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Harnessing Useful Rhizosphere Microorganisms for Nematode Control

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Abstract

Nematodes are very diverse and parasitize various plants including vegetables, and their management is of concern. Biological control of nematodes provides an environmentally friendly management option and there are various micro-soil-borne organisms which can be considered for this purpose. The primary goal of this chapter is to provide a review on the progress made so far, in application of biological control agents in nematode management in vegetables, cereals, and root and tuber crops. This chapter will be divided into five (5) sections: (1) herbivore-induced plant volatiles, (2) root exudates and nematode control, (3) inhibitory metabolites in bacteria for nematode management, (4) fungi and symbiotic reprogramming in host cells, and (5) fungi antagonists of nematodes.

Keywords: arbuscular mycorrhizal fungi (AMF), biocontrol, volatile organic compounds (VOCs)

1. Introduction

Plant-parasitic nematodes (PPNs) represent serious threat to the world economy and are responsible for great losses in production systems worldwide [1]. In monetary terms, world agricultural economy losses are approximately \$215.8 billion annually, because of 12.6% crop loss inflicted on top 20 life-sustaining crops by PPN based on 2010–2013 production figures and prices. These figures do not cover all crops throughout the world especially crops produced in the developing countries which will probably exceed these estimates if combined. Therefore, nematode management is a major constraint in food security efforts worldwide. However, PPNs are difficult to control compared to other pests because nematodes mostly

inhabit the soil, and usually attack the underground parts of the plants [2]. Although chemical nematicides are effective, easy to apply, and show rapid effects, the growing dissatisfaction with chemical nematicides due to environmental and health issues has created redirections in the type and choice of applicable nematicides [3]. In view of these challenges posed by traditional nematicides, for the past 20 years the search for novel, environmentally friendly alternatives with which to manage PPN populations has therefore become increasingly important. The role of different beneficial microorganisms in the soil ranks high as environmentally friendly biological alternatives to synthetic nematicides [3].

Volatile compounds are emitted both by eukaryotes and by prokaryotes; these volatile organic compounds (VOCs) are lipophilic, with a molecular mass of about 300 Da or less, and a vapor pressure of 0.01 kPa. These chemicals evaporate easily and are produced through diffusion; however, other mechanisms (passive or active) for their emission and transmission exist [4]. Three chemical groups can be associated with the volatile compounds (terpenoids, phenylpropanoids, and fatty acid derivatives). Volatile compound penetration and movement in soils is greatly influenced by the mineral type, soil texture, and particle design [5]. The rhizosphere has within it various microorganisms because of its conducive environment; furthermore, about 20% of carbon can be released by roots [6]. Root exudates are made up of various chemical compounds, among these are amino acids and amides, organic acids, sugars, phenols, polysaccharides, secondary metabolites, and proteins [7]. Volatile metabolites effused in the soil could have an impact on the organism within the soil community. Mycorrhizal and non-mycorrhizal plants also release distinct root exudates which contain organic acids and sugars [8].

Plant-parasitic nematodes move toward their host and this phenomenon is important in agriculture [9]. Carbon dioxide is a root volatile with specific roles in luring plant-parasitic nematodes, for example, to their hosts *Meloidogyne incognita* [10], *Caenorhabditis elegans* [11], and *Ditylenchus dipsaci* [12]. In a previous study, a tracking system linked to a computer was implored to monitor the responses of second-stage juveniles of *M. incognita* exposed to carbon dioxide [10]. Results revealed a positive correlation among carbon dioxide concentration increase and nematode locomotion rate. Higher carbon dioxide concentrations (>10%) resulted in a reduction of nematode movement. In a second experiment, the movement of nematodes was monitored on a gradient, maintaining the carbon dioxide concentration constant. Thresholds were maintained either above or below 0.01% CO₂/cm. The migration rate under optimal CO₂ concentrations was 0.7 cm/h. Plants secrete chemicals, for example, benzaldehyde, thymol, limonene, neral, geranial, and carvacrol which are needed for defense against other pathogens in the soil [13–18]. These chemicals may have within them nematocidal properties.

2. Herbivore-induced plant volatiles

Herbivore-induced plant volatiles (HIPVs) are generated after a herbivore feeds on its host roots and their roles to attract nematodes and other predators are still been explored [19–21]. Lima bean (*Phaseolus lunatus*) releases volatiles after the feeding activities of spider mites (*Tetranychus urticae*); this volatile attracts *Phytoseiulus persimilis* which is a predatory mite [22].

Among the compounds present in the oral secretions of herbivores are volicitin and fatty acid amides, which stimulate volatile release in plants [23, 24].

