutanol vapor. On the other hand, benzene, ether, and chloroform had no effects, suggesting that some unknown factors controlled this extraordinary event (Zachariah 1989). Twelve species of hyphomycetes have been identified as forming constricting rings, varying in size from 20 to 40  $\mu\text{m}$  internal diameter (Poinar 2012).

#### **Egg and female parasitic fungi**

These fungi use appressoria, lateral mycelial branches, and penetrating pegs to parasitize eggs, females, and other growth stages of PPNs (Lopes et al. 2021). The

parasitism of ten isolates of *Pochonia chlamydosporia* was assessed in vitro against the eggs of *Globodera pallida*, with pathogenicity ranging from 34 to 49%. Impulsive hatching was observed when *P. chlamydosporia* isolates parasitized immature eggs more aggressively than eggs with second-stage juveniles. The efficacy of *Beauveria bassiana* 08F04 on *Heterodera filipjevi* in vitro was investigated, and significant differences in growth rate and bio-control potential were found between some of the transformants, mainly G10. Also, the use of wild-type *Beauveria bassiana* 08F04 and transformant G10 significantly minimized the population of cereal cyst nematodes (female) in the roots (Zhang et al. 2020). Similarly, in a greenhouse experiment, the AMF *Glomus etunicatum* on *Heterodera glycines* caused a 28% reduction in female nematodes in the root systems of mycorrhizal plants, compared to the untreated roots, suggesting that *G. etunicatum* encourages host plants to tolerate the presence of the soybean cyst nematode (SCN) (Benedetti et al. 2021).

#### **Endoparasitic fungi**

Endoparasitic fungi produce spores (conidia, zoospores) to infect nematodes. The spores either are ingested by nematodes or adhere to the nematode epidermis before the infection (Braga and de Araújo 2014; Zhang et al. 2020). *Drechmeria coniospora* is a nematode-aggressive endoparasitic fungus. The strain YMF1.01759 had high infection efficiency against nematodes. It inhibited egg hatching, infected nematodes with spores, and produced active metabolites to kill nematodes (Wan et al. 2021). In greenhouse experiments, *D. coniospora* can reduce the number of root-knot nematodes forming galls on tomatoes and alfalfa (Liu et al. 2009; Wan et al. 2021). Studies have shown variation in the number of conidia produced by fungi on a single infected nematode. *D. coniospora* fungi produce a large number of conidia compared to hyphal material, which produces 10,000 conidia, and *Hirsutiella rhossoliensis* produces 100–1000 conidia on each infected nematode. Upon infection, conidia rapidly geminate, and assimilative hyphae grow and ultimately penetrate the outer layer of nematodes and enter their body.

#### **Toxin production**

Some nematophagous fungi produce toxins that kill nematodes. Toxin-producing fungi come from a wide range of orders and families. The fungus attacks nematodes without physical contact by secreting inhibitory metabolites. Once the nematodes immobilized, the hyphae penetrate their cuticle. Fungi that produce toxins are mostly basidiomycetes. Many *Pleurotus* species produce toxins with nematotoxic activity. For example, *P. ostreatus* produces trans-2-decanoic acid, a compound derived from

linoleic acid that is toxic to insects, nematodes, and other fungi. It is important to note that basidiomycetes are not the only fungi that produce such toxins; certain fungi produce toxins that are harmful to nematodes but are not nematophagous. These compounds have a wide range of chemical properties, including simple fatty acids and other organic acids such as lactone pyrones, anthraquinones, benzoquinones, alkaloids, furans, peptaibiotics, and cyclodepsipeptides. The mechanisms of these toxins against nematodes are diverse and multifaceted, as shown by recent studies on the basidiomycetous fungi (*Coprinus comatus* and *Stropharia rugosoannulata*) (Luo et al. 2006).

