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Nematophagous fungi as biocontrol agents for Root-Knot nematodes: A study of *Trichoderma*, *Fusarium*, *Cladosporium*, and *Drechslerella*

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Abstract

Root-Knot nematodes (RKNs), which belong to *Meloidogyne* spp., are considered the most devastating plant pathogens that limit the production of the majority of the cultivated crops worldwide. These nematodes placed the first rank among the top ten plant-parasitic nematodes and are responsible for more than 50% of yield losses caused by plant-parasitic nematodes worldwide. Morphological characteristics of RKNs have been used for a long time for identification. Nowadays, many molecular marker PCR-based methods have evolved for identification. Biological control was the strategy that got more attention and has been used recently for managing nematodes. In this regard, *Trichoderma, Fusarium, Cladosporium,* and *Drechslerella* have received more attention for the management of RKNs. These fungi developed their ability to reduce nematode populations in soil. They attack nematodes directly via parasitism or by producing metabolites and enzymes that degrade nematode cell walls or produce trapping organs that catch the nematodes. Thus, it is crucial for accurate nematode identification by different methods for employing the best management strategy. Prospect studies should focus on the isolation, identification, and screening of nematophagous fungi applications for controlling RKNs.

Introduction

Plant-parasitic nematodes (PPNs) are a group of nematodes that feed on living plant cells. They belong to the kingdom Animalia and are placed among the most serious plant pathogens for agricultural crops worldwide. More than 4100 species of PPNs have been described around the world (Jones *et al*., 2013). According to Hunt *et al*. (2018), PPNs are classified according to their parasitism as ectoparasites (Nematode doesn't enter plant tissues and remains in soil), semi-endoparasites (The anterior part of the nematode penetrates the plant root while the posterior part remains in soil), and endoparasites (The whole nematode body penetrates the root tissues). There are two kinds of endoparasites: migratory endoparasites (Still moving inside plant tissues and have no fixed feeding site) and sedentary endoparasites (They have a fixed site of feeding and induce nurse cells or syncytia, mostly become obese,

and thereby lose their mobility). The annual losses caused by PPNs are 8.8-14.6% worldwide (Nicol *et al.*, 2011). This estimation may be less than the real estimation due to the default estimation in different countries. In 2023, Quintanilla and Fazlabadi reported that PPNs cause more than 60% yield losses. By direct and indirect damage, PPNs decrease yield and crop quality as well as increase production costs and income losses. Damage caused by PPNs is characterized by stunting, premature wilting, leaf yellowing, root malformation, and nutrient deficiencies that occur in patches throughout the field as a result of irregular distribution of nematodes in the soil. Root-Knot nematodes (*Meloidogyne* spp.), cyst nematodes (*Heterodera* and *Globodera*), and root-lesion nematodes (*Pratylenchus* spp.) are among the most destructive plant-parasitic nematodes worldwide (Quintanilla and Fazlabadi, 2023).

Root-Knot nematodes (*Meloidogyne* spp.) are polyphagous, sedentary endoparasites that pose a serious threat to crop production (Peiris *et al*., 2020). Relying on economic and scientific importance, RKNs ranked first among the top ten PPNs worldwide (Jones *et al*., 2013). This genus involves more than 100 species described; the most important of them worldwide are *M. incognita, M. javanica, M. arenaria*, and *M. hapla* (Elling, 2013; Coyne *et al*., 2018, and Sikandar *et al*., 2020). According to Elling (2013), the host range of RKNs exceeds 3000 plant species. RKNs caused losses in agricultural production crops of about $78 billion annually around the world (Lima *et al*., 2017). According to Wendimu (2021), the taxonomic classification of RKNs is Domain: Eukaryota, Kingdom: Metazoa, Phylum: Nematoda, Class: Secernentea, Order: Tylenchida, Family: Heteroderidae, Genus: *Meloidogyne*.

Many strategies have been used for controlling RKNs, including chemical control, cultural control, physical methods, and biological control. Chemical control is a widespread practice; they have proved to be a useful and reliable means of controlling a wide range of PPNs. Recently, the exaggerated use of nematicides has caused soil and environmental pollution and hazards (El-Qurashi *et al.,* 2025). Additionally, farmers are not careful when using nematicides and sometimes use more than the recommended dose. Chemical control also became more expensive due to the rise of synthesis costs of new compounds. Cultural methods like adding plant amendments or changing planting time can be effective in controlling RKNs but are not economical. Physical methods can also be used for controlling RKNs. Soil fallowing during hot and dry weather, immersing soil with water, and plowing soil more times are also used for reducing RKNs population but are not economically effective as well.

Regarding botanical nematicides, more than 100 plant species have been evaluated for controlling PPNs. Plant extracts and crude extracts have exhibited inhibitory effects against RKNs. Most fungal, bacterial, yeast, and actinomycete isolates have been used for controlling RKNs. Fungal antagonists of nematodes include both nematophagous and non-nematophagous fungi that have detrimental effects on nematodes (Chen and Dickson, 2004). The benefits of biocontrol agents are that they can compete and persist in the environment, colonize the niches rapidly, and proliferate on newly formed roots.

Nematophagous fungi were categorized as predacious fungi, endoparasites of vermiform worms, parasites of sedentary females and eggs,

fungi that produce antibiotic compounds, and vesicular-arbuscular mycorrhizal fungi (Chen and Dickson, 2004). Some individual fungi can belong to different categories, so there is no clear-cut distinction between these categories. Predacious fungi capture nematodes by forming specific devices, then kill and consume their prey. These devices are adhesive hyphae, branches, nets and knobs, non-constructing and constructing rings and stephanocysts (Barron, 1977). Regarding RKNs management, *Fusarium, Trichoderma, Arthrobotrys, Dactylella, Aspergillus, Purpureocillium,* and *Verticillium* have been successfully used to control RKNs (Barron, 1977).

Root-Knot nematodes (*Meloidogyne* spp.):

The first recorded instance of Root-Knot nematode disease transpired in the mid-19th century, when galls were seen on the roots of cucumber (*Cucumis sativus*) in a greenhouse (Berkeley, 1855). *Anguillula marioni* Cornu, 1879, was the first species of Root-Knot nematode to be found; it formed galls on the roots of sainfoin (*Onobrychis sativus*) in France (Hunt and Handoo, 2009). Chitwood separated the genera *Meloidogyne* and *Heterodera* in 1949 based on morphological differences, whereas Göldi established the name *Meloidogyne* in 1887 (Chitwood, 1949 and Moens *et al*., 2009). The descriptions of *Meloidogyne arenaria* (Neal, 1889) Chitwood, 1949, *Meloidogyne incognita* (Kofoid and White, 1919) Chitwood, 1949, *Meloidogyne javanica* (Treub 1885) Chitwood, 1949, and *Meloidogyne hapla* Chitwood, 1949 were among the later updates (Moens *et al.,* 2009).

Root-Knot nematodes (*Meloidogyne* spp.) are considered one of the most crucial plant pathogens that limit plant production for most cultivated plants worldwide. Their world distribution, massive host range, and their interaction with other plant pathogens causing disease complexes rank them among the major pathogens affecting the world food supply (Sasser, 1980). In 2013, Jones *et al*. ranked RKNs as the first plant pathogens out of the top ten plant nematodes that caused economic losses for crops. In Saudi Arabia, *M. javanica* is the most dominant species and causes very severe damage to vegetables, followed by *M. incognita*, which occurs mostly on shrubs and trees (Al-Hazmi *et al*., 1995). Moreover, ornamentals and horticultural trees were also found to be attacked with *Meloidogyne* spp. (Mokbel, 2014). *Meloidogyne* spp. were also recorded to infect coffee trees in the Jazan region (Al-Hazmi *et al*., 2009, and Mohamed *et al.,* 2023) and some greenhouse vegetable crops in the Riyadh region as well (Almohithef *et al.,* 2018).

Root-Knot nematode life cycle:

The life cycle of RKNs consists of four juvenile stages (J1 in eggs, J2, J3, and J4) and adults. Inside roots (Figure 1), females lay eggs containing J1 that develop into J2 and hatch from eggs. J2s infect plant roots and develop into J3 and J4 (sedentary phases). Then, J4 molts to adult females, which remain in roots and produce egg masses (Sikandar *et al*., 2020). In RKNs, especially *M. incognita* and *M. javanica*, mitotic parthenogenesis was the common reproductive method (Hussey and Janssen, 2002).

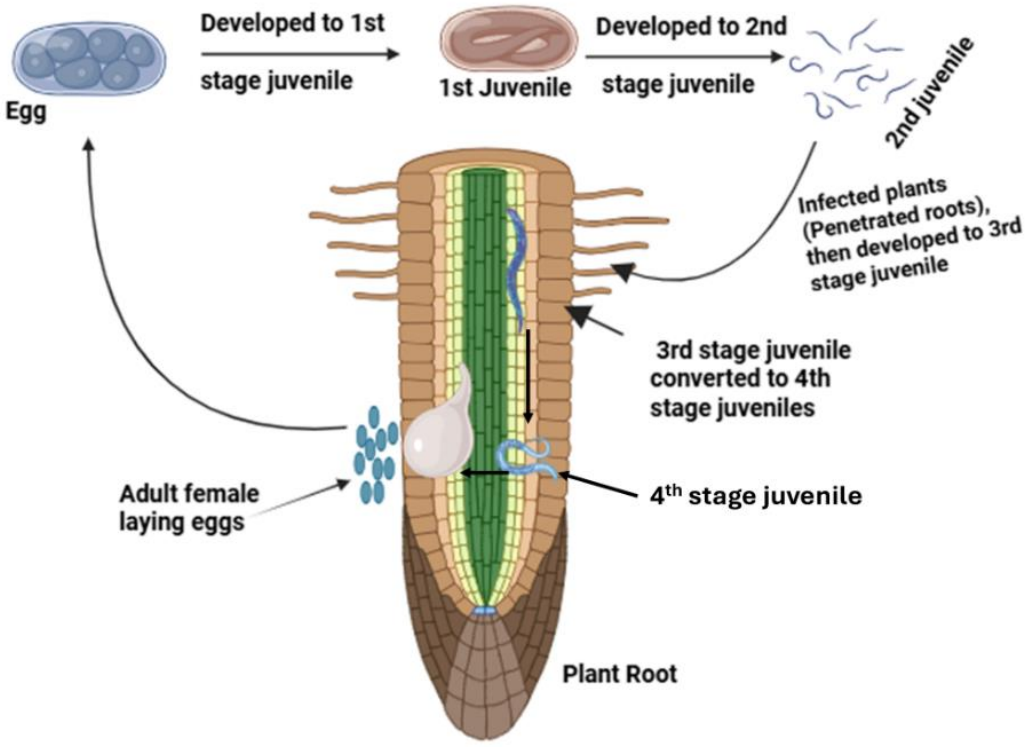

Figure (1): The life cycle of Root-Knot nematodes (El-Qurashi and Al-Yahya, 2025).