The roles herbivores play in relation to nematode parasitism on plants have been investigated [25, 26]. Signals released from plant roots, which are also parasitized by insects, influence the actions of entomopathogenic nematodes (EPNs) [27, 28]. Feeding mechanisms of herbivores stimulate the release of EPN-attracting volatiles, especially in annual grasses [29]. A hybrid root stock "*Swingle citrumelo*" lures EPNs (*Steinernema diaprepesi*) toward its roots after parasitism by larval *Diaprepes abbreviatus* root weevils; this is because of the production of subterranean volatiles (terpenoid) [30]. The citrus nematode *Tylenchulus semipenetrans* is a devastating pest of citrus causing damage to about 8–12% of citrus species; however, higher infection rates (53–89%) have been observed on citrus in Florida [31]. This nematode life cycle has the second-stage juvenile (J2) as the most infective stage. These nematodes are attracted to citrus roots that have been parasitized by weevil larvae (*D. abbreviatus*) compared to non-parasitized plants [26]. In their experiment, the response of four entomopathogenic nematodes (*S. diaprepesi*, *S. carpocapsae*, *S. riobrave*, and *Heterorhabditis indica*) and a plant-parasitic nematode (*T. semipenetrans*) to *D. abbreviatus* parasitism on citrus root stocks (*Poncirus trifoliata*, *S. citrumelo* (*C. paradisi* × *P. trifoliata*), and *Citrus aurantium*) was investigated. Results revealed high nematode numbers that moved toward *S. citrumelo* weevil-infested roots, compared to the non-infested ones in spite of the foraging strategy implored by the nematode-foraging strategy and its trophic status. Further, parasitism or non-parasitism of *D. abbreviatus* on the citrus parent line *P. trifoliata* did not influence the attraction level of nematodes, because the nematode responses to the root stock were similar. Production of the volatile, pregeijerene was released after feeding activity by *D. abbreviatus* only within the root zone and absent in the upper portions of shoots. Feeding activity by the adult beetle (*D. abbreviatus*) on the shoots did not stimulate the production of pregeijerene; however, limonene was released. Within the *P. trifoliata* roots, pregeijerene was released; however, the feeding activity of *D. abbreviatus* had no influence in its production.

Maize root volatiles can be associated with the ability of entomopathogenic nematodes in controlling the western corn rootworm. The roots of maize release the volatile (*E*)- β -caryophyllene (E β C) after parasitism by the larvae of *Diabrotica virgifera virgifera*. This chemical, which is a sesquiterpene, serves as an attractant to some species of entomopathogenic nematodes [29, 32, 33]. The volatile (*E*)- β -caryophyllene (E β C) was investigated on the EPN *H. bacteriophora*, *H. megidis*, and *S. feltiae* against *D. v. virgifera* larvae in southern Hungary. The maize variety that released (*E*)- β -caryophyllene (E β C) was protected from *H. megidis* and *S. feltiae*.

The roots of cotton (*Gossypium herbaceum*) also emit terpenoid volatiles after the feeding activity of the larvae of the chrysomelid beetle *D. balteata* [25]. This sesquiterpenoid aristolene may be a useful volatile for attraction of the nematode *H. megidis*.

3. Root exudates and nematode control

Plant root exudates and their impact on root-knot nematode egg hatchability are an important development for nematode management. The chemicals within root exudates may either

attract or repel nematodes to their host roots. There is experimental evidence to show the influence of root exudates on nematode egg hatch [34–36]. There are specific signals which are generated from exudates of roots; these enable nematodes to be attracted to their hosts. Known compounds that attract second-stage juveniles to host roots include tannic acids, flavonoids, glycoside, fatty acids, and volatile organic molecules [37, 38]. Semiochemicals, for example, small lipophilic molecules produced from root exudates of tomato and rice, enable stylet movement into host cells [39].

Root exudates have within them organic acids and sugars which are generated from mycorrhizal and non-mycorrhizal plants [8]. Flavonoids [40], phenolic compounds [41], amino acids [42], and the plant hormone strigolactone [43] are also constituents of root exudates. Root exudates released by mycorrhizal plants have the potential of attracting *Pseudomonas fluorescens* [44] and the fungus *Trichoderma* spp. [45], both organisms poses nematicidal properties for biocontrol of nematodes [46, 47]. Tomato plants, which formed symbiosis with *Funneliformis mosseae*, had low juvenile numbers of *M. incognita* compared to control plots [48].

In a recent study, the impact of tomato root exudates on *M. incognita* was investigated. These exudates were obtained from the root stocks Baliya (highly resistant, HR), RS2 (moderately resistant, MR), and L-402 (highly susceptible, T). These had varying impacts on *M. incognita* egg hatch and the movements of the second-stage juveniles (J2) [49]. The various root exudates obtained from the tomato root stocks (HR, MR, and T strains) decreased *M. incognita* egg hatchability; furthermore, populations of J2 decreased with the highest mortality rate associated with exudates from the HR plants. There was a much higher repelling rate from the HR genotypes to *M. incognita* J2 compared to the other genotypes. However, exudates from the susceptible genotype (T) attracted the juveniles. *The root exudates are made up of varying constituents from the different AMF species* [50]. Microbial diversity occurring within soils is positively influenced by root exudates [51], and AMF in soils may also produce high facultative anaerobic bacteria, for example, *Streptomyces* species, and actinomycetes [52–54].

4. Soil bacteria and nematode control

Nematodes in soil are subject to infections by bacteria and fungi. This creates the possibility of using soil bacteria to control PPN [55–57]. An effective natural enemy of nematodes is nematophagous bacteria which are ubiquitous with wide host ranges. These organisms have been isolated from soil, plant tissues, cysts, and eggs of nematodes. They directly suppress the activities of nematodes through the production of antibiotics, toxins, as well as enzymes; they also compete for nutrients and space through parasitizing, and therefore provide systemic resistance for plant growth. Their activities promote plant growth through facilitating rhizosphere colonization and enhanced microbial antagonism. Antagonism may be direct, which might result from physical contact, or indirect, which includes activities that do not involve sensing or targeting the PPN. Nematophagous bacteria may be grouped into parasitic and non-parasitic bacteria, opportunistic parasitic bacteria, rhizobacteria, Cry protein-forming bacteria, endophytic bacteria, and symbiotic bacteria based on their mode of parasitism [58].

Biocontrol agents, for example, *Agrobacterium*, *Alcaligenes*, *Bacillus*, *Clostridium*, *Desulfovibrio*, *Pseudomonas*, *Serratia*, *Streptomyces*, and *Pasteuria penetrans* have potentials for nematode control, have shown great potential for the biological control of nematodes [59, 60]. Nematophagous bacteria affect nematodes by the following modes of action: parasitizing; producing toxins, antibiotics, or enzymes; interfering with nematode-plant-host recognition; competing for nutrients; inducing systemic resistance of plants; and promoting plant health [58].