#### **Enzymes of NF**

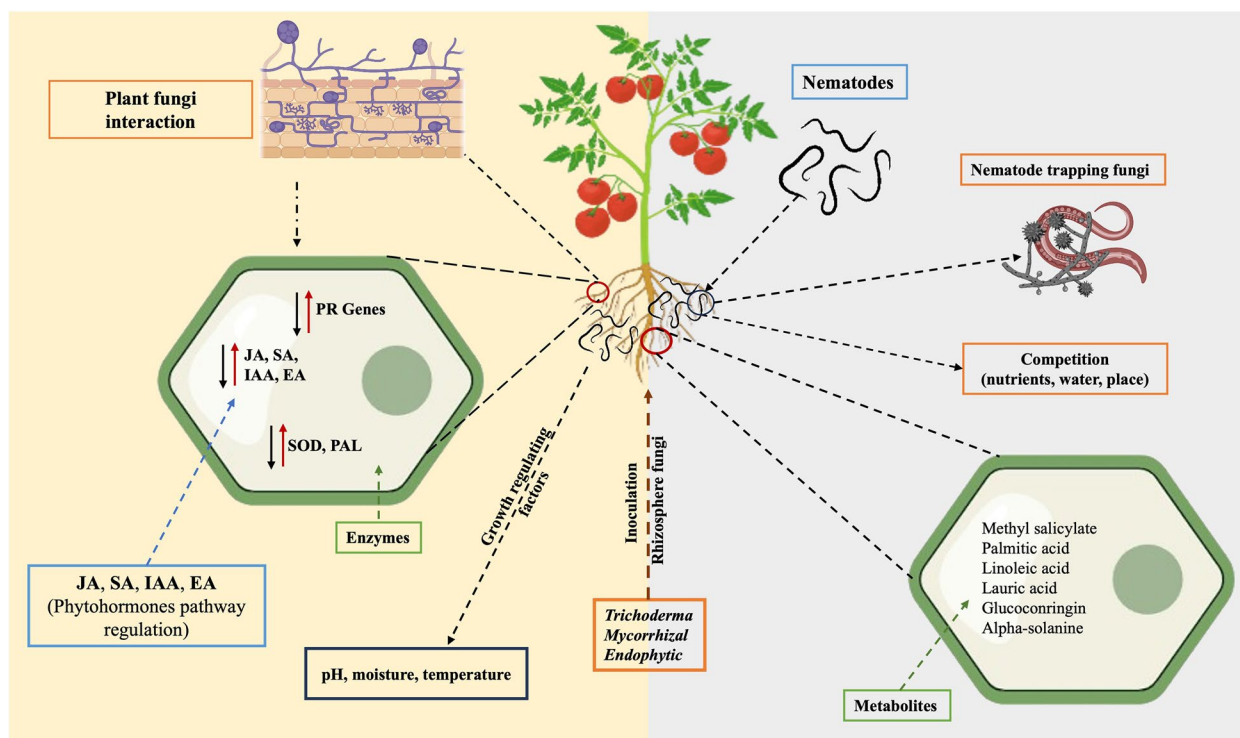
Physical barriers are present in the composition of nematodes, protecting them from the activities of natural predators (Ekino et al. 2017). NF can overcome this barrier by penetrating the nematode cuticle and eggshell using mechanical and enzymatic (protease and chitinase) means (Liang et al. 2010). There is an abundance of proteins belonging to these enzymes. The key enzymes involved in cuticle degradation are alkaline and neutral serine proteases, which catalyze the hydrolysis of the peptide bonds of cuticle proteins (Rao et al. 1998). Serine proteases hydrolyze peptide bonds by using a specifically triggered serine residue in the substrate-binding pocket (Siezen and Leunissen 1997). Alkaline serine protease induced cuticle destruction within hours and inhibited the nematode *Panagrellus redivivus* (Yang et al. 2005). Neutral serine protease produced by *A. oligospora* can control *Haemonchus contortus* and *Caenorhabditis elegans in vitro* (Junwei et al. 2013). High levels of serine protease produced by the fungus *Monacrosporium thaumasium* are destructive to *Meloidogyne javanica* eggs (de Souza Gouveia et al. 2017). Serine protease is, therefore, a vital enzyme in the fungus-initiated infection process. In addition, the shell of nematode eggs is rich in chitin and proteins. Endochitinases and exochitinases catalyze the hydrolysis of glycosidic linkages between the N-acetylglucosamine groups of chitins (Tikhonov et al. 2002). *M. thaumasium* is an NF that produces chitinases and showed nematocidal activity against the nematode *Panagrellus redivivus* (de Freitas Soares et al. 2014; Soares et al. 2015). Furthermore, these enzymes have shown nematocidal activity alone in the absence of fungi (Soares et al. 2015). Thus, chitinases also play an important role in infection and the digestion of shells (Khan et al. 2004).

#### **Fungal-induced defense against nematodes**

Some fungal species, such as *Trichoderma*, mycorrhizal, and endophytic fungi, can induce plant resistance against nematodes. This is an indirect mechanism

that fungi mitigate the harm caused by plant-parasitic nematodes (Martinez-Medina et al. 2016; Kubicek et al. 2019). *Trichoderma's* alteration in transcripts, proteins, and metabolites leads to systemic defense stimulation, enhancing the plant's immunological response for quicker reactions to future pathogen attacks. As a result, the likelihood of the disease spreading is reduced (Mendoza-Mendoza et al. 2018). This induced systematic resistance (ISR) is controlled by the hormone (JA/ET/SA) signaling pathways (Fig. 4). SA signaling is reduced during the first phases of *M. javanica* infection in tomato roots. Conversely, the response mediated by JA/ET is stimulated in tomato roots treated with the fungus, suggesting that *Trichoderma* triggers the activation of ISR inside the plant (Martínez-Medina et al. 2017). However, new research has shown that the SA route plays an active role in this regulation (Jogaiah et al. 2018).