Crop losses caused by Root-Knot nematodes:

In 1987, Sasser and Freckman estimated the crop losses due to plant-parasitic nematodes at 8.8-14.6% worldwide. However, in 2020, there was a high increase in crop losses caused by plant-parasitic nematodes, which were estimated to be 21.3% of production (Kumar *et al*., 2020). The majority of crop losses are caused by RKNs, which affect virtually every crop plant (Mukherjee *et al.*, 2011). *Meloidogyne* spp. caused losses for peanuts, tobacco, soybean, and vegetable crops by more than 50% of total nematode losses worldwide (McSorley *et al*., 1987, and El-Qurashi *et al.,* 2023). *M. javanica* and *M incognita* caused 20 to 30% losses in chickpea production in India (Ali and Sharma, 2003). *M. graminicola* caused losses of 16-32% of rice yield (Mukherjee *et al.,* 2011). While in 2020, Kumar *et al.* estimated losses caused by *M. graminicola* by 16% in rice. Additionally, *Meloidogyne* spp. Caused 25, 18, 23, 23, 4.5- 16, and 19.75% losses in fruit, vegetables, horticultural, pulse, oilseed, and fiber crops, respectively.

Root-Knot nematode identification:

Traditionally, RKNs were identified using morphometric methods such as the morphology of the perineal pattern, male head morphology, size and shape of the stylet, and the distance from the stylet base to the dorsal esophageal gland orifice (DGO) (Cunha *et al.*, 2018). For males, supplementary characteristics encompass body size, labial cap morphology and height, number of annulations, diameter of the labial region in relation to the first body annule (Figure 2), stylet length, configuration of the stylet cone, shaft, and basal knobs, length of the stylet cone, distance between the stylet knobs and the dorsal gland opening, metacarpus lumen lining, distance from the anterior end to the excretory pore, phasmid position and length, and spicule morphology.

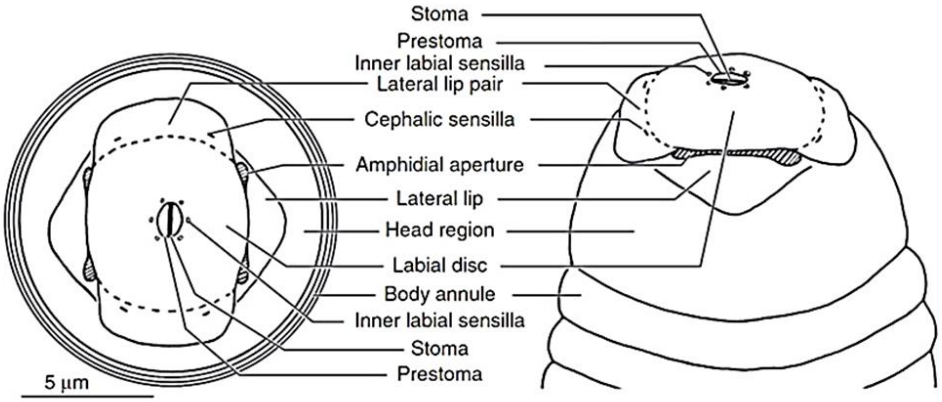

Figure (2): Drawings of the anterior end of a *Meloidogyne* male (Eisenback and Hunt, 2009).

Measurements of juvenile body and stylet length, morphology of the labial region, configuration of stylet knobs, location of the hemizonid, distance from the anterior end to the stylet knobs, distance from the stylet base to the dorsal gland orifice (DGO), enumeration of lines in the lateral field, along with the shape, length of the tail, and length of the hyaline terminus, are also considered.

For decades, the female perineal pattern (Figure 3) has been the only main technique used for RKN species identification (Seesao *et al*., 2017). In 1981, Eisenback *et al.* reported that host plants were used for differentiating between the four major species of *Meloidogyne* (Table 1). These morphological characteristics are perhaps not satisfying due to the RKN species being close in morphological characteristics like stylet shape and size. Perineal patterns and host differential plants are used mainly for differentiating between the four major RKN species only.

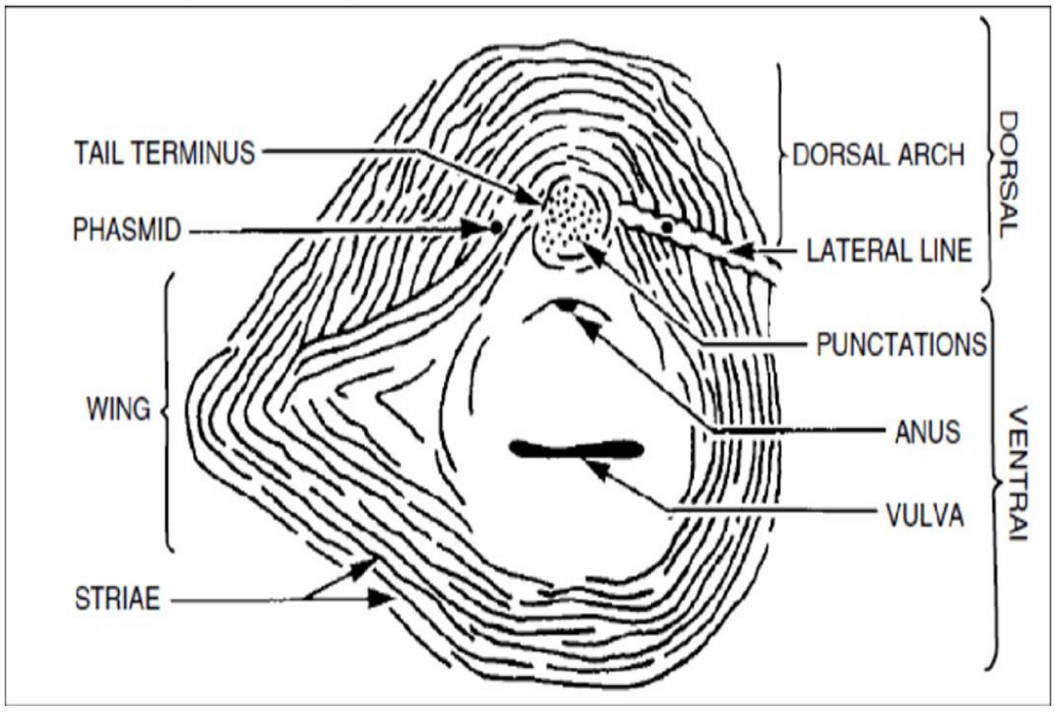

Figure (3): Different characteristics of RKN female perineal pattern (Karssen and Moens, 2006).

Table (1): Response of the differential hosts to the four major species of Root-Knot nematodes and their races.

RKN species	Differential hosts					
	Cotton (Deltapine 16)	Tobacco (NC 95)	Pepper (California Wonder)	Watermelon (Charleston Gray)	Peanut (Florunner)	Tomato (Rutgers)
Meloidogyne incognita race 1	-	-	+	+	-	+
Meloidogyne incognita race 2	-	+	+	+	-	+
Meloidogyne incognita race 3	+	-	+	+	-	+
Meloidogyne incognita race 4	+	+	+	+	-	+
Meloidogyne arenaria race 1	-	+	+	+	+	+
Meloidogyne arenaria race 2	-	+	-	+	-	+
Meloidogyne javanica	+	+	-	+	-	+
Meloidogyne hapla	-	+	+	-	+	+

(-) indicates not host (Resistant); (+) indicates good host (Susceptible), (Eisenback *et al*., 1981).

So, other methods should be used, like biochemical and molecular DNA-based techniques. Isozyme phenotypes are used successfully for diagnosing the RKNs worldwide. This technique was used for the first time by Esbenshade and Triantaphyllou (1985) when they reported different esterase patterns from 16 RKN species. The stability of isozyme phenotypes within different individuals of RKNs make it a crucial tool to use worldwide (Blok and Powers, 2009).

A drawback of this method is that it can only be used with mature females, as the specific gene required for its success is only expressed in mature females. DNA-based techniques for the identification of *Meloidogyne* species were first documented in the 1980s, with Curran *et al.* (1985) using restriction fragment length polymorphisms (RFLPs). In the last ten years, molecular diagnostics for nematodes have advanced markedly due to the invention and use of polymerase chain reaction (PCR) (Nega, 2014). Root-Knot nematode species have been identified using a variety of DNA-based methods, including satellite DNA probes and PCR, ribosomal DNA (rDNA) PCR, mitochondrial DNA (mtDNA) PCR, sequence-characterized amplified regions (SCARs), random amplified polymorphic DNA (RAPDs), microarrays, amplified fragment length polymorphisms (AFLP), PCR targeting rDNA, mt DNA, internal transcribed spacer (ITS), and ribosomal intergenic spacer (IGS) sequences, and real-time PCR (Blok and Powers, 2009). Molecular approaches for the identification of *Meloidogyne* species are always evolving, with the anticipation of more advanced methodologies emerging with advancements in molecular technology.

Biochemical techniques:

Isozymes and antibodies are two biochemical methods that have been applied to identify *Meloidogyne* species (Blok and Powers, 2009). The use of isozyme phenotypes for identification began with Esbenshade and Triantaphyllou (1985), who demonstrated that different esterase patterns could differentiate 16 species of Root-Knot nematodes. Since then, researchers have adopted isozyme phenotypes, particularly carboxylesterase/esterase, as a routine method for identifying *Meloidogyne* species (Blok and Powers, 2009). While isozyme phenotypes remain consistent across different individuals, making it a valuable identification tool, a drawback of this method is that it can only be applied to mature females. The specific gene required for this process is only expressed in mature females (Blok and Powers, 2009).

An antibody-based capture technique was created to enhance nematode extraction from soil since plant-parasitic nematodes are tiny and have an uneven distribution in soil, making it difficult to identify them in plant samples. This technique utilizes an antibody that adheres to the surface

of the target nematode after incubation with extracted worms (Chen *et al.,* 2001; Blok and Powers, 2009, and Nega, 2014). Subsequently, magnetic beads coated with a secondary antibody are added, and a magnet seizes the target species, eliminating non-targets (Chen *et al*., 2003). The immunomagnetic capture approach enables the recovery of *Meloidogyne* species from soil samples with a success rate of up to 80% (Chen *et al.,* 2001 and 2003).