Among microorganisms occurring in soil, only few have been identified as biocontrol agents for phytonematodes, and some species of fungi and bacteria are the most common parasites of nematodes [57]. Some bacteria are potent antagonists of phytonematodes, and currently some have been developed into commercial bionematicides which are being used to control on the field mainly in advanced countries [61] (**Table 1**). These nematophagous bacteria can be categorized into two groups based on their mechanisms of infection: (i) bacteria that are pathogenic to nematodes or nematode diseases producing bacteria and (ii) bacteria whose secretions or metabolic products are harmful to nematodes or the nematode toxin-producing bacteria. The genus *Pasteuria* are endospore forming which are parasites of nematodes and water fleas [62, 63]. The control of most economically important genera of phytonematodes using nematophagous bacteria has been associated with this genus—*Pasteuria*. The other group includes strains of *Agrobacterium radiobacter*, *Azotobacter chroococcum*, *Bacillus* spp., *Clostridium* spp., and *Streptomyces* spp.

Actinobacteria are a group of soil bacteria of importance as biocontrol agents with nematocidal properties [64–67]. The diversity and biocontrol ability of nematicidal actinobacteria have been investigated [67]. In their study, 200 soil samples were obtained from 20 provinces within China. Results revealed 4000 actinobacteria, and these isolates 533 (13.3%) and 488 (12.2%) have some nematicidal activities on the nematodes *Panagrellus redivivus* and *Bursaphelenchus xylophilus*, respectively. Actinobacteria are generally Gram positive bacteria, and have G+C content of >55%. There has been over 70% of bioactive compounds released by these microorganisms with their usage in agriculture and pharmaceutical industry. These organisms release lytic enzymes, and secondary metabolites. One group of metabolites are avermectins which are produced by *S. avermitilis* [68]. Avermectins are useful for nematode control [69]. A previous screen of 502 actinobacteria showed 15 of these with nematicidal impact on *P. redivivus*, a free-living nematode [65].

Streptomyces isolate (CR-43) from Costa Rica had inhibitory impacts on *C. elegans* after a laboratory experimentation [69]. Other studies conducted in the greenhouse showed CR-43 with the potential of reducing root galls on tomato inoculated with *M. incognita*. Furthermore, field studies in Puerto Rico revealed pepper and tomato plants that received CR-43 as treatments having the least gall numbers compared to controls. In an in vitro investigation, *Streptomyces* sp. (CMU-MH021), which is an actinomycete isolated from nematode-infested soils in Thailand, showed the release of secondary metabolites which prevented *M. incognita* egg hatch, and also a decrease in juvenile numbers [70]. The nematicidal properties of various culture filtrates were explored. The modified basal (MB) medium gave the highest activity against *M. incognita*. The broth microdilution technique was applied for understanding the nematicidal activity of fervenulin. Inhibitory concentrations for both egg hatch (30 µg/ml)

Product name	Microbial origin	Company or institution	Country	Nematode target	References
Econem	<i>Pasteuria usgae</i> (or <i>P. penetrans</i>)	Bayer Crop Science	Multinational	Sting (or root knot)	[76]
Avid 0.15EC (or Abamectin)	<i>Bacillus thuringiensis</i>	Syngenta Group company	Multinational	Root-knot and other nematodes	[190]
Bionem-WP, BioSafe-WP, and Chancellor-WP	<i>B. armus</i>	Agro Green	Multinational	Root-knot and other nematodes including	[190]
Nortica VOTIVO PONCHO/ VOTIVO	<i>B. armus</i>	Bayer CropScience	Multinational	<i>Heterodera avenae</i>	[76]
Deny Blue circle	<i>Burkholderia capacia</i>	Stine Microbial Wisconsin Products	USA	<i>Meloidogyne incognita</i>	[191]
Biostart®	<i>Bacillus subtilis</i>	Bio-Cat	USA	Root knot nematodes	[192]
BiostartL™	<i>B. laterosporus</i> , <i>B. ncheniformis</i> (mixture)	Rhcon-Vltova			
Nemix	<i>Bacillus subtilis</i> , <i>B. ncheniformis</i>	AgriLife/Chr. Hansen	Brazil		[192]
Nemaless	<i>Serratia marcescens</i>	Agricultural Research Centre	Giza, Egypt	Root-knot and other phytonematode	[193]
SHEATHGUARD (or Sudozone)	<i>Pseudomonas</i> , <i>P. fluorescens</i>	Agri Life (Ind Limited or Agri Land Biotech)	Hyderabad, India	Nematode such as root-knot, cyst and Citrus nematode	http://www.agrilife.in/biopestl_microrigin_sheathguard_pf.htm
Xlan Mile	<i>Bacillus cereus</i>	XlnYI Zhong kai Agro-Chemical Industry Co., Ltd	China	<i>Meloidogyne</i> spp. on vegetables	[194]
Pathway Consortia®	<i>Bacillus</i> spp., <i>Trichoderma</i> spp., <i>P. fluorescens</i> , <i>Streptomyces</i> spp.	Pathway Holdings	USA	Phytonematodes	[1]
Micronema	<i>Bacillus</i> sp., <i>Pseudomonas</i> sp., <i>Rhizobacterium</i> sp., <i>Rhizobium</i> sp.	Agricultural Research Centre	Giza, Egypt	Root-knot and other phytonematodes	[195]

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Table 1. Commercial products of bacteria for phytonematode control.

and *M. incognita* juvenile mortality (120 µg/ml) were noted. An evaluation of both *in vitro* and *in vivo* nematocidal potential of extracts from *S. hydrogenans* strain DH16 against *M. incognita* prevented egg hatch (>95%) and a high mortality rate (95%) of juveniles after 96 h [71].