Mycorrhizal fungi can also activate ISR in plants, protecting against nematodes, as evaluated by multiple studies (Vos et al. 2012a; Xu et al. 2019). The introduction of *Funneliformis mosseae* to tomato roots decreased infection rates of *M. incognita* and *Pratylenchus penetrans* by modifying the release of substances from the roots. These mechanisms involve the activation of specific genes responsible for encoding chitinases, PR (pathogenesis-related) proteins, enzymes that aid in the detoxification of ROS (which accumulate due to nematode-induced cell hypertrophy and death), such as glutathione S-transferase and superoxide dismutase (SOD) (Sharma and Sharma 2017; Balestrini et al. 2019). Similarly, the split root system methodology has been utilized to study systemic resistance caused by endophytic fungi, such as *F. oxysporum* against *M. incognita* in tomatoes and bananas against *Radopholus similis* (El-Fattah Adnan Dababat and Alexander Sikora 2007; Martinuz et al. 2015). Root nematodes may be effectively controlled with the help of bio-control microorganisms. The endophytic fungi that possess the ability to produce nematotoxic metabolites have significant promise as viable biocontrol agents. By lowering nematode penetration, postponing development, or limiting reproductive potential, these fungi can efficiently inhibit and suppress nematodes (Grabka et al. 2022). Endophytic fungi such as *Acremonium sclerotigenum* (Yao et al. 2023), *Neotyphodium coenophialum* (Choi et al. 2022), and *Chaetomium globosum* (Bairwa et al. 2023) play pivotal roles in regulating nematode pathogenesis in various crops. The fungi and nematodes compete for space and nutrients in the soil as both are required for survival. Metabolites released by plants are also overtaken by fungi and nematodes for their survival. Nematodes do not decompose organic matter but act as parasites for plants, while fungi decompose organic matter available to plants (Brady et al. 2008). The plants take



**Fig. 4** Mechanisms of *Trichoderma*, mycorrhizal, and endophytic fungi benefiting plants against nematodes. JA (Jasmonic acid), SA (salicylic acid), IAA (indole-3-acetic acid), and EA (ethyl acetate) are hormones released, and SOD (superoxide dismutase) and PAL (phenylalanine ammonia-lyase) are enzymes released by plants due to the expression of pathogenesis-related (PR) genes as a result of plant and fungi association which protect the plant against nematodes. Plants provide metabolites, and the fungi and nematodes compete against each other for nutrients, water, and space in the soil

deep roots to allocate carbon and other nutrients to horizontal soil volume (Iversen et al. 2011).

#### Biological control against nematodes in horticultural crops

Fungal bio-control has been studied and applied in various horticultural crops with promising results. Many notable case studies have been reported. For example, the application of certain fungi *P. lilacinus* in tomatoes can effectively reduce populations of root-knot nematodes, resulting in improved plant growth and yield (Moreno-Gavira et al. 2020; Giri et al. 2022). In another study of tomatoes, a strain of the fungus *Verticillium chlamydsporium* has been found to control root-knot nematodes effectively. This fungus colonizes the roots and nematode galls, reducing the nematode population and improving plant health. One study showed that the application of the fungal species *T. harzianum* and *Gliocladium virens* in tomato crops reduced root-knot nematode populations and improved plant growth and yield (Khan et al. 2022; Tyśkiewicz et al. 2022). Additionally, *Phanerochaete chrysosporium* has been used to control the population of nematodes (Du et al. 2020). In carrots, the use of the fungus *G. virens* has been shown to reduce populations

of dagger nematodes, resulting in healthier and more productive crops (Villate et al. 2012). Similarly, in strawberries, the application of fungal bio-control agents (*Aureobasidium pullulans*) has effectively reduced populations of root-lesion nematodes, leading to improved plant growth and fruit yield (Hong et al. 2022). Thus, the application of the fungus can significantly reduce nematode populations and improve plant growth and yield.

In controlling cyst nematodes, the fungus *P. lilacinum* has been shown to infect and parasitize the nematode eggs, effectively reducing the hatching rate and nematode population in the soil (Rumbos et al. 2008). The fungal species *H. rhossiliensis* has been shown to control potato cyst nematodes (Gartner et al. 2021; Dubovskiy et al. 2023). In ornamental crops, such as roses and chrysanthemums, strains of the fungus *P. lilacinum* have been found to control root-knot nematodes effectively (Sánchez and Cardona 2018).

#### Fungal control against root-knot nematodes

Root-knot nematodes are one of the most destructive plant-parasitic nematode species, causing extensive damage to root systems and reducing crop yields. The fungus



*Metarhizium anisopliae* has been shown to effectively control root-knot nematodes in tomato, cucumber, and eggplant crops (Youssef et al. 2020; Panyasiri et al. 2022). Besides, *P. lilacinum* is commonly used to control root-knot nematodes in tomatoes, pepper, and cucumber (Osman et al. 2020), and *Verticillium lecanii* has been shown to suppress root-knot nematodes in several vegetable and ornamental crops (Uddin et al. 2023). Additionally, several *Trichoderma* species have been used to suppress root-knot nematodes in tomatoes and other crops (d'Errico et al. 2022); *Coniothyrium minitans* has been successfully used in several crops, including tomatoes, cotton, and peanuts (Forghani and Hajihassani 2020); *Pasteuria penetrans* species, which can infect the root-knot nematode larvae and form spores inside the nematode body (Kariuki and Dickson 2007), has been demonstrated to be efficient at lowering root-knot nematode populations in crops like tomatoes, peppers, and cotton. The genus *Arthrobotrys* spp., containing numerous species that produce sticky traps to capture and eliminate root-knot nematodes, has been demonstrated to lower nematode numbers in crops like tomatoes and cotton (Philbrick et al. 2020).