Ribosomal and mitochondrial DNA PCR:

While SCAR-PCR has demonstrated significant efficacy in differentiating various *Meloidogyne* species, several universal primers have been evaluated in the last few years for the identification of *Meloidogyne* spp. (Tigano *et al.*, 2010; Onkendi and Moleleki, 2013a; Onkendi *et al.,* 2014; Bekker *et al.,* 2016; Janssen *et al*., 2016 and El-Qurashi *et al.*, 2017). Nonetheless, the majority of these primers have had difficulties in consistently distinguishing between *Meloidogyne* species. Research conducted by Onkendi and Moleleki (2013b) using IGS-rDNA and mtDNA sequences demonstrated that *M. incognita*, *M. javanica*, and *M. arenaria* grouped as a singular clade. Simultaneously, examination of D2-D3 28S rDNA sequences categorized *M. incognita* and *M. enterolobii* as a single clade, while *M. arenaria* and *M. javanica* constituted distinct clades. Furthermore, partial 18S and 28S rDNA sequences from the *M. incognita* population in China exhibited 99% similarity with other tropical species such as *M. incognita*, *M. arenaria*, *M. javanica*, and *M. floridensis* (Zeng *et al*., 2014), underscoring the inadequacies of these primers in precisely distinguishing these species. Specific DNA sections, including 18S, ITS, and 28S, may distinguish specific tropical species such as *M. incognita*, *M. javanica*, and *M. arenaria*, as shown in research on *M. hispanica* (Landa *et al*., 2008) and *M. enterolobii* (Bekker *et al*., 2016). Janssen *et al.* (2016) determined that the COI, COII, COIII, and 16S segments were insufficient for differentiating *M. incognita*, *M. arenaria* and *M. javanica*. The low sequence diversity in the ITS1, ITS2, and 5.8S regions among the mitotically parthenogenetic species *M. arenaria*, *M. incognita*, and *M. javanica* renders these areas inadequate for distinction (De Ley *et al*., 1999 and Blok, 2005). The COII/16S (C2F3/1108) marker has been effectively utilized for the identification of *Meloidogyne* spp. (Powers and Harris, 1993; Blok *et al*., 2002 and Powers *et al*., 2005); however, it did not yield amplification products for Turkish *Meloidogyne* spp. (Devran and Söğut, 2009), rendering it unreliable for precise species identification.

SCAR-PCR:

Given the limitations of various recently developed universal primers in reliably distinguishing *Meloidogyne* species, other established molecular methods such as RAPD and SCAR-PCR are essential for confirming species identification (El-Qurashi *et al*., 2017). SCAR-PCR, developed specifically for diagnostic use, focuses on a specific DNA segment and is particularly effective for identifying species with minimal genetic differences based on DNA fragment length (Blok and Powers, 2009). For example, three RAPD markers have effectively differentiated the Root-Knot nematode species; *M. arenaria*, *M. incognita*, and *M. javanica*. Three species-specific primers developed for SCAR-PCR have successfully identified many *Meloidogyne* species, precisely distinguishing the thermophilic species: *M. arenaria*, *M. incognita*, *M. javanica*, and *M.*

enterolobii. This technique also efficiently distinguishes the cryophilic species: *M. hapla*, *M. fallax*, and *M. chitwoodi* (Zijlstra, 2000). Furthermore, three pairs of species-specific primers have been used in multiplex PCR for the quick identification of *M. incognita*, *M. enterolobii*, and *M. javanica* from DNA recovered from individual galls (Hu *et al*., 2011).

Genotyping using Sequencing:

Genotyping by Sequencing (GBS) is one of the high-throughput molecular approaches that has recently gained popularity and proved useful for genetic research (Elshire *et al*., 2011). According to Jarquín *et al.* (2014), GBS is a simple technique that employs next-generation sequencing of genomic fragments, such as those from nematodes, produced by certain restriction enzymes, followed by analysis using a bioinformatics pipeline. This approach demonstrates significant accuracy in elucidating intricate genetic information across several species. GBS is especially advantageous for investigating nematode genes by identifying the Single Nucleotide Polymorphisms (SNPs) across several loci and has been successfully used to assess genetic diversity in cyst nematodes (Mimee *et al*., 2015). GBS, on the other hand, is not an identifying tool. In contrast, Rashidifard *et al.* (2018) used GBS for the first time to investigate genetic diversity and perform phylogenetic analysis of *Meloidogyne* spp. populations.

Biological control of Root-Knot nematodes:

Plethora strategies have been used for managing RKN worldwide. Chemical nematicides are considered the most effective strategy. However, it is causing harmful effects on the environment, microflora, animal, and human, and polluting underground water. So, most nematicides have been banned from global markets. Recently, a lot of attention has been given to biological control. Biological control is defined as using organisms or their metabolites to decrease the population density of another organism (Bale *et al*., 2008). Different strains of bacteria, fungi, actinomycetes, yeasts, nematodes, and mites have been utilized for managing RKN. Fungal antagonists of nematodes are categorized based on their mechanisms of action as predacious fungi, endoparasites of vermiform worms, parasites of sedentary stages, antibiotic-producing fungi, and vesicular-arbuscular mycorrhizal fungi (Chen and Dickson, 2004). Predacious fungi attack nematodes by producing special devices, including adhesive hyphae, branches, nets, and knobs, and non-constructing and constructing rings (Figure 4). Fungal endoparasites of vermiform nematodes are obligate (*Hirsutella, Verticillium*, and *Haptoglossa*) or facultative (*Catenaria* and *Verticillium*) parasites. Fungi that attack nematode females, egg masses, cysts, and eggs are known as sedentary parasitic fungi. The final group is fungi that produces toxic metabolites or enzymes that may inhibit or stimulate egg hatches. *Trichoderma, Fusarium Paecilomyces, Penicillium, Aspergillus, Arthrobotrys, Drechslerella* (Chen and Dickson, 2004 and Al-Hazmi *et al.,* 2019). The potency of certain fungi against RKNs, such as *T. harzianum, T. hamatum,* and *T. viride*, has been proved by Javeed *et al.* (2016), who provided the ability of these fungi to control *M. javanica in vitro* and *in vivo*. *P. lilacinus, T. harzianum* were suppressed *M. javanica* egg hatch and increased J2s mortality percent alone and combined with humic acid (Al-Hazmi and Javeed, 2015; Javeed and Al-Hazmi, 2015 and Al-Hazmi *et al*., 2019).

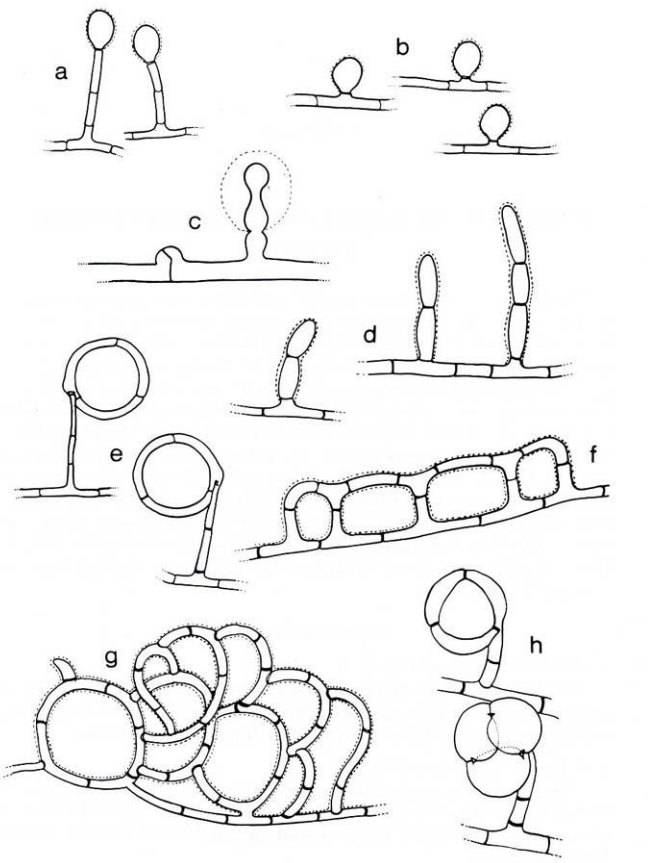

Figure (4): Structures created by predatory fungi. (a) Adhesive knobs on stalks. (b) Sessile sticky knobs. (c) Adhesive knob of *Nematoctonus*. (d) Adhesive branches. (e) Non-constricting rings. (f) Two-dimensional sticky mesh. (g) Three-dimensional sticky net. (h) Constricting rings (Barron, 1977).

Microbial pesticides mechanisms:

Comprehending the mechanisms of biocontrol in microbial pesticides is essential for the effective reduction of pathogens in their hosts. Certain strains utilize a singular biocontrol method, whereas others employ a combination of strategies. Antibiosis, a phenomenon in which microbes suppress plant-pathogenic bacteria and fungi, is frequently observed in fruit trees. *Bacillus subtilis* synthesizes cyclolipopeptides, such as fengycins, which serve to protect apple fruits from gray mold (*Botrytis cinerea*) (Ongena *et al*., 2005). Additional approaches involve phenolic antifungal compounds, such as pyrrolnitrin derived from *Pseudomonas cepacia* (Janisiewicz and Roitman, 1988), bacteriocins like herbicolin and pantocins sourced from *Pantoea* species (Ishimaru *et al*., 1988; Wright *et al*., 2001, and Smits *et al*., 2010), and lytic enzymes from *Trichoderma harzianum* aimed at controlling *Penicillium expansum* in apples (Batta, 2004). Competitive exclusion occurs when biocontrol agents outcompete pathogens for essential nutrients and colonization sites. This mechanism is prevalent in the postharvest decay of pome fruits and in the management of fire blight (Sharma *et al.,* 2009 and Cabrefiga *et al*., 2007).

Various hyperparasites, such as yeasts and fungi, including *Pichia* and *Trichoderma*, have the capability to directly degrade fungal cells, synthesize antimicrobial compounds, establish hyperparasitism, disrupt pathogen signaling, or trigger resistance in plant

hosts (Harman, 2006). Fungal viruses and bacteriophages may be employed to target specific pathogens (Jones *et al.,* 2007; Ghabrial and Suzuki, 2009). Spadaro and Gullino (2004) indicate that certain microbes, including bacterial and fungal strains, can activate plant defense mechanisms through the release of elicitors, such as cell wall components, or signaling molecules, such as salicylic acid. Finally, specific biocontrol agents impede pathogens by breaking down chemical signals essential for quorum sensing, which pathogens use to initiate infection (e.g., acyl homoserine lactones) (Molina *et al.*, 2003).

***Trichoderma* vs Root-Knot nematodes:**

Trichoderma strains are extensively used as biocontrol agents against Root-Knot nematodes all over the world. By entering egg masses and juveniles, *Trichoderma* species have shown efficacy in regulating RKNs both *in vitro* and *in vivo*. This decreases egg hatching and raises the mortality rate of second-stage juveniles (J2s) (Sahebani and Hadavi, 2008). According to Khan *et al.* (2020), the species and growth medium composition have an impact on *Trichoderma*'s effectiveness. Furthermore, *Trichoderma* generates several compounds and enzymes that degrade the cell walls of RKN stages and paralyze J2s and eggs (Sidhu *et al*., 2014). In addition to its ability to suppress nematodes, *Trichoderma* also generates phytohormones that stimulate plant development and stimulate plant systemic resistance against plant diseases (Goswami *et al*., 2008). *T. harzianum* promotes plant development by the synthesis of secondary metabolites, including harzianic acid, harzianolide, auxin, abscisic acid, and 6-pentyl-2H-pyran-2-one (Goswami *et al*., 2008, and Zin and Badaluddin, 2020). These compounds enhance lateral root development, root length, root surface area, root tips, seed germination, and seedling growth (Vinale *et al*., 2013, and Cai *et al*., 2013).

The effects of *Trichoderma* on enhancing plant defense mechanisms against nematodes and inducing systemic resistance are illustrated in the next key points: Increased Enzyme Activities: *T. harzianum* markedly enhances the activity of defense-related enzymes such as phenylalanine ammonia-lyase (PAL), peroxidase (POX), and polyphenol oxidase (PPO). This signifies an induced resistance response in plants. Howell *et al.* (2000), Evans *et al.* (2003), and Coppola *et al.* (2019) have shown that *T. harzianum* colonization may enhance the levels of certain defensive enzymes, such as chitinase, β-1,3-glucanase, and lipoxygenase.