Furthermore, two compounds [10-(2,2-dimethyl-cyclohexyl)-6,9-dihydroxy-4,9-dimethyl-dec-2-enoic acid methyl ester] purified from the streptomycete were evaluated for their efficacy against *M. incognita*. The juvenile nematode mortality varied with the concentration rates with high mortality observed at high concentrations, for example, a concentration of 100 µg/ml caused 95% mortality after 96 h.

The marine bacteria *B. firmus* strain YBf-10 shows its efficacy as a biocontrol agent on *M. incognita* (eggs and juveniles) through a systemic action [72]. The application of this strain through drenching of tomato plants inoculated with *M. incognita* produced plants with reduced galls and egg masses, and nematode numbers in soil samples.

Pasteuria, which is an endospore-forming bacteria with various species within this genus, may be implored as biocontrol agents and there are four nematode antagonists within this genus. Among these, *P. penetrans*, *P. thornei*, *P. nishizawae*, and *P. usgae* are parasites on root-knot nematodes, lesion nematodes [73], and *Belonolaimus* spp. [74]. Commercialization of *Pasteuria* products for nematode control is, however, limited by two factors: (i) a narrow host range [75] and (ii) growth *in vitro* is slow and production is tedious [76]. *In vitro* production of *Pasteuria* spp. was initiated after *Pasteuria*. Bioscience Alachua (Florida, USA) filed a patent in 2004, for the production of the product Econem™, a product which is target-specific and has been designed to control sting nematodes (*Belonolaimus* spp.) in turf.

5. Fungi and symbiotic reprogramming in host cells

Arbuscular mycorrhiza fungi (AMF) are in the phylum Glomeromycota [77]; these fungi form symbiotic associations with plant roots and provide phosphorus, nitrogen, and water to plants [78]. Another advantage derived from this association is tolerance to biotic and abiotic stresses by host plants [79, 80]. Native strains of AMF are used as bio-fertilizers for enhanced plant growth, including root and tuber crops and for nematode management [81, 82]. The AMF releases signal that are transmitted systemically and these are to target non-infected parts of roots [83, 84]. Within the soil microbes with beneficial properties, for example, AMF are recognized by plants as invaders leading to the triggering of an immune response (**Figure 1A**) [85], and this signaling is associated with microbe-associated molecular patterns (MAMPs), which further induce MAMP-triggered immunity (MTI) [86, 87]. Second, there symbiotic activities within cells can be activated through mycorrhizal Myc factors if perceived (**Figure 1B**). The SP7 effector within the AMF *Glomus intraradices* is a characteristic defense signal in the fungi [88], and its expression occurs in host roots [85].

Plant cells with roots undergo reprogramming activities for successful establishment of symbiosis with symbionts (e.g., arbuscular mycorrhizal (AM) and root-nodule (RN) symbiosis) [89] (**Figure 2B**). However, this reprogramming phenomenon is absent in an asymbiotic root