#### Fungal control against cyst nematodes

Cyst nematodes cause severe economic loss and are a pest of several crops worldwide. Fungus bio-control has also been used to suppress cyst nematode populations, *G. virens* have been used for bio-control of cyst nematodes in a variety of crops, including potato, cotton, and soybean. *Trichoderma* species can reduce populations of cyst nematodes in crops such as tomatoes and cotton (Khan et al. 2022; Mhatre et al. 2022). *Penicillium funiculosum* has also been used to reduce populations of cyst nematodes in tomato and cucumber crops (Martinez-Beringola et al. 2013). Other examples include *Pythium oligandrum*, which has been used for bio-control of cyst nematodes in crops such as tomato and cotton (Luca et al. 2022), *Coniothyrium minitans* in crops such as soybean and potato (Sun et al. 2022), *Hirsutella minnesotensis* in crops such as soybean and potato (Sun et al. 2015), and *Metarhizium anisopliae* in a variety of crops including cotton, soybean, and tomato (Liu et al. 2022).

#### Fungal control against root-lesion nematodes

The majority of root-lesion nematodes' habitat is within plant roots, making them difficult biological control targets (Stirling 1991). However, using biological control of nematodes in potatoes is promising, although its use in agriculture is restricted, and its efficacy is unknown (Palomares-Rius et al. 2014). Several "trapping" fungi have been studied for their potential biological control of *P. penetrans*, including *A. oligospora*, *H. rhossiliensis*,

*Monacrosporium ellipsosporum*, *Verticillium balanoides*, *Drechmeria coniospora*, and *Nematoctonus* spp. that produce adhesive conidia; however, only *H. rhossiliensis* (24–25% reduction of population) has proven to be successful in potatoes (Timper and Brodie 1993). In a different investigation, *H. rhossiliensis* similarly suppressed nematode penetration, resulting in a 25% reduction in *P. penetrans* penetration of potato roots (Timper and Brodie 1994). Similarly, the quantity of *Pratylenchus brachyurus* per gram of root in pineapple was considerably reduced by the arbuscular endomycorrhizal *Glomus* spp. injected with pineapple microplants (Guillemin et al. 1994). Another study examined the effects of AMF on nematodes. Potted apple seedlings were modified with several AMF species in the presence of nematode *P. penetrans*. A positive relationship was found between the percentages of root length when colonized by AMF species, while a significant reduction of nematodes in the soil of the apple seedlings was observed (Ceustermans et al. 2018). Additionally, the development of carrots was inhibited by the root-lesion nematode *P. penetrans*; however, the soil densities of *P. penetrans* were reduced by 49% through soil inoculation with *Glomus* spp. spores (Talavera et al. 2001), and similarly, *G. mosseae* systematically reduced the soil densities of *P. penetrans* in tomatoes (Vos et al. 2012b). Moreover, AMF mitigated the damage caused by *Pratylenchus coffeae* to banana cultivars (*Musa* spp.) in their roots (Elsen et al. 2003a, b). These case studies demonstrate the potential of fungal bio-control as a valuable tool in managing plant-parasitic nematodes in horticultural crops and suggest that further research and development in this field could lead to even more widespread adoption of this approach.