Parasitism and Enzyme Secretion: *Trichoderma* can directly parasitize nematode eggs and juveniles by secreting enzymes such as chitinase and protease, which aid in breaking down the protective structures of the eggs. Sharon *et al.* (2001) demonstrated direct parasitism by *T. harzianum* T-203 on *M. javanica*, with extracellular protease being involved, although the rate of parasitism was low. The involvement of chitinases in attacking nematode eggs also been documented in other fungi like *Purpureocillium lilacinum* (formerly *Paecilomyces lilacinus*) and *Pochonia* spp., which were found in infected nematode eggs (Khan *et al*., 2003; Tikhonov *et al*., 2002, and Hao *et al*., 2025). This supports the concept that these enzymes facilitate the infection and degradation of nematode eggs by breaking down the chitinous structure of the eggshell.

Implications for Plant Health: The use of *Trichoderma* can be seen as a dual approach, providing direct antagonistic action against nematodes and boosting the plant's defensive

responses, making it a valuable agent in biological control strategies against nematode pests. Ahmed *et al.* (2010) documented the potential of five *Trichoderma* species, namely *T. harzianum, T. hamatum*, *T. lignorum, T. glaucum* and *T. koningii* were applied as seed dressing for enhancing plant fresh weight of sunflower, okra, and cowpea and mitigating *M. incognita* Root-Knot nematode infection.

Increase in Defense Hormones: In cucumber cotyledons, inoculation with *T. asperellum* T34 led to increased concentrations of salicylic acid (SA) and jasmonic acid (JA) within a timeframe of 3 to 48 hrs. (Segarra *et al*., 2007). Both SA and JA are crucial signaling molecules in plant defense pathways. Salicylic acid is generally associated with systemic acquired resistance (SAR) against biotrophic pathogens, while jasmonic acid is linked to resistance against necrotrophic pathogens and herbivores (Kamle *et al*., 2020).

Enzymatic Activity in *Trichoderma*: *Trichoderma*, like the other nematophagous fungi, can produce extracellular chitinase and protease enzymes. These enzymes help the fungus to penetrate the chitinous and proteinaceous barriers of nematode eggs. So, it's noted that there was an increase in the proportion of infected nematode eggs as chitinase activity rose.

Chitinase Role: Chitinases are inducible enzymes that break down chitin, which is an essential component of fungal cell walls, nematode and insect eggshells, and insect cuticles. They are necessary for various fungal functions, including hyphal growth (Takaya *et al*., 1998).

Extracellular Enzymes and Egg Penetration: Besides chitinase, *Trichoderma* may produce other lytic enzymes that contribute to egg penetration. So, a medium enriched with colloidal chitin can induce the production of various extracellular proteins, indicating the involvement of additional enzymes in degrading the eggshell structure.

Implications for Plant Immunity: *T. asperellum* T34 can act as a biological control agent by priming the plant's innate immune system. The primed state enables the plant to respond more effectively to subsequent pathogen attacks, highlighting the potential of using beneficial fungi to enhance crop resistance naturally (Sahebani and Hadavi, 2008).

Mechanism of Action: While *Trichoderma* is generally found in the soil or plant root tissues and not directly within nematode-affected plant tissues, it can still reduce nematode impact. It achieves this through:

- Direct parasitism and egg infection.
- Inducing systemic resistance in the plant, which may limit nematode penetration, feeding, and egg hatching.
- Potential production of metabolites with anti-nematode activity.

Trichoderma based products *Trichoderma* spp., are among the most commonly used microbial biological control agents in agriculture and are presently marketed as biopesticides, biofertilizers, growth enhancers, and stimulants of natural resistance, reducing environmental impact and the risk of agrochemical residues in crops.

Fusarium vs Root-Knot nematodes:

Fusarium spp. has been evaluated in different countries against RKNs. *Fusarium* strains have successfully managed RKNs *in vitro* and *in vivo*. Their effectiveness comes from producing many components in the media. Fungal strains of *Fusarium* parasitize directly on eggs and juveniles of RKNs (Sahebani and Hadavi, 2008). These fungi penetrate egg masses and

consequently decrease their hatching (Sahebani and Hadavi, 2008, and Zhang *et al*., 2015). El-Qurashi *et al.* (2019) and Qureshi *et al.* (2012) reported that *Fusarium* and *Trichoderma* strains have nematocidal activities against RKNs.

Plethora compounds have been excreted from *Fusarium* strains, showing a high potential in controlling RKNs. These compounds are found in culture filtrate, inducing a suppression of egg hatch or immobilization of juveniles. Mani *et al.* (1986) established that a blend of long-chain alkanes was accountable for the toxicity of *F. solani* to *M. incognita*. Ciancio (1995) outlined that several commercially available mycotoxins, typically generated by *Fusarium* species, were evaluated and determined to have a nematicidal effect against *M. javanica* at low doses.

Trichothecenes, such as diacetoxyscirpenol and 4,15-Diacetylnivalenol, are a significant category of tricyclic sesquiterpene mycotoxins that impede protein synthesis and are synthesized by *Fusarium* species (Sweeney and Dobson, 1998). These chemicals generated by *F. equiseiti* have efficacy against plant-parasitic nematodes (Nitao *et al*., 2001).

Mode of Action:

- Some *Fusarium* species can parasitize nematode eggs or juveniles, disrupting their life cycle.
- Others produce secondary metabolites toxic to nematodes, reducing their populations.
- Competitive exclusion by colonizing root zones, *Fusarium* strains outcompete nematodes for space and nutrients.

Fusarium-based products are gaining attention for their potential to control plant-parasitic nematodes. Through different mechanisms such as parasitism, competition, or the production of nematotoxic compounds.

Eco-Friendliness: *Fusarium*-based products are a sustainable alternative to chemical nematicides, reducing environmental impact and the risk of chemical residues in crops.

Plant Growth Promotion: Many strains also have beneficial effects on plant health by stimulating root growth or enhancing nutrient uptake.

Example products or strains:

Some non-pathogenic strains of *Fusarium oxysporum* are commercially developed as biocontrol agents. *F. oxysporum* strain 162 (Fo162) is known for its ability to suppress nematode populations while promoting plant health (Dababat and Sikora, 2007).

Application and usage:

Soil Treatment: Incorporating the product into the soil where nematodes are active.

Seed Treatment: Coating seeds to establish protective root-zone colonization.

Drip Irrigation: Delivering spores or formulated products through irrigation systems.

Limitations:

Fusarium-based biocontrol agents require optimal environmental conditions (e.g., soil pH, moisture) for effectiveness. Therefore, their activity may vary based on nematode species, population density, and crop type. So, for best results, these products are often integrated into broader Integrated Pest Management (IPM) strategies, which include crop rotation, resistant crop varieties, and other biological or cultural controls.

Types of formulations:

1. Spore-Based formulations:

These formulations rely on live *Fusarium* spores that germinate and colonize the rhizosphere (root zone), exerting biocontrol effects against nematodes. For instance: dried spore powders or granules and liquid suspensions containing fungal spores. Application methods include: a) seed

coating: coating seeds with fungal spores before planting. b) soil drench: spores are mixed with water and applied to the soil around plants. C) Drip irrigation: spores are delivered via irrigation systems for targeted nematode control.

2. Mycelium-Based formulations:

These formulations use fungal mycelium instead of spores, offering rapid establishment in the soil. Features: Effective for immediate colonization and competition in the root zone. Applications: Mixed into the soil during planting or as a pre-planting soil amendment.

3. Bio-Fertilizer Mixtures with *Fusarium*:

Fusarium strains are sometimes included in bio-fertilizers with multiple benefits involving: a) enhanced root health and nutrient uptake. b) nematode suppression through root colonization. For example, Bio-fertilizer formulations containing *Fusarium oxysporum* combined with beneficial bacteria or fungi.

4. Encapsulated Formulations:

In these products, *Fusarium* spores or metabolites are encapsulated in protective materials, ensuring longer shelf life and better survival under field conditions. Advantages: improved stability, controlled release, and compatibility with other IPM tools. Application: direct soil application or seed treatment.

5. Fermentation-Derived Metabolites:

Some products are based on nematotoxic compounds produced by *Fusarium* during fermentation. These metabolites attack nematodes directly or interfere with their reproduction. For example: liquid concentrates or dried powders derived from fungal metabolites.

6. Pre-Mixed Soil Amendments:

Fusarium is integrated into organic soil conditioners or compost-like materials to improve soil health while reducing nematode populations.

Selecting a commercial product:

The choice depends on factors like

- Target Nematode: Products are often specific to the nematode species.
- Crop Type: Some products are tailored for particular crops (e.g., vegetables, cereals, ornamentals).
- Application Method: Compatibility with your existing farming practices (e.g., seed coating, irrigation).

***Cladosporium* vs. Root-Knot nematodes:**

Cladosporium species, which belong to the Fungi imperfect group, are pigmented molds commonly found in the air, organic matter, and food. Some species are primarily present in tropical and subtropical regions (Tasic and Tasic, 2007). They are saprophytic fungi that have been isolated from both indoor and outdoor air (Park *et al*., 2004), humans (Yew *et al*., 2016), and various plant sources such as dead plants, wood, food, straw, soil, dyes, and textiles (Pereira *et al*., 2002). This genus belongs to the family Dematiaceae, characterized by fungi with melanin in the cell walls of hyphae and conidia, forming colonies with colors ranging from olive-grey to black (Răut *et al*., 2021).

This genus can break down complex carbohydrates and proteins, and its genome (UM843) encodes numerous proteins involved in melanin biosynthesis, siderophore production, cladosins, and survival in high-salinity environments (Yew *et al*., 2016). On the other hand, *Cladosporium* species are endophytic fungi isolated from different plant tissues (Hamayun *et al*., 2009, and Răut *et al*., 2021), like medicinal plants, so they do not produce plant damage. They are known as plant protectants against different

biotic and abiotic stresses. These species improve the ability of plants to adapt to new habitats and to sustain the plant's performance and health via secretion of secondary metabolites. Among the secreted metabolites, gibberellins and hormones which are responsible for stimulating plant growth, especially in seed germination, stem elongation, and leaf expansion (Archard and Genschik, 2009). Due to their secondary beneficial metabolites, *Cladosporium* can be used in agro-industrial applications, in the discoloration of textile dyes and the degradation of keratin-containing wastes from the natural environment (Ademakinwa and Agboola, 2014; Nwadiaro *et al*., 2015; Guan *et al*., 2016, and Jakovljevic and Vrvic, 2018).

According to Amatuzzi *et al.* (2018), *C. sphaerospermum*, isolated from strawberry leaves, has also been used as a biocontrol agent against the moth, *Duponchelia fovealis*. *Cladosporium* spp. have the ability to degrade the cell wall of RKN eggs and juveniles. Also, they developed their potential to paralyze eggs and juveniles. In a previous study (Figure 5), *Cladosporium* suppressed egg hatch of *M. javanica* and increased mortality percent of second-stage juveniles as well.