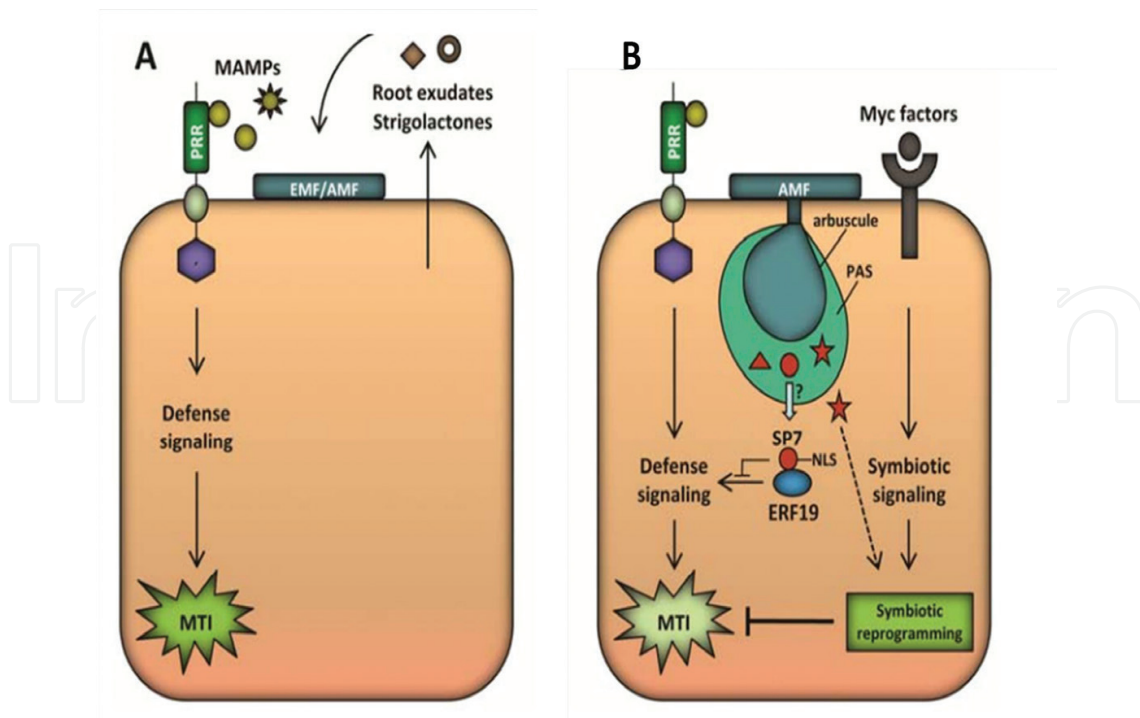


Figure 1. Model for the modulation of host immunity in ectomycorrhizal (EMF) and arbuscular mycorrhizal (AMF) fungi. (A) Root exudates recruit symbiotic mycorrhizal fungi and prime them for the interaction. Host plants initially recognize ectomycorrhizal (EMF) and arbuscular mycorrhizal (AMF) fungi as potential invaders; pattern recognition receptors (PRR) in the host perceive microbe-associated molecular patterns (MAMPs) and a signaling cascade is initiated that results in MAMP-triggered immunity (MTI). (B) The establishment of the symbiotic program in plant cells, which is activated upon perception of the mycorrhizal Myc factors, counteracts MTI with mechanisms yet to be defined. Molecules secreted in the apoplastic or peri-arbuscular space (PAS) may act as either apoplastic or cytoplasmic effectors to suppress the MTI response or promote the symbiotic program. The AMF *Glomus intraradices* secretes the SP7 effector which is translocated into the plant cytosol; a nuclear localization signal (NLS) targets SP7 to the nucleus, where it interacts with the defense-related transcription factor ERF19 to block the ERF19-mediated transcriptional program [85].

cell (**Figure 1B**). Within the soil, roots of plants continuously produce and release root exudates and strigolactones as observed in an asymbiotic root cell. Signals are transmitted to the nucleus through transcription factors, gene expression occurs, and there is cell-to-cell communication. There are also plant receptors within the root cells that detect mineral concentration in soils. In a root cell that either interacts with AM or RN fungi, there is release of both flavonoids and strigolactones, two factors (Nod and Myc) are released from the symbionts and these turn on the calcium spiking. Within the RN symbiosis, flavonoids from the plant root turn on the Nod transcription factor, and enables bacteria to produce lipochitooligosaccharide nod factors. These Nod factors stimulate root-nodule development, which are needed by rhizobia. Strigolactones further stimulate AM fungi and hyphal branching occurs [90]. The root cortex is usually colonized by AM fungi and produces substantial hyphae (arbuscules). During the development of the arbuscule, it becomes enveloped within the peri-arbuscular membrane (PAM), and essential proteins are moved to the plant cell within the PAM [91]. Jasmonic acid (JA) and methyl jasmonate (MeJA) can stimulate the expression of Nod genes [92] and release of Nod factors [93], in rhizobia after their application exogenously.

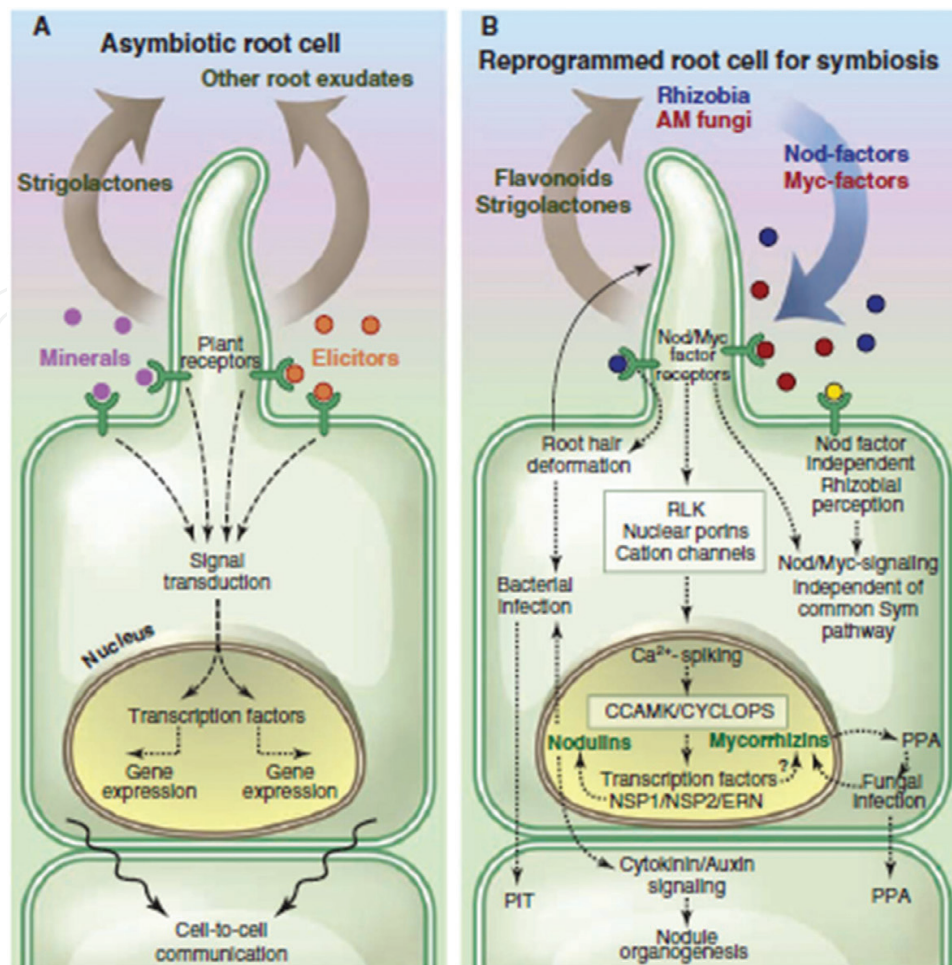


Figure 2. Signal exchange during symbiosis. (A) An asymbiotic cell constitutively releases root exudates, including strigolactones. The root cell monitors the concentration of minerals and microbial organisms in the soil and transduces the respective signals. Integration of the signals occurs at the cellular and organismic levels and includes cell-to-cell communication. (B) A root-hair cell primed for interaction with rhizobia or AM fungi, respectively. Plant roots release flavonoids and strigolactones that prime the rhizobia and AM fungi. Nod and Myc factors act as signals from the symbionts to plant root cells that activate calcium spiking via the Sym pathway (boxed). The potential differential activation of CaMK/Cyclops leads to differential induction of nodulation-specific transcription factors (NSP1, NSP2, and ERN) and unknown mycorrhizal-specific transcription factors. Rhizobial and mycorrhizal infection require the common Sym pathway but also exhibit recognition and signaling independent of this pathway. The path for fungal infection and the IT is predicted by the PiT and the PPA, respectively, indicating directed signaling to neighboring cells. Nodule organogenesis is induced in inner cortical cells after nod-factor perception by epidermal cells. This requires cytokinin signaling and is associated with changes in auxin levels [89].