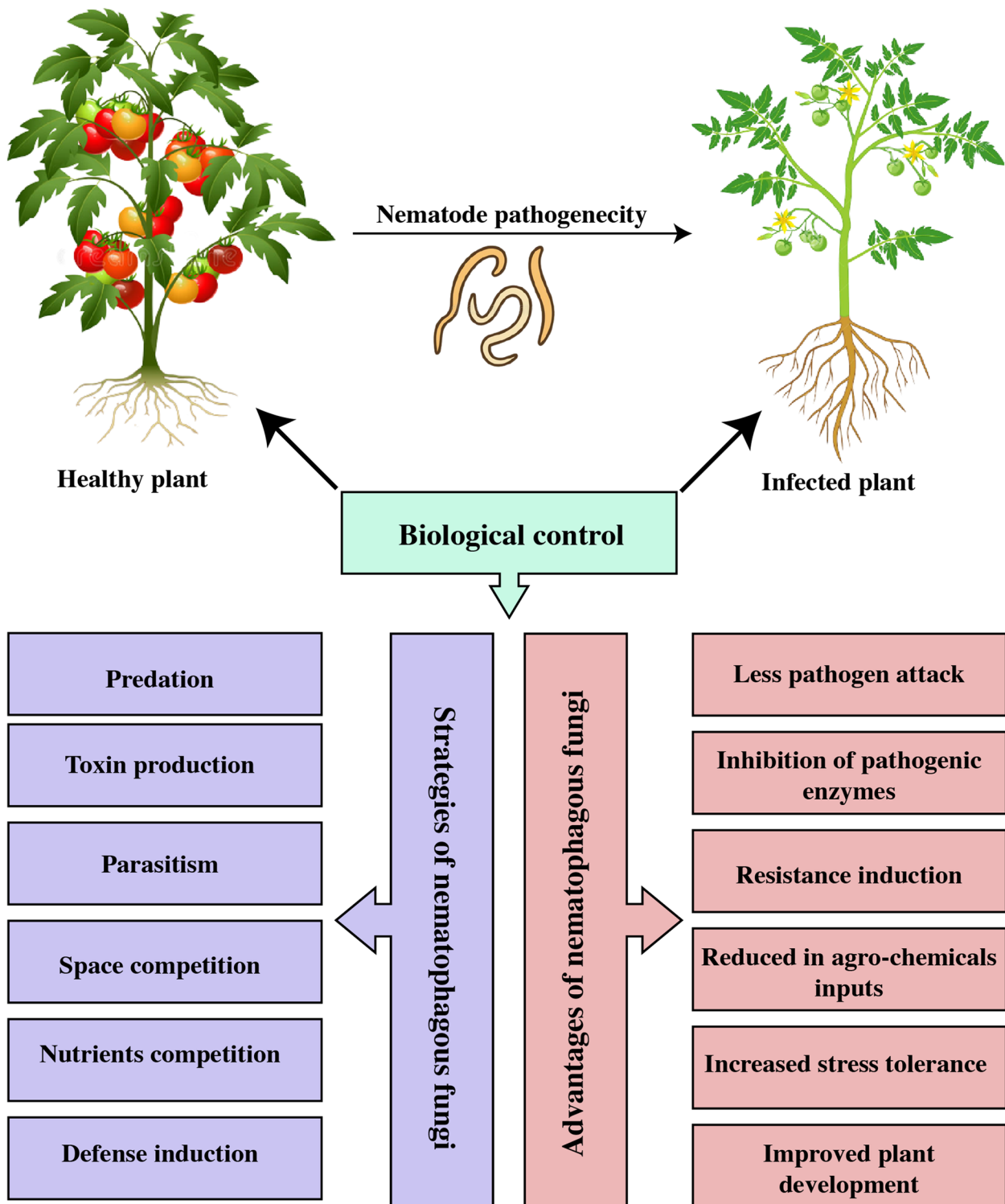
#### Advantages of using fungi for biological control

Using fungi as nematode control agents has several advantages over chemical or physical control methods (Fig. 5). The advantages of using fungi for bio-control include selectivity, environmental safety, long-term effectiveness, sustainability, and compatibility with other management strategies, which are discussed separately below.

#### Selectivity and environmental safety

One of the most significant benefits of bio-control is its specificity. In contrast to chemical control approaches, which can be dangerous to a broad variety of organisms, fungi can selectively target and control nematode populations, lowering the potential of injury to non-target organisms such as beneficial microorganisms, insects, pollinators, and wildlife (Sandhu et al. 2012; Gill et al. 2014; Sponsler et al. 2019). This is important because these non-target organisms play important roles in soil





**Fig. 5** Essential mechanisms involved in the biological suppression of plant nematocidal infection by fungal antagonists. Antibodies, enzymes, secondary metabolites, nutrients, mycoparasitism, and space are the factors where nematodes and fungi compete with each other and act as biological controls for plant safety and development. The advantages of biological control include less pathogen attack, increased resistance and stress tolerance, better plant development, reduced agro-chemical inputs, and inhibition of pathogenic enzymes

health and productivity, such as breaking down organic matter, cycling nutrients, and maintaining soil structure or other biodiversity. These organisms are expected not to be killed by pesticides. Fungal selectivity also helps reduce the risk of developing nematode populations resistant to bio-control agents (Khan et al. 2022). When nematodes are exposed to non-selective nematicides, they may develop resistance over time, making it more difficult to manage them in the future (Lima et al. 2018; Wram et al. 2022). However, using fungal bio-control agents, which are specific to nematodes, it is less likely that they will develop resistance. Fungal selectivity is a major benefit of using fungal bio-control agents for managing plant-parasitic nematodes (Liarzi et al. 2016). Due to the specificity, fungal bio-control agents are generally more environmentally friendly than chemical control.