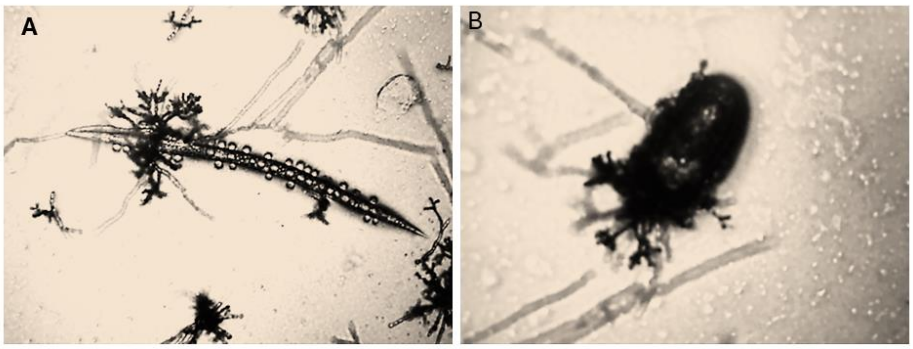

Figure (5): The parasitism of *Cladosporium sphaerospermum* on *Meloidogyne javanica* juveniles (A) and eggs (B), (Taken by the Corresponding author).

Key features of *Cladosporium* as a biocontrol agent:

Mode of Action:

- Parasitism:

Cladosporium can directly attack nematode eggs by colonizing their surfaces, penetrating the eggshells, and degrading them.

- Antagonistic activity: Produces secondary metabolites with nematotoxic effects that suppress nematode populations.
- Competition: Colonizes the rhizosphere and root surfaces, effectively competing with nematodes for space and nutrients.
- Induced Resistance: Some strains can stimulate plant defenses, enhancing the plant's ability to resist nematode infections.

Environmental and Crop Safety:

Cladosporium spp. are generally considered safe for the environment and non-toxic to plants and beneficial soil organisms. It is also compatible with other IPM practices and sustainable farming systems. Applying with other biocontrol agents (e.g., *Trichoderma* spp. or *Pseudomonas fluorescens*) often enhances efficacy.

Potential advantages:

- Sustainability: Offers an eco-friendly alternative to chemical nematicides, reducing the risk of soil and water contamination.
- Ease of Cultivation: *Cladosporium* fungi can be mass-produced using agricultural residues,

making them cost-effective for large-scale applications.

- Adaptability: Suitable for use in diverse agricultural systems, including field crops, horticulture, and greenhouses.

Limitations:

- Environmental Sensitivity: The effectiveness of *Cladosporium* may depend on soil conditions, temperature, and moisture levels.
- Field Performance: While laboratory results are promising, consistent efficacy under field conditions can vary.
- Product Availability: Few commercial products are currently available, as the use of *Cladosporium* for nematode control is still under development in many regions.

Application methods:

- Soil Drench: Liquid formulations containing *Cladosporium* spores can be applied to the root zone.
- Seed Coating: Spores are used to coat seeds, allowing fungal colonization of roots as the plant grows.
- Compost or Organic Amendments: Incorporating *Cladosporium*-enriched compost into soil.

Drechslerella vs. Root-Knot nematodes:

Drechslerella species belong to the order Orbiliales, which includes a large group of fungi. These fungi can produce devices for trapping to attack different animals. *Drechslerella*, which is known for forming constricting rings, has been isolated from nematode-infested roots or soil (Murga-Gutierrez *et al*., 2012). Besides, it was isolated from different soil types, decayed root galls of tomato, and leaf litter (Elshafie *et al*., 2006; Cho *et al*., 2008, and Singh *et al*., 2019). This genus evolved around 17 species that trap nematodes by producing constricting rings (Zhang and Hyde, 2014). The constricting ring consists of three cells as outlined by Yu *et al.* (2014). *Drechslerella* has been shown to effectively control RKNs both *in vitro* and *in vivo* (Singh *et al*., 2019). According to Hastuti *et al.* (2023), *Drechslerella* reduced *M. hapla* by 97.7% after 72 hrs. Moreover, constricting ring-forming fungus (*Arthrobotrys dactyloides*) attacked *M. javanica* J2s with more than 90% after 3 days (Galper *et al*., 1995).

Drechslerella successfully consumed RKN juveniles after 3 days (unpublished data). When juveniles of *M. javanica* moved through the constricting rings, nematodes stimulated constricting ring cells, which increased in size and closed on nematodes, preventing them from moving. Finally, the fungus consumes the nematode contents and grows (Figure 6).

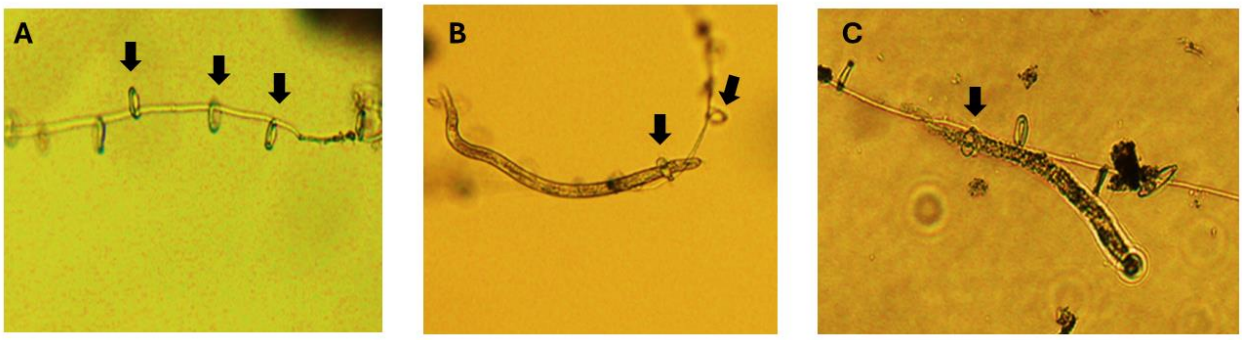

Figure (6): The constricting rings of *Drechslerella*. Where a) constricting rings of *D. brochopaga*, b) Root-Knot nematodes J2 attached to constricting ring, c) J2 after *D. brochopaga* consumed the nematode body content (Taken by the Corresponding author).

Key Features of *Drechslerella* in nematode control:

Mode of Action

Nematode Trapping: *Drechslerella* produces trapping structures, such as constricting rings, that physically capture nematodes. Once trapped, the fungus penetrates the nematode's cuticle, invades its body, and digests its contents.

Parasitism: The fungus directly parasitizes nematode juveniles, thereby significantly reducing their populations in the soil.

Secondary Metabolites: The fungus produces enzymes (e.g., proteases) and other compounds that degrade nematode cuticles and contribute to nematode mortality.

Target Nematodes

The fungus is highly effective against Root-Knot nematodes (*Meloidogyne* spp.). Also, targets other plant-parasitic nematodes, such as *Pratylenchus* (lesion nematodes) and *Heterodera* (cyst nematodes).

Plant Protection:

The fungus controls nematodes in the rhizosphere, protecting plant roots and reducing root galling. Promotes healthier root systems and indirectly improves plant growth and yield.

Advantages of *Drechslerella*:

- Eco-Friendly: Provides an environmentally sustainable alternative to chemical nematicides, with no harmful residues.
- Broad Adaptability: Functions across diverse soil types and agricultural systems.
- Synergy with IPM: The fungus is compatible with other biological control agents and practices, such as organic amendments and beneficial microorganisms.
- Durability: Once established in the soil, *Drechslerella* can persist and reproduce, providing long-term nematode control.

Limitations:

Environmental Sensitivity: Requires favorable soil conditions (moisture, organic matter) to thrive and produce trapping structures.

Field Efficacy: Laboratory and greenhouse studies have demonstrated effectiveness, but field performance can vary due to environmental factors.

Commercial Availability: Products based on *Drechslerella* are still under development, with limited commercial formulations currently available.

Application methods:

Soil Drench: Spores or fungal biomass can be applied to the soil, where the fungus colonizes and establishes a presence in the root zone.

Seed Treatment: Seeds coated with fungal spores allow early colonization of the rhizosphere.

Organic Matter Enrichment: Incorporating organic materials into the soil may enhance fungal growth and nematode-trapping activity.

Importance of biological control:

According to the biological control definition, many microorganisms and/or their products are used successfully for controlling pathogens. In this regard, many products composed of viruses, bacteria, yeasts, and fungi are marketed and essential for sustainable agriculture; nonetheless, their actual use remains constrained (Montesinos and Bonaterra, 2009). Cook and Baker (1983) contended that microbial products provide benefits, including a) the lack of residues, b) eco-friendliness, and c) low manufacturing costs, relative to chemical pesticides. Numerous biological control agents, such as *Trichoderma,* and *Cladosporium,* which stimulate plant growth and induce systemic acquired resistance, have been advocated for use as plant fertilizers.

One of the most notable benefits of biological control is its enduring

efficacy. This indicates that it might be a very economical pest management strategy, with advantages potentially surpassing the original project expenses by significant margins (Hoddle, 2004). A significant benefit of effective biological control is the reduction in the use of large quantities of pesticides, which are recognized as detrimental to non-target species, vertebrates, and people. Over 100 types of advantageous organisms are marketed for the management of significant pests and infections. Biocontrol agents provide distinct benefits, particularly in scenarios where pests exhibit resistance to insecticides. Moreover, the primary benefit of using biological management is its potential to serve as the only remedy for the restoration of ecosystems affected by invasive species (Blossey *et al*., 2001).

Limitations of using biological control

Biological control applications have disadvantages, such as the different efficiency influenced by many biotic and abiotic factors. Additionally, their specificity is at a high level against the target disease and pathogen, which may require the application of multiple microbial pesticides (Bonaterra *et al.,* 2012). Biocontrol, including the introduction of non-native species, may result in considerable ecological risks. These species may become invasive, disseminating beyond their introduction area and adversely impacting the ecosystem (Jennings *et al*., 2017). Furthermore, while biocontrol is often implemented on a limited scale, its viability on a broader scale is still questionable. Despite the genetic stability of biocontrol agents, their success has been limited, partly due to the effects of climate change. Certain biocontrol agents display predatory behavior only in nutrient-deficient conditions, rather than in normal environments. For example, *Trichoderma* species do not attack *Rhizoctonia solani* in the presence of bark compost, since the availability of cellulose affects the activation of genes that encode chitinase, an enzyme involved in parasitic behavior (Pal and Gardener, 2006).

The suboptimal efficacy of microbial pesticides is often ascribed to the failure of biocontrol agents to adequately colonize and last in the applied environment, where their fitness diminishes under field circumstances. This is particularly true for the phyllosphere and, to a lesser extent, the rhizosphere, both of which experience significant variations in environmental and phenological conditions. Additionally, these regions possess a robust native microbiota that is difficult for non-native microbes to supplant. Improving the competitiveness of biocontrol agents in the plant environment is essential for augmenting their biocontrol efficacy, and many ways may be used to accomplish this (Bonaterra *et al*., 2012).