6. Fungi antagonists of nematodes

Biological control, defined as the management of plant diseases and pests by means of other living organisms, mainly concerns the exploitation of microbial agents [94]. Under natural conditions, biocontrol agents that are associated with plant-parasitic nematodes usually exist [95]. These organisms act through parasitism, predation, antagonism, or competition [96], but their successful activity depends on a number of parameters, including soil environmental factors [97]. Many beneficial organisms were found to attack plant-parasitic nematodes

but most research has been focused on bacteria and fungi [94, 98]. Although few biological agents had been until recently adopted for nematode control with successful use, the current progress in studies of biological control has gradually led to the development of commercial biocontrol products with proven efficacy against plant-parasitic nematodes. Studies on fungal antagonists of nematodes have been started since 1874 with the first observations of *Harposporium anguillulae*, by Lohde.

7. Types of nematode-antagonistic fungi and their mode of action

Species of several fungal genera have been reported to have biological activity against plant-parasitic nematodes [58]. Hallmann et al. [98] classified these beneficial fungi into nematophagous fungi, saprophagous fungi, and endophytic fungi.

7.1. Nematophagous fungi

Nematophagous fungi are the largest and the most studied group of the fungi involved in the biological control against plant-parasitic nematodes. Among nematophagous fungi, which have been tested for their efficacy in controlling nematodes, some are obligate parasites (e.g., *Nematophthora gynophila*), others are facultative or opportunistic parasites (e.g., *Pochonia chlamydosporia*) [98].

Obligate parasites require a residual population of nematodes for their survival. Infection is initiated when fungal spores penetrate the host nematode either through the gastrointestinal tract after being ingested or directly after adhering to the cuticle [98]. Among the obligate fungal parasites, *Hirsutella* spp. and *Drechmeria coniospora* have shown to be interesting in terms of their biology, mode of action, and nematode control potential. Infection of these fungi is initiated by the adhesion of small conidia to the nematode cuticle. However, obligate parasites are difficult to grow in culture.

The facultative parasites are able to switch between saprophytic state in soil and rhizosphere into parasites that infect nematodes, depending on environmental circumstances. Nematode infection occurs either by way of adhesive spores or by trapping structures, or through an appressorium [94]. Depending on their mode of action, nematophagous fungi can attack nematodes during all stages of their life cycle.

In addition to the fungi described above, some form a mycelium able to capture plant-parasitic nematodes. They are called predacious fungi or nematode-trapping fungi and act through different trapping structures including fungal hyphae covered with adhesive secretions (e.g., *Stylopage* spp.), adhesive branches (e.g., *Monacrosporium cionopagum*), adhesive spores (*Meristacrum* spp.), or adhesive knobs (*Arthrobotrys* spp., *Nematoctonus* spp.) [99, 100]. These fungi also produce nematocidal compounds such as linoleic acid (e.g., *A. oligospora*) or pleurotin (e.g., *N. robustus*) [101].

7.2. Saprophagous fungi

Among the saprophagous fungi present in the bulk soil, some have been reported to be antagonistic toward plant-parasitic nematodes. This group was represented by the genus

Trichoderma, a ubiquitous soil fungus that also colonizes the root surface and cortex [98]. *Trichoderma* spp. was first reported to be parasite of other fungi [102], before being identified as an antagonist of plant-parasitic nematodes [103, 104]. A number of *Trichoderma* species, for example, *T. asperellum*, *T. hamatum*, *harzianum*, and *T. viride*, were reported to infect eggs and juveniles of root-knot nematodes [105, 106]. Several possible mechanisms including the production of antifungal metabolites, competition for space and nutrients, mycoparasitism, plant growth promotion, and induction of the defense responses in plants have been suggested as mechanisms for their biocontrol activity [107, 108]. Other saprophagous fungi with antagonistic activity against plant-parasitic nematodes include species of the genus *Gliocladium*, *Acremonium*, and *Cylindrocarpon* [109–111].

7.3. Endophytic fungi

Endophytic fungi have been considered as important fungi in the biological control of plant-parasitic nematodes. The implication of endophytic fungi in root-knot nematode reduction was first demonstrated with arbuscular mycorrhizal fungi on vegetables [112].

AMFs are obligate fungi, which form symbiotic associations with numerous plant species, with the primary function of improving plant nutrient uptake [113]. Arbuscular mycorrhizal fungi are obligate plant symbionts. According to Harley and Smith [114], AMFs establish with their host plant an interdependent mutualistic relationship (symbiosis) where the host plant receives mineral nutrients, while the fungus obtains photosynthesis-derived carbon compounds from the plant [115]. Three major types of mycorrhizal associations—ectomycorrhiza, endomycorrhiza, and ectomycorrhizal—endomycorrhizal intermediate type—have been distinguished [116]. Their endophytic nature enables associated (infected) plants to overcome biotic [117] and abiotic stresses [118]. Potential modes of actions developed by AMF during the protective activity against plant pathogens reviewed by Whipps [119] include (1) the direct competition or inhibition, (2) enhanced or altered plant growth, morphology, and nutrition, (3) biochemical changes associated with plant defense mechanisms and induced resistance, and (4) development of an antagonistic microbiota. Other studies have recently reported the ability of AMF to induce systemic resistance against plant-parasitic nematodes in the root system [120].