#### **Long-term effectiveness**

Fungal bio-control can provide long-term control of plant-parasitic nematodes (Balla et al. 2021), which helps reduce the need for repeated applications and improve the sustainability of agricultural systems. Fungal bio-control provides long-term control of plant-parasitic nematodes through several mechanisms. First, they can persist in the soil for extended periods, allowing them to infect and control nematodes continuously over time (Usta 2013). This persistence is attributed to the ability of some fungal species to form resistant structures, such as spores and sclerotia, which can survive in the soil for long periods. Second, fungal bio-control agents can reproduce and spread in the soil, allowing them to reach new areas and infect additional nematodes (Loulou et al. 2022). This reproduction helps maintain and increase the population of fungal bio-control agents in the soil over time, providing a long-term source of control for nematodes. Third, fungal bio-control agents can induce systemic resistance in plants, helping reduce the impact of nematode-feeding damage. By inducing systemic resistance, fungal bio-control agents protect plants from future nematode infections and provide long-term control of nematodes (Walters et al. 2013; Fontana et al. 2021). Finally, the integration of fungal bio-control with other nematode management strategies, such as cultural practices and chemical nematicides, can help to improve the efficacy and sustainability of nematode management in crops (Devi 2018; Yigezu Wendimu 2021).

#### **Sustainability**

Fungal bio-control is economically sustainable, particularly in the long term, as the fungi can persist in the soil and control nematode populations over multiple cropping cycles (Dutta et al. 2019; Forghani and Hajihassani 2020). Additionally, fungal bio-control is often less

labor-intensive and requires fewer inputs, such as fertilizer, water, and energy, than chemical control (Chaudhary et al. 2022). The use of fungi can help maintain soil health by preserving soil structure, improving nutrient cycling, and promoting the growth of beneficial microorganisms (Chamkhi et al. 2022). Taken together with other advantages shown above, fungal bio-control is a sustainable management strategy that offers environmental, economic, and agronomic benefits.

#### **Compatibility with other management strategies**

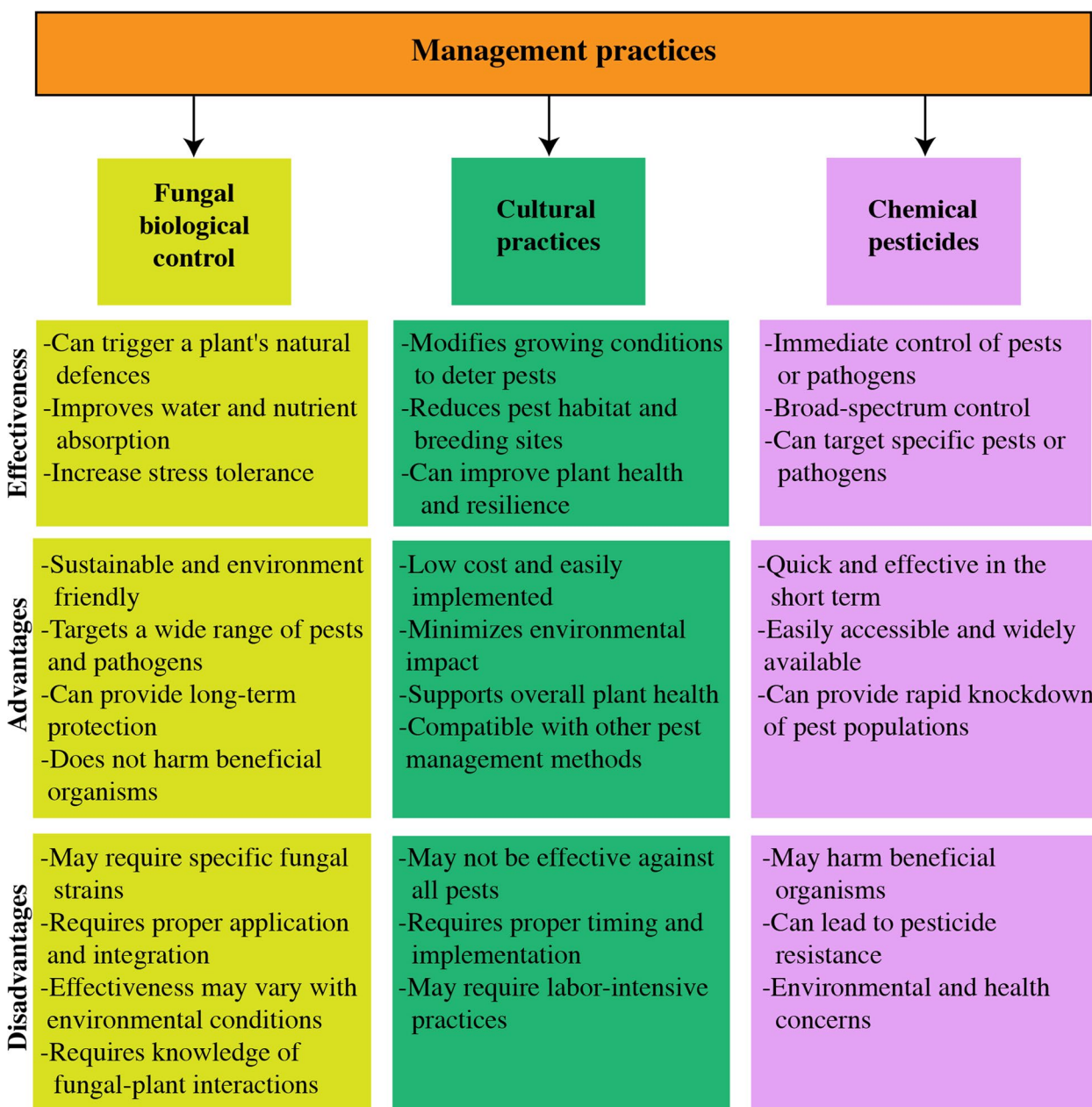
Fungal bio-control can be combined with other nematode management strategies, such as crop rotation, resistant varieties, and chemical nematicides. The integration of multiple management strategies allows for a more comprehensive approach to controlling nematodes, reducing the risk of developing nematode populations resistant to any single control method (Fourie et al. 2016). For example, using a combination of cultural practices, such as crop rotation and nematode-resistant varieties, with fungal bio-control can help reduce the nematode population in the soil over time (Xiang et al. 2018). Cultural practices can help reduce the number of nematodes in the soil, creating a less favorable environment for nematode survival and reproduction, while fungal bio-control agents can directly control nematodes and help maintain the reduced nematode population (El-Saadony et al. 2021). Another example is the integration of fungal bio-control with chemical nematicides. Chemical nematicides provide quick and effective control of nematodes in the short term, while fungal bio-control can help reduce the nematode population over the long term (Abd-Elgawad 2020). This combination can help reduce the required chemical nematicides (Kawanobe et al. 2019; Gowda et al. 2022). Finally, fungal bio-control agents can also be used with biostimulants, such as compost and microbial inoculants, which can help improve soil health and plant growth while also reducing nematode populations (Naik et al. 2020; Aioub et al. 2022; Jindo et al. 2022).