Overcoming the biological control limitations:

An effective strategy involves enhancing the nutritional environment for the biological control agents to boost their growth within the plant ecosystem and/or to inhibit the growth of competing microorganisms. This can include using specific chemicals alongside a biocontrol agent strain to suppress competing or antagonistic native microbes or adding nutrients to formulations that the biocontrol agent can utilize more effectively than the pathogen. Such approaches have been shown to improve the biocontrol agent's survival, adaptability, and biocontrol effectiveness against various plant pathogens (Guetsky *et al*., 2002, and Druvefors *et al*., 2005). For example, the effectiveness of biocontrol for fire blight infections using *Pseudomonas fluorescens* 62e was enhanced by adding glycine and Tween

80, without impacting the infection potential of the bacterium *Erwinia amylovora* (Cabrefiga *et al*., 2011). Another approach involves modifying the physiology of the biological control agent to help it withstand challenging conditions after being applied in natural environments (Such as soil, rhizosphere, or phyllosphere). Many microorganisms survive osmotic stress by a process called osmoadaptation, where they accumulate compatible solutes (Like sugars, glycosides, amino acids, and their derivatives) within their cells. This adaptation can be triggered by cultivating the microorganisms under suboptimal conditions, allowing them to endure drought, salinity, freezing, and high temperatures, thereby enhancing their ecological fitness (Csonka and Hanson, 1991; Miller and Wood, 1996; and Welsh and Herbert, 1999). Combining osmoadaptation with strategies like nutritional enhancement further strengthens the fitness of biocontrol agents on aerial plant surfaces. A method using both approaches has been developed to boost colonization and survival in the phyllosphere of Rosaceous plants, thereby improving the fitness and effectiveness of the fire blight biocontrol agent, *Pseudomonas fluorescens* EPS62e (Cabrefiga *et al*., 2011).

Another approach to enhancing biological control involves combining antagonistic agents with different biocontrol mechanisms (Spadaro and Gullino, 2005, and Stockwell *et al*., 2011). When compatible strains are used together, they can achieve broader colonization of the plant surface and enhance key biocontrol traits, which improves pathogen suppression across a wider range of environmental conditions than when applied individually. For instance, combining two *P. fluorescens* strains improved the control of *Phytophthora* root rot in strawberries and reduced variability in treatment outcomes (Agustí *et al*., 2011).

Enhancing biocontrol agents can also be achieved through genetic modification, which has the benefit of embedding sustainable traits in the biocontrol agent's progeny. Breeding-based approaches may be used to overexpress genes that produce existing metabolites, introduce new genes, or develop strains that generate higher levels of antimicrobial compounds, as well as manipulate the timing of their production (Walsh *et al.*, 2001). Various genetic modifications have been applied to improve biocontrol in the rhizosphere, including the overproduction of antimicrobial compounds, as seen in *T. harzianum* and *P. fluorescens* CHAO (Flores *et al*., 1997, and Girlanda *et al*., 2001). The use of genetically engineered biocontrol agent strains is restricted by the European United (EU) regulations due to potential environmental and ecological risks. EU legislation sets stringent and comprehensive requirements for the environmental release and commercial use of genetically modified biological control agents, including extensive environmental impact assessments and risk analyses for both the biological control agent and its products. Although, these risks may be reduced by carefully selecting genetic constructs, opting for chromosomal rather than plasmid-based gene insertions, and using delivery systems that limit translocation and dispersal (van Elsas and Migheli, 1999).

Conclusion

Root-Knot nematodes are causing more severe damage for most cultivated crops worldwide. The initial step for regulating *Meloidogyne* is identifying the pest accurately using conventional and molecular methods. Accurate identification is crucial for selecting

management strategies. Biological control nowadays is important as an alternative to chemical control. Many advantages and disadvantages have been reported for biological control. Thus, we can assume that the advantages of biocontrol overcome their cons. *Trichoderma*, *Fusarium, Cladosporium*, and *Drechslerella* are known as bioagents against *Meloidogyne.* The ability of *Trichoderma* to trigger hormone-mediated defense responses illustrates its potential for integrated disease management in agriculture. The ability of *Cladosporium* to degrade the extensive disulfide crosslinking of keratin polypeptides and solubilize the keratin by secreting specialized enzymes can be used to obtain plant biostimulants and recommend *Cladosporium* as a fungal agent to promote plant growth. *Drechslerella* traps J2s of *Meloidogyne* and decreases their population densities in soil. On the other hand, *Trichoderma* and *Fusarium* successfully managed *Meloidogyne* by producing many metabolites and enzymes that degrade and toxic to nematodes.

Declaration of interest:

The authors declare there is no competing interest.

Data availability:

All available data has been published in the article. Figures (5 and 6) were captured and are available from the corresponding author upon reasonable request.

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References

A**demakinwa, N.A. and Agboola, F.K. (2014):** Production of Laccase by *Auerobasidium pullulans* and *Cladosporium werneckii* under optimized conditions: Applications in decolourization of textile dye. Res. Rev. J. Microbiol Biotechnol, 3: 32–40.

Agustí, L.; Bonaterra, A.; Moragrega, C.; Camps, J. and Montesinos, E. (2011): Biocontrol of root rot of strawberry caused by *Phytophthora cactorum* with a combination of two *Pseudomonas fluorescens* strains. J. Plant Pathol., 93:363–372.

Ahmed, S.M.M.; Mostafa, F.A.M., and Mazaty, M.A.A. (2010): Evaluation of five species of *Trichoderma* for the biocontrol of *Meloidogyne incognita* infecting sunflower, okra and cowpea .1. Seed dressing application. Egypt. J. Agronematol., 9(2):157-171.

Al-Hazmi, A. S.; Al-Yahya, F. A. and Abdul-Razig, A.T. (1995): Occurrence, distribution and plant associations of plant nematodes in Saudi Arabia. Research Bulletin No. 52, Agricultural Research Center, College of Agriculture, King Saud University Pp.45.

Al-Hazmi, A.S. and Javeed, M.T. (2015): Effects of different inoculum densities of *Trichoderma harzianum* and *Trichoderma viride* against *Meloidogyne javanica* on tomato. Saudi Journal of Biological Sciences, 23: 288- 292. http://dx.doi.org/10.1016/j.sjbs.2015.04.007

Al-Hazmi, A.S.; Al-Yahya, F.A.; AbdelRafaa, O.A., and Lafi, H.A. (2019): Effect of humic acid, *Trichoderma harzianum,* and *Paecilomyces lilacinus* on *Meloidogyne javanica.* International Journal of Agriculture, Environment and Bioresearch, 4: 61- 74.

Al-Hazmi, ASA.S.; Dawabah, A.A.M,; Al-Yahya, F.A., and Al-Nadary, S.N. (2009): Plant parasitic nematodes associated with coffee, a newly introduced crop to South

WestSouthwest Saudi Arabia. Pak. J. Nematol., 27 (2): 401-407.

Ali, S.S. and Sharma, S.B. (2003): Nematode survey of chickpea production areas in Rajasthan, India. Nematol. Medit., 31:147–149.

Almohithef, A.H.; Al-Yahya, F.A.; Al-Hazmi, A.S.; Dawabah, A.A.M. and Lafi, H.A. (2018): Prevalence of plant-parasitic nematodes associated with certain greenhouse vegetable crops in Riyadh region, Saudi Arabia. Journal of the Saudi Society of Agricultural Sciences. https: //doi.org/10.1016/j.jssas.2018.05.00 1

Amatuzzi, R.F.; Cardoso, N.; Poltronieri, A.S.; Poitevin, C.G.; Dalzoto, P.; Zawadeneak, M.A. and Pimentel, I.C. (2018): Potential of endophytic fungi as biocontrol agents of *Duponchelia fovealis* (Zeller) (Lepidoptera: Crambidae). Brazilian Journal of Biology, 78: 429-435. http://dx.doi.org/10.1590/1519-6984.166681

Archard, P. and Genschik, P. (2009): Releasing the brakes of plant growth: How GAs shutdown DELLA proteins. J. Exp. Bot., 60:1085–1092.

Bale, J.S.; van Lenteren, J.C. and Bigler, F. (2008): Biological control and sustainable food production. Philos. Trans. R. Soc. Lond. B Biol. Sci., 363: 761–776. doi:10.1098/rstb.2007 .2182

Barron, G.L. (1977): The nematode-destroying fungi 1st ED., Guelph-Ontario, Canada. Canadian Biological Publications Ltd. Pp 140. https://doi.org/10.1002/jobm.19790 190412

Batta, Y.A. (2004): Effect of treatment with *Trichoderma harzianum* Rifai formulated in invert emulsion on postharvest decay of apple blue mold. International Journal of Food Microbiology, 96(3): 281-288. https://doi.org/10.1016/j.ijfoodmicr o.2004.04.002

Bekker, S.; Fourie, H.; Rashidi, M.; Daneel, M.; Shokoohi, E. and Nel, A. (2016): Discriminating between the eggs of two egg-mass-producing nematode genera using morphometric and molecular techniques. Nematology, 18(9): 1119-1123. doi:10.1163/156 85411-00003022.

Berkeley, M.J. (1855): Vibrio forming cysts on the roots of cucumbers. Gardener's Chronicle and Agricultural Gazette, 14: 220.

Blok, V.C. (2005): Achievements in and future prospects for molecular diagnostics of plant-parasitic nematodes. Canadian Journal of Plant Pathology, 27(2): 176-185. https://doi.org /10.1080/07060660509507214

Blok, V.C. and Powers, T.O. (2009): Biochemical and molecular identification. In: Perry, R.N.; Moens, M. and Starr, J.L. (Eds.), Root-Knot nematodes (pp. 98-118). Wallingford: CAB International. https://doi.org/10.1079/9781845934 927.0098

Blok, V.C.; Wishart, J.; Fargette, M.; Berthier, K. and Phillips, M.S. (2002): Mitochondrial DNA differences distinguishing *Meloidogyne mayaguensis* from the major species of tropical Root-Knot nematodes. Nematology, 4(7): 773-781. doi10.1163/156854102760402 559

Blossey, B.; Skinner, L.C. and Taylor, J. (2001): Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. Biodiversity Conserv., 10:1787–1807.