Another important endophytic fungus in nematode control but with saprophytic nature is the non-pathogenic *Fusarium* species, *Fusarium oxysporum*. Reduction of nematode penetration into the host plant root and induction of systemic resistance to plants have been considered as the main mechanisms by which *F. oxysporum* reduced nematode parasitism [121–123].

8. Potential of antagonistic fungi in nematode control

A large number of fungi have been tested for their potential as biological control agents of plant-parasitic nematodes. Until recently, few had been adopted for nematode control with successful use [98]. However, the current progress in studies of biological control has gradually led to the development of commercial biocontrol products with proven efficacy against plant-parasitic nematodes. In this section, most fungal studies will be discussed.

8.1. *P. chlamydosporia*

Species of *Pochonia* are widely distributed in agricultural soils and infect eggs of plant-parasitic nematodes, snails, and slugs [96].

Within the genus *Pochonia*, *P. chlamydosporia* appears the most effective in infecting nematode eggs [124]. *P. chlamydosporia* includes two subspecies *P. chlamydosporia* var. *chlamydosporia* and *P. chlamydosporia* var. *catenulatum* [125] which are considered non-pathogenic to plants, higher animals, and humans [126]. This species is one of the major facultative antagonistic fungi that can parasitize egg and female stages of root-knot nematodes and female cyst nematodes [96, 127, 128]. Parasitism of this fungus is based on appressorial formation developed from undifferentiated hyphae, which allows the colonization of the egg surface and penetration through both mechanical and enzymatic actions [129]. Observations during the infection process have shown that the penetration of the eggshell occurs from both the appressorium and the lateral branch of the mycelium, and leads to the disintegration and the dissolution of three layers composing the eggshell: the vitelline layer, chitin layer, and lipoprotein layer [130, 131]. The infection process is affected by the nematode host [130], suggesting that fungal growth, development, and penetration of the eggshell may be influenced by signals from the eggs [132]. Different enzymes, in particular proteases and chitinases, are important for the infection processes, and VCP1 proteases being the most known proteases with enzymatic activity against the nematode eggshells [94, 130].

The efficacy of *P. chlamydosporia* has been reported to be affected by three key factors: the fungal density in the rhizosphere, the rate of egg development in the egg masses, and the size of the galls in which the female nematodes develop [133]. *P. chlamydosporia* is found to be more abundant in the rhizosphere and on nematode-infected roots, and parasitism may promote the long-term survival of the fungus in soil [96]. However, the extent of colonization depends on the fungus isolate and the plant species [134, 135]. Although isolates of *P. chlamydosporia* differ significantly in their ability to parasitize the eggs of different nematode species, they have shown little host specificity [136].

Formulations based on *P. chlamydosporia* have been developed and are currently being commercialized (e.g., KlamiC® based on *P. chlamydosporia* var. *catenulata* RES 392 from Cuba) [98, 137].

8.2. *Trichoderma* spp

Species of *Trichoderma* are ubiquitous soil-borne fungi that can colonize the root surface as well as the cortex [138, 139]. Several species of *Trichoderma* have been considered for biocontrol of plant-parasitic nematodes [104]. Some species were found to be associated with eggs of root-knot nematodes in vegetable fields [106].

Against nematodes, *Trichoderma* spp. can provide excellent control and are viewed as strong contenders for development as biocontrol agents [104]. In various studies, species of *Trichoderma* were reported to show antagonistic activity against eggs and juveniles of root-knot nematodes in *in vitro* conditions [105] and to infect nematode egg masses and reduce juvenile populations in non-sterilized field soil [140]. *Trichoderma* spp. were shown to efficiently

control root-knot nematodes when they were applied before planting [104, 141]. Methods suggested for their application include seed treatment, dry formulation, or soil drench [98]. However, isolates of the same species of *Trichoderma* can differ markedly in their rhizosphere competence, biocontrol potential toward nematodes, and plant growth promotion [141].

Different mechanisms have been suggested as mechanisms developed by *Trichoderma* against nematodes. The first observable interaction between *Trichoderma* spp. and its host is expressed by direct growth of the mycoparasite hyphae initiated by a chemotropic reaction toward the host [105]. The hyphae, upon contact, coil around and penetrate the host. This process involves the release of lytic enzymes by *Trichoderma* spp. [142], which serves to partially degrade the host cell wall. Lytic enzymes such as chitinases, glucanases, and proteases, seem to be particularly important in the mycoparasitic process. Induction of defense responses in plants by *Trichoderma* spp. was also observed through increased peroxidase and chitinase activities following fungal inoculation and a strengthening of the epidermal and cortical cell walls as the deposition of newly formed barriers [143]. These authors also reported increased enzyme activities in the leaves, suggesting a systemic defense response to the presence of *Trichoderma* in the rhizosphere. When monitoring fungus-nematode interactions, Sharon et al. [105] observed that in pre-inoculated soil, the fungus colonizing the roots interacts with the penetrating juveniles and colonizes their penetration sites, indicating also a competition for spaces. *Trichoderma*-based products are commercially available and used to control plant-parasitic nematodes on different crops. Successful examples include BioNem® [144] and T-22™ Planter Box [145].