#### **Factors limiting the efficacy of fungal biological control**

The efficacy of fungal bio-control agents as a nematode management strategy depends on several factors, which can significantly limit the ability of the fungi to reduce nematode populations and improve plant health. These factors must be considered when deciding on the most appropriate management strategy for controlling plant-parasitic nematodes (Fig. 6). Some key factors affecting the efficacy of fungal bio-control are discussed below.

#### **Environmental conditions**

Environmental conditions, such as temperature, moisture, and light, can considerably influence the efficacy of



**Fig. 6** A comparison of fungal and other management (cultural and chemical) shows fungal bio-control's effectiveness

fungal bio-control agents (Velásquez et al. 2018; Bamisile et al. 2021). For example, changes in these conditions can affect the growth and activity of fungal agents, leading to variations in their efficacy. High temperatures or low moisture levels can reduce the growth and viability of fungal agents, while high moisture levels can increase the risk of fungal disease and reduce their efficacy (Mohapatra et al. 2017; Davies et al. 2021). Additionally, some fungi may be sensitive to light and may perform poorly in brightly light areas, which can limit their use in some

crops or growing regions (Losi and Gärtner 2021). Environmental sensitivity can bring out inconsistent performance (Chandler et al. 2011).

Soil characteristics, such as pH, nutrient content, and texture, also affect the efficacy of fungal bio-control agents (Neina 2019; Scavo et al. 2019; Sharma et al. 2021). Fungal bio-control agents may perform poorly in soils with low moisture levels, as the fungi require a certain level of moisture to grow and reproduce (Dannon et al. 2020; Stenberg et al. 2021). Similarly, some fungi

require specific nutrients to grow and reproduce effectively (Kowalska et al. 2022), so they may not work well in a barren field. The pH of the soil can affect the performance of fungal bio-control agents, as some fungi prefer slightly acidic or alkaline soils, while others perform best in neutral soils (Zhang et al. 2016; Msimbira and Smith 2020). In addition, soil structure, such as the presence of organic matter, can also influence fungal performance by changing the penetration and persistence of the fungal agents in the soil (Meurer et al. 2020).

In general, if the fungi are not well-suited to the environmental conditions of the crop or growing region, they may not establish well or effectively control nematode populations. Some fungi may require specific temperature or moisture conditions to grow and control nematodes, and if these conditions are not present, the fungi may not perform well. Therefore, it is important to consider the environmental conditions and select fungal bio-control agents well-suited to the specific soil and environmental conditions of the target area.

#### **Nematode diversity and abundance**

Nematode diversity and abundance play a significant role in the efficacy of fungal bio-control of plant-parasitic nematodes. A high level of nematode diversity can reduce the efficacy of fungal bio-control agents, as different nematode species may have different levels of susceptibility to the fungal agents (Chanu et al. 2015; Garcia et al. 2022). In addition, high nematode abundance can increase the challenge of controlling nematode populations, as a large number of nematodes can quickly repopulate the soil and reduce the impact of the fungal bio-control agent (Büttner et al. 2021; Sukhanova et al. 2022). This information can help select the most appropriate fungal bio-control agent and determine the best application rate and timing to achieve the desired level of nematode control.