Bonaterra, A.; Badosa, E.; Cabrefiga, J.; Frances, J. and Montesinos, E. (2012): Prospects and limitations of microbial

pesticides for control of bacterial and fungal pome fruit tree diseases. Trees, 26: 215- 226. doi 10.1007/s00468-011-0626-y

Cabrefiga, J.; Bonaterra, A. and Montesinos, E. (2007): Mechanisms of antagonism of *Pseudomonas fluorescens* EPS62e against *Erwinia amylovora*, the causal agent of fire blight. International Microbiology, 10(2): 123. http://hdl.handle.net/10256/7763

Cabrefiga, J.; Francés, J.; Montesinos, E. and Bonaterra, A. (2011): Improvement of fitness and efficacy of a fire blight biocontrol agent via nutritional enhancement combined with osmoadaptation. Appl. Environ. Microbiol., 77: 3174–3181. https://doi.org/10.1128/ AEM. 02760-10

Cai, F.; Yu, G.; Wang, P.; Wei, Z.; Fu, L.; Shen, Q. and Chen, W. (2013): Harzianolide, a novel plant growth regulator and systemic resistance elicitor from *Trichoderma harzianum*. Plant Physiol. Biochem., 73:106-113. https://doi.org/10.1016/j.plaphy.201 3.08.011

Chen, Q.; Brown, D.J.F.; Curtis, R.H. and Jones, J.T. (2003): Development of a magnetic capture system for recovery of *Xiphinema americanum*. Annals of Applied Biology, 143(3): 283-289. doi: 10.1111/j.1744-7348. 2003.tb00296.x

Chen, Q.; Robertson, L.; Jones, J.T.; Blok, V.C.; Phillips, M.S., and Brown, D.J.F. (2001): Capture of nematodes using antiserum and lectin-coated magnetized beads. Nematology, 3(6): 593-601. doi: 10.1163/156854101753389202

Chen, S. and Dickson, D.W. (2004): Biological control of nematodes by fungal antagonists. In: Chen, Z.X.; Chen, S.Y. and Dickson, D.W. (eds) Nematology-Advances and Perspectives Vol2 Nematode Management and Utilization. CABI CABI, Wallingford, UK, Pp. 979-1039.

Chitwood, B.G. (1949): Root-Knot nematodes, part I. A revision of the genus *Meloidogyne* Goeldi, 1887. Proceedings of the Helminthological Society of Washington, 16(2): 90-104.

Cho, C.H.; Kang, D.S.; Kim, Y.J. and Whang, K.S. (2008): Morphological and phylogenetic characteristics of a nematophagous fungus, *Drechslerella brochopaga* Kan-23. Korean Journal of Microbiology, 44: 63- 68.

Ciancio, A. (1995): Observations on the nematicidal properties of some mycotoxins. Fundam. Appl. Nematol., 18:451–454.

Cook, R.J. and Baker, K.F. (1983): The nature and practice of biological control of plant pathogens. American Phytopathological Society, Minnesota, USA.

Coppola, M.; Diretto, G.; Digilio, M.C.; Woo, S.L.; Giuliano, G.; Molisso, D. and Rao, R. (2019): Transcriptome and metabolome reprogramming in tomato plants by *Trichoderma harzianum* strain T22 primes and enhances defense responses against aphids. Frontiers in Physiology, 10: 745. https://doi.org/10.3389/fphys.2019. 00745

Coyne, D.L.; Cortada, L.; Dalzell, J.J.; Claudius-Cole, A.O.; Haukeland, S.; Luambano, N. and Talwana, H. (2018): Plant-parasitic nematodes and food security in Sub-Saharan Africa. Annu. Rev. Phytopathol., 56:381-403. doi: 10.1146/annurev-phyto-080417-045833

Csonka, L.N. and Hanson, A.D. (1991): Prokaryotic osmoregulation: genetics and physiology. Annu. Rev.

Microbiol., 45:569–606. https://doi.org/10.1146/annurev.mi. 45.100191.00303 3

Cunha, T.G.; Visotto, L.E.; Lopes, E.A.; Oliveira, C.M.G. and God, P.I.V.G. (2018): Diagnostic methods for identification of Root-Knot nematodes species from Brazil. Ciência Rural, Santa Maria, 48: 02. http://dx.doi.org/10.1590/0103-8478cr2017044

Curran, J.; Baillie, D.L. and Webster, J.M. (1985): Use of genomic DNA restriction fragment length differences to identify nematode species. Parasitology, 90(1): 137-144. doi:10.101 7/S0031182000049088

Dababat, A.A. and Sikora, R.A. (2007): Influence of the mutualistic endophyte *Fusarium oxysporum* 162 on *Meloidogyne incognita* attraction and invasion. Nematology, 9(6): 771-776. https://doi.org/10.1163/1568541077 82331225

De Ley, I.; Karssen, G.; De Ley, P.; Vierstraete, A.; Waeyenberge, L.; Moens, M. and Vanfleteren, J. (1999): Phylogenetic analyses of internal transcribed spacer region sequences within *Meloidogyne*. Journal of Nematology, 31(4): 530-531.

Devran, Z. and Söğut, M. (2009): Distribution and identification of Root-Knot nematodes from Turkey. Journal of Nematology, 41(2): 128–133. PMCID: PMC3365313 PMID: 22661785

Druvefors, U. A.; Passoth, A. and Schnurer, J. (2005): Nutrient effects on biocontrol of *Penicillium roqueforti* by Pichia anomala J121 during airtight storage of wheat. Appl. Environ. Microbiol., 71:1865–1869. doi: 10.1128/AEM.71.4.1865 -1869.2005

Eisenback, J.D. and Hunt, D.J. (2009): General morphology. In: Perry, R.N.; Moens, M. and Starr, J.L. (Eds.), Root-Knot nematodes (pp. 18-54). Wallingford: CAB International. https: //doi.org/10.1079/9781845934927.0 018

Eisenback, J.D.; Hirschmann, H.; Sasser, J.N. and Triantaphyllou, A.C. (1981): A guide to the four most common species of Root-Knot nematodes (*Meloidogyne* spp.), with a pictorial key 1st ED., The United States Agency for International Development, Raleigh, North Carolina.

Elling, A.A. (2013): Major emerging problems with minor *Meloidogyne* species. Phytopathology, 103: 1092-1102. http://dx.doi.org/10.1094/PHYTO-01-13-0019-RVW

El-Qurashi, M. A.; Al-Yahya, F.A.; Al-Hazmi, A.S., and Saleh, A.A. (2023): Efficacy of biologically synthesized nanoparticles on suppression plant-parasitic nematodes: a review. Egyptian J. Agronematology, 22(2): 41- 60. doi: 10.21608/ejaj.2023.323776

El-Qurashi, M.A. and Al-Yahya, F. (2025): A comprehensive review of biological agents against plant-parasitic nematodes. Egyptian J. Phytopathol., 53(2): 51- 72. doi: 10.21608/EJP.20 25.399978.1147

El-Qurashi, M.A.; Al-Yahya, F.; Almasrahi, A., and Shakeel, A. (2025): Growth and resistance response of eleven eggplant cultivars to infection by the javanese Root-Knot nematode – *Meloidogyne javanica* under greenhouse conditions. Plant Protect. Sci., 61(3):291-300. doi:10.17221/185/2024-PPS.

El-Qurashi, M.A.; El-Zawahry, A.M.I.; Abd-El-Moneem, K.M.H. and Hassan, M.I. (2017): Morphological and molecular identification of Root-Knot

nematodes infecting pomegranate in Assiut Governorate, Egypt. Journal of Phytopathology and Pest Management, 4: 30-37. https://ppmj.net/index.php/ppmj/article/view/111

El-Qurashi, M.A.; El-Zawahry, A.M.I.; Abd-El-Moneem, K.M.H. and Hassan, M.I. (2019): Occurrence, population density and biological control of Root-Knot nematode, *Meloidogyne javanica* infecting pomegranate orchards in Assiut Governorate, Egypt. Assiut J. Agri. Sci., 50: 176-189. https://doi.10.21608/ajas.2019.41818

Elshafie, A.E.; Al-Mueini, R.; Al-Bahry, S.N.; Akindi, A.Y.; Mahmoud, I. and Al-Rawahi, S.H. (2006): Diversity and trapping efficiency of nematophagous fungi from Oman. Phytopathologia Mediterranea, 45: 266- 270. http://www.jstor.org/stable/26463263

Elshire, R. J.; Glaubitz, J.C.; Sun, Q.; Poland, J.A.; Kawamoto, K.; Buckler, E.S. and Mitchell, S.E. (2011): A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PloS One, 6(5): e19379. doi: 10.1371/journal.pone.0019379.

Esbenshade, P.R. and Triantaphyllou, A.C. (1985): Use of enzyme phenotypes for identification of *Meloidogyne* species (Nematoda: Tylenchida). Journal of Nematology, 17(1): 6-20.

Evans, H.C.; Holmes, K.A. and Thomas, S.E. (2003): Endophytes and mycoparasites associated with an indigenous forest tree, *Theobroma gileri*, in Ecuador and a preliminary assessment of their potential as biocontrol agents of cocoa diseases. Mycol Progress, 2: 149–160. https://doi.org/10.1007/s11557-006-0053-4

Flores, A.; Chet, I. and Herrera-Estrella, A. (1997): Improved biocontrol activity of *Trichoderma harzianum* by over-expression of the proteinase-encoding gene prb1. Curr. Genet., 31:30–37. doi: 10.1007/s002940050173

Galper, S.; Eden, L.M.; Stirling, G.R. and Smith, L.J. (1995): Simple methods of assessing the predacious activity of nematode-trapping fungi. Nematologica, 41: 130- 140. https://doi.org/10.1163/003925995X00107

Ghabrial, S.A. and Suzuki, N. (2009): Viruses of plant pathogenic fungi. Annual Review of Phytopathology, 47(1): 353-384. https://doi.org/10.1146/annurev-phyto-080508-081932

Girlanda, M.; Perotto, S.; Moenne-Loccoz, Y.; Bergero, R.; Lazzari, A.; Defago, G.; Bonfante, P. and Luppi, A.M. (2001): Impact of biocontrol *Pseudomonas fluorescens* CHAO and a genetically modified derivative on the diversity of culturable fungi in the cucumber rhizosphere. Appl. Environ. Microbiol., 67:1851–1864. doi: 10.1128/ AEM.67. 4.1851-1864.2001

Göldi, E.A. (1887): Relatorio sobre a molestia do cafeeiro na provincia do Rio de Janeiro. Rio de Janeiro: Imprensa Nacional.

Goswami, J.; Pandey, R.K.; Tewariand, J.P. and Goswami, B.K. (2008): Management of root knot nematode on tomato through application of fungal antagonists, *Acremonium strictum* and *Trichoderma harzianum*. Environ. Sci. Health J., 43: 237-240. doi:10.1080/0360123 0701771164

Guan, G.Q.; Zhao, P.X.; Zhao, J.; Wang, M.J.; Huo, S.H.; Cui, F.J. and Jiang, J.X. (2016): Production

and Partial Characterization of an Alkaline Xylanase from a Novel Fungus *Cladosporium oxysporum*. Hindawi Publishing Corporation. BioMed Res. Int. 4575024.