9. Arbuscular mycorrhizal fungi

A number of studies have demonstrated the contribution of arbuscular mycorrhizal fungi in improving soil structure [146], plant mineral uptake, and plant growth [113, 147, 148] enhancing plant tolerance to pollution with toxic metals [149, 150], resistance to drought stress [151], and reducing the effect of plant diseases [117, 152–154]. AMFs have also been reported to protect host plants against plant-parasitic nematodes [81, 98, 155]. The interaction between AMF-colonized plants and plant-parasitic nematodes has been reviewed by several authors [98, 156, 157]. AMFs have also been shown to suppress the effect of damage [112, 158], although some studies have shown no effects against these pests [159, 160]. However, the efficacy of AMF against nematodes may be influenced by a number of factors including prevailing environmental conditions [161], cultivar [159], nutrient status of the field [162], and the timing of application [163]. Existing knowledge suggests the application of the fungi in the nursery or to introduce suitable mycorrhizal crops into the rotation pattern for efficient pest control [98]. Pre-inoculation of seedlings with AMF, for example, has resulted in high levels of root colonization, followed by a significant reduction of nematode infection [164]. However, recent studies showed that the level of reduction of RKN was not necessarily dependent on high-root mycorrhization, while the interaction between crop cultivar-AMF strains is also important [165]. Furthermore, direct inoculation of AMF inoculum into the transplanting hole prior to planting may provide plant protection against root-knot nematodes, indicating possible use

of AMF for seed-growing crops [165]. Some studies on the combination of AMF with other antagonists have provided promising clues for their successful integration into nematode control strategies [166, 167]. Different formulations based on AMF strains (e.g., *F. mosseae*- and *G. dussii*-based products from BIORIZE® in Dijon, France) were commercially developed for use in crop protection against plant-parasitic nematodes [81, 165].

9.1. *Paecilomyces lilacinus*

Paecilomyces lilacinus (Thom) Samson seems to be most frequent in warmer regions, although it has been reported in different parts of the world and from various habitats [126, 168]. Investigations on the biocontrol activity of the fungus toward plant-parasitic nematodes started after Jatala et al. [169] discovered infection of eggs and females of *M. incognita* and eggs of *Globodera pallida*. Both mechanical and enzymatic activities may be involved in the host penetration. *P. lilacinus* first colonizes the gelatinous matrix of *Meloidogyne*, *Tylenchulus*, and *Naccobus*, and cysts of cyst nematodes, develops a mycelium network, then engulfs and penetrates the nematode eggs through an appressorium or simple hyphae [126, 169]. Following penetration, the fungus grows on the early embryonic development, depletes all nutrients in the eggs, breaks the cuticle of the infected egg and infects other eggs. Although *P. lilacinus* is considered as egg-pathogenic fungus, Holland et al. [170] observed in *in vitro* experiment infection of third- and fourth-stage juveniles and adult females of *M. javanica*.

P. lilacinus is among the most widely studied microorganisms used for the management of plant-parasitic nematodes. Its success in controlling plant-parasitic nematodes has led to the development of commercial products such as MeloCon® WG by Bayer in Germany and PAECILO® by AgriLife in India [171].

9.2. *Fusarium oxysporum*

The interest in the non-pathogenic *Fusarium oxysporum* for nematode control is stimulated after several isolates were reported to reduce the banana root rotting caused by *Pratylenchus goodeyi* [172]. This endophytic fungus was reported as the most abundant endophytes of banana (*Musa* spp.), for example, in Uganda [173, 174]. In various studies, the strain *F. oxysporum* FO162 has shown the ability to reduce penetration of damage caused by plant-parasitic nematodes on tomato and banana [175–178]. Dababat and Sikora [123] reported that plants colonized by *F. oxysporum* were less attractive or exuded substances that were repellent toward nematodes. The endophytic fungus can infect nematodes at any stages and reduce significantly the plant damage [121, 179]. Recent studies indicate that the non-pathogenic *F. oxysporum* is a successful biocontrol agent for plant-parasitic nematodes with positive effect on the plant growth [180].

9.3. *Arthrobotrys* spp

Arthrobotrys species are trapping fungi which immobilize nematodes [189] using different trap structures [181]. The species *A. oligospora* was the first recognized nematode-trapping fungus [182]. *A. conoides* and *A. oligospora* makes three-dimensional adhesive network to trap

soil-inhabiting nematodes [94, 183]. *A. candida* usually forms non-constructing rings [184] but Al kader [181] reported a formation of adhesive hyphae capturing nematodes and then trophic hyphae within nematodes' body to digest nematode contents. *A. brochopaga* forms ring traps that constrict around the body of a nematode passing through them [185]. The presence of the nematode is important in the initiation of the trapping structures [186]. Nematode species did not affect the type of trap structure but most probably the quantity of these traps. Santos et al. [187] reported substantial variability in virulence among isolates of the same species. Host recognition and adhesion by the fungus were the first steps in the infection of the host nematode. This recognition has been attributed to a molecular interaction of certain proteins on the fungal surface with sugar molecules on the nematode cuticle [183]. Substantial variability in virulence among isolates of the same species was observed [187]. Nordbring-Hertz et al. [188] reported that *Aphelenchus avenae* can avoid to be captured by the fungi structures, especially for the young nematode.

10. Conclusions

Beneficial microbial inocula can be applied for large-scale field management of nematodes which will result in increased yields. However, further research into the various biocontrol measures used by organisms is necessary, and this can be achieved through genomic approaches; this will enhance understanding of the various complex mechanisms used by these organisms on nematodes. Strains of these organisms may be effective in their local occurrences, and therefore countrywide surveys of soils will enable location-specific strains to be isolated and characterized. These local strains once characterized can be produced in large quantities and distributed to farmers for applications in their fields.

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