#### **Crop management practices**

Crop management practices, such as tillage, fertilization, and pest management, also impact the efficacy of fungal bio-control agents (Manik et al. 2019; Pirttilä et al. 2021). Certain practices, including tillage or heavy pesticide use, may disturb or kill the fungi, reducing their effectiveness, while other practices, such as reduced tillage or integrated pest management, help maintain and promote fungal populations, their distribution, and longevity (Alyokhin et al. 2020; Kumar et al. 2021; Orrù et al. 2021). Crop rotation is reported to result in an altered nematode population density (Rueda-Ramírez et al. 2022). Growing crops that are not hosts for particular nematode species lowers their numbers and enhances the effectiveness of fungus-based bio-control treatments.

The kind and quantity of fertilizer used on the crops affect how well nematodes are controlled by biological agents (El-Saadony et al. 2022). A high-nutrient environment caused by excessive use of fertilizer may encourage the establishment of nematodes and lessen the effectiveness of fungal bio-control treatments (Zin and Badaluddin 2020). Irrigation techniques influence soil moisture levels, whose impact on the effectiveness of bio-control agents has been discussed above (Café-Filho et al. 2018; Lüneberg et al. 2019). The growth and reproduction of fungal bio-control agents can be aided by maintaining the ideal soil moisture levels through proper watering techniques.

#### **Limitations of using fungi for biological control**

Fungi typically take time to establish in the soil, colonize roots, and reduce nematode populations (Molinari et al. 2022). Furthermore, the inconsistency or slow-acting performance of fungal agents often makes it difficult for farmers to predict the outcome of fungal bio-control applications. Another affecting factor is the cost. Currently, chemical nematicides are often cheaper and more readily available. However, the production, formulation, and distribution of fungal bio-control agents are often complex and time-consuming, and therefore their costs can be passed on to growers and farmers (Mawar et al. 2021). Additionally, the cost of fungal bio-control agents can be influenced by factors such as the availability and cost of the raw materials used to produce the fungi, the size of the market for fungal bio-control, and the levels of competition among suppliers (Daou et al. 2021).

Additionally, some fungal bio-control agents may be subject to regulatory restrictions. Regulatory hurdles can include requirements for the registration of fungal bio-control agents, the approval of their use for specific crops, and the establishment of performance standards (Palmieri et al. 2022). These requirements can be time-consuming, complex, and costly to meet, and they can limit the availability and feasibility of fungal bio-control agents for farmers. Taken together, all these factors or limitations can have a significant impact on their effectiveness as bio-control agents for plant-parasitic nematodes.

#### **Future directions and research recommendations**

Further research is needed to identify the most effective fungi for controlling certain nematode pests in horticultural crops. To optimize their integration into pest management programs, it is necessary to conduct studies to determine the compatibility of fungal bio-control agents with other nematode management strategies, such as chemical treatments. It is crucial to create scalable, affordable manufacturing techniques for fungal



bio-control agents to make this strategy more available and useful for growers. For fungal bio-control products to operate better in the field, it is important to understand how environmental factors like temperature and moisture affect their efficiency. More investigation is required to determine the long-term effects of fungal bio-control on nematode populations and plant health to guarantee that fungal bio-control is sustainable as a management method. New and efficient procedures for identifying and quantifying fungal bio-control agents in soil and plant tissues must be developed to track their effectiveness and enhance their application in the field. It is also important to perform studies to assess the capability of fungal bio-control in various agricultural systems and to ascertain its applicability to varied agro-ecological circumstances. The future of fungal bio-control as a viable and successful management technique against nematode pests in horticulture crops will be secured by implementing these suggestions.

## Conclusion

This review discussed using fungi as a bio-control agent against plant-parasitic nematodes and how fungi can effectively reduce nematode populations and improve plant health in horticulture crops. The emphasis was given to thoroughly detail the key elements, including environmental circumstances, nematode diversity and abundance, soil properties, and crop management practices that may impact the effectiveness of fungal bio-control. Several case studies have also been detailed, including fungi that control cyst, root-knot, and lesion nematodes. We also discussed the pros and cons of employing fungi for biocontrol and concluded that despite certain drawbacks, using fungi for bio-control can be a viable and efficient method for controlling plant-parasitic nematodes in horticulture crops when correctly combined with other management practices. Future studies should emphasize the importance of the complexity of microbial communities in soil and their interactions with other soil biotas to properly comprehend their potential for bio-control.

## Abbreviations

ISR	Induced systemic resistance
JA	Jasmonic acid
MIR	Mycorrhizal induced resistance
NF	Nematophagous fungi
SA	Salicylic acid
SAR	Systemic acquired resistance
SLs	Strigolactones (SLs)

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## Authors' contributions

The idea was gestated by MR and FB. MR and MU drafted, and FB revised the manuscript. XZ visualized and updated the figures. FB supervised the whole study and helped with funding. All authors carefully read and approved the article for submission.

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## Availability of data and materials

All the data is presented in the main text file.

## Declarations

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analysis, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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