Guetsky, R.; Elad, Y.; Shtienberg, D. and Dinoor, A. (2002): Improved biocontrol of *Botrytis cinerea* on detached strawberry leaves by adding nutritional supplements to a mixture of *Pichia guilermondii* and *Bacillus mycoides*. Biocontrol Science and Technology, 12: 625–630. doi:10.1080/0958315021000016289

Hamayun, M.; Ahmad, N.; Tang, D.S.; Kang, S.M.; Na, C.I.; Sohn, E.Y.; Hwang, Y.H.; Shin, D.H. and Lee, I.J. (2009): *Cladosporium sphaerospermum* as a new plant growth-promoting endophyte from the roots of *Glycine max* (L.) Merr. World J. Microbiol. Biotechnol., 25: 627–632. Doi: 10.1007/s11274-009-9982-9

Hao, L.; Zhao, F.; Guo, Y.; Ma, Y.; Li, Z.; Wang, W. and Wang, R. (2025): Antagonistic activity of *Pochonia chlamydosporia* against three helminth eggs and characterization of its serine protease. Veterinary Parasitology 334: 110374. https://doi.org/10.1016/j.vetpar.2024. 110374

Harman, G.E. (2006): Overview of Mechanisms and Uses of *Trichoderma* spp. Phytopathology, 96(2): 190-194. https://doi.org/10.1094/PHYTO-96-0190

Hastuti, L.D.; Sari, R.W.; Fauzi, F.; Naibaho, D.C.; Purba, R.T. and Putri, Q.A. (2023): Nematophagous fungi isolated from municipal wast-contaminated soil in Medan city, north Sumatera: morphological identification, phylogeny analysis and assessment as Root-Knot nematodes biocontrol. Yuzuncu Yil University. Journal of Agricultural Sciences, 33. https://doi.org/10.29133/yyutbd.1230261

Hoddle, M.S. (2004): Restoring balance: using exotic species to control invasive exotic species. Conserv. Biol., 18: 38–49.

Howell, R.; Hanson, E.L.; Stipanovic, R.D. and Puckhaber, L.S. (2000): Induction of terpenoid synthesis in cotton roots and control of *Rhizoctonia solani* by seed treatment with *Trichoderma virens*. Phytopathology, 90: 248–252.

Hu, M.X.; Zhuo, K. and Liao, J.L. (2011): Multiplex PCR for the simultaneous identification and detection of *Meloidogyne incognita*, *M. enterolobii*, and *M. javanica* using DNA extracted directly from individual galls. Phytopathology, 101(11):1270-1277. doi:10.1094/PHYTO-04-11-0095. PMID: 21770774

Hunt, D.J. and Handoo, Z.A. (2009): Taxonomy, identification and principal species. In: Perry RN, Moens M, Starr JL (Eds.), Root-Knot nematodes. CAB International, Wallingford, pp 55- 97. https://doi.org/10.1079/9781845934927.005

Hunt, D.J.; Palomares-Rius, J.E. and Manzanilla-Lopez, R.H. (2018): Identification, morphology and biology of plant parasitic nematodes. In: Sikora, R.A.; Coyne, D.; Hallmann, J. and Timper, P. (eds) Plant Parasitic Nematodes in Subtropical and Tropical Agriculture. CABI, Wallingford, UK, Pp. 20-61.

Hussey, R.S. and Janssen, G.J.W. (2002): Root-Knot nematodes: *Meloidogyne* species. In: Starr, J.L.; Cook, R. and Bridge, J. (eds.) Plant Resistance to Parasitic Nematodes. CABI Wallingford, UK, Pp. 43- 70.

https://doi.org/10.1079/9780851994666.0043

Ishimaru, C.A.; Klos, E.J. and Brubaker, R.R. (1988): Multiple antibiotic production by *Erwinia herbicola*. Phytopathology, 78(6): 746- 750.

Jakovljevic, V.D. and Vrvic, M.M. (2018): Potential of pure and mixed cultures of *Cladosporium cladosporioides* and *Geotrichum candidum* for application in bioremediation and detergent industry. Saudi J. Biolol. Sci., 25: 529–536.

Janisiewicz, W.J. and Roitman, J. (1988): Biological control of blue mold and gray mold on apple and pear with *Pseudomonas cepacia*. Phytopathology, 78(12): 1697- 1700.

Janssen, T.; Karssen, G.; Verhaeven, M.; Coyne, D. and Bert, W. (2016): Mitochondrial coding genome analysis of tropical Root-Knot nematodes (*Meloidogyne*) supports haplotype-based diagnostics and reveals evidence of recent reticulate evolution. Scientific Reports, 6: 1-13. doi:10.1038/srep22591

Jarquín, D.; Kocak, K.; Posadas, L.; Hyma, K.; Jedlicka, J., Graef, G. and Lorenz, A. (2014): Genotyping by sequencing for genomic prediction in a soybean breeding population. BMC Genomics, 15: 740. doi:10.1186/1471-2164-15-740

Javeed, M.T. and Al-Hazmi, A.S. (2015): Effect of *Trichoderma harzianum* on *Meloidogyne javanica* in tomatoes as influenced by time of the fungus introduction into soil. Journal of Pure and Applied Microbiology, 9: 535- 539.

Javeed, M.T.; Al-Hazmi, A.S. and Molan, Y.Y. (2016): Antagonistic effects of some indigenous isolates of *Trichoderma* spp. against *Meloidogyne javanica*. Pakistan Journal of Nematology, 34 (2): 183-191. http://dx.doi.org/10.18681/pjn.v34.i02.p183

Jennings, D.E.; Duan, J.J. and Follett, P.A. (2017): Environmental impacts of arthropod biological control: an ecological perspective. In: Coll, M. and Wajnberg, E. (eds) Environmental pest management: challenges for agronomists, ecologists, economists and policymakers. Wiley, Chichester, p 105. https://doi.org/10.1002/9781119255574.ch5

Jones, J.B.; Jackson, L.E.; Balogh, B.; Obradovic, A.; Iriarte, F.B. and Momol, M.T. (2007): Bacteriophages for plant disease control. Annu. Rev. Phytopathol., 45(1): 245- 262. https://doi.org/10.1146/annurev.phyto.45.062806.094411.

Jones, J.T.; Haegeman, A.; Danchin, E.G.; Gaur, H.S.; Helder, J.; Jones, M.G.; Kikuchi, T.; Manzanilla-López, R.; Palomares-Rius, J.E.; Wesemael, W.M. and Perry, R.N. (2013): Top 10 plant-parasitic nematodes in molecular plant pathology. Mol. Plant Pathol., 14(9): 946- 61. DOI: 10.1111/mpp.12057

Kamle, M.; Borah, R.; Bora, H.; Jaiswal, A.K.; Singh, R.K. and Kumar, P. (2020): Systemic acquired resistance (SAR) and induced systemic resistance (ISR): Role and mechanism of action against phytopathogens. Fungal Biotechnology and Bioengineering, 457- 470. https://doi.org/10.1007/978-3-030-41870-0_20

Karssen, G. and Moens, M. (2006): Root-Knot nematodes. In: Perry, R.N. and Moens, M. (Eds.), Plant Nematology, pp. 59-90. CABI. https://doi.org/10.1079/9781845930561.0059

Khan, A.; Williams, K.; Molloy, M.P. and Nevalainen, H. (2003): Purification and characterization of a serine protease and chitinases from *Paecilomyces lilacinus* and detection of chitinase activity on 2D gels. Protein Expression and Purification, 32: 210-220. https://doi.org/101016/j.pep.2003.07.007

Khan, R.A.A.; Najeeb, S.; Mao, Z.; Ling, J.; Yang, Y.; Li, Y. and Xie, B. (2020): Bioactive secondary metabolites from *Trichoderma* spp. against phytopathogenic bacteria and Root-Knot nematode. Microorg, 8: 401. https://doi.10.3390/microorganisms 8030401

Kumar, V.; Khan, M.R. and Walia, R.K. (2020): Crop loss estimations due to plant-parasitic nematodes in major crops in India. Natl. Acad. Sci. Lett., 43(5): 409–412. https://doi.org/10.1007/s40009-020-00895-2

Landa, B.B.; Rius, J.E.P.; Vovlas, N.; Carneiro, R.M.D.G.; Maleita, C.M.N.; de O Abrantes, I.M. and Castillo, P. (2008): Molecular characterization of *Meloidogyne hispanica* (Nematoda, Meloidogynidae) by phylogenetic analysis of genes within the rDNA in *Meloidogyne* spp. Plant Disease, 92(7): 1104-1110. doi: 10.1094/PDIS-92-7-1104

Lima, F.S.O.; Correa, V.R.; Nogueira, S.R. and Santos, P.R.R. (2017): Nematodes affecting soybean and sustainable practices for their management. In: Kasai M (eds) Soybean-the Basis of Yield, Biomass and Productivity. In Tech. http://dx.doi.org/10.5772/67030

Mani, A.; Sethi, C.L. and Devkumar (1986): Isolation and identification of nematoxins produced by *Fusarium solani* (Mart) Sacc. Indian J. Nematol., 16: 247–251.

McSorley, R.; Arnett, J.D.; Bost, S.C.; Carter, W.W.; Hafez, S.; Johnson, A.W.; Kirkpatrick, T.; Nyczepir, A.P.; Radewald, J.D.; Robinson, A.F. and Schmitt, D.P. (1987): Bibliography of estimated crop losses in the United State due to plant-parasitic nematodes. Annals of Applied Nematology, 1: 6-12.

Miller, K.J. and Wood, J.M. (1996): Osmoadaptation by rhizosphere bacteria. Annu. Rev. Microbiol., 50: 101-136. https://doi.org/10.1146/annurev.micro.50.1.101

Mimee, B.; Duceppe, M.O.; Véronneau, P.Y.; Lafond-Lapalme, J.; Jean, M.; Belzile, F. and Bélair, G. (2015): A new method for studying population genetics of cyst nematodes based on Pool-Seq and genomewide allele frequency analysis. Molecular Ecology Resources, 15(6): 1356-1365. doi:10.1111/1755-0998.12412

Moens, M.; Perry, R.N. and Starr, J.L. (2009): *Meloidogyne* species a diverse group of novel and important plant parasites. In: Perry, R.N.; Moens, M. and Starr, J.L. (Eds.) Root-Knot nematodes. CAB International, Wallingford, pp. 1-17. https://doi.org/10.1079/9781845934927.0001

Mohamed, M.M.M.; Al-Yahya, F.; Yassin, M.; El-Qurashi, M.; Gboyega, Y. and Yousif, H. (2023): Plant nematodes associated with crop plants in Jazan Region, southwest of Saudi Arabia. Journal of Agricultural & Marine Sciences (JAMS), 28 (2): 89- 89.

Mokbel, A.A. (2014): Nematodes and their associated host plants cultivated in Jazan province, Southwest Saudi Arabia. Egypt. J. Exp. Biol. (Zool.), 10 (1): 35- 39.

Molina, L.; Constantinescu, F.; Michel, L.; Reimmann, C.; Duffy, B. and Défago, G. (2003):

Degradation of pathogen quorum-sensing molecules by soil bacteria: a preventive and curative biological control mechanism. FEMS Microbiology Ecology, 45(1): 71-81. https:/ /doi.org/10.1016/S0168-6496(03)00125-9

Montesinos, E. and Bonaterra, A. (2009): Microbial pesticides. In: Schaechter M (ed), Encyclopedia of Microbiology, 3rd Edition, Elsevier, Amsterdam, 110-120. http://dx.doi.org/10.1016/b978-012373944-5.00125-5

Mukherjee, A.; Ghosh, A.; Chatterjee, C.; Mitra, A. and Mandal, F.B. (2011): Diversity nematodes inhibiting some major crop plants of India with a note on their biocontrol. J. Environ. Sociobiol., 8(1): 103- 107.

Murga-Gutierrez, S. N.; Colagiero, M.; Rosso, L.C.; Finetti Sialer, M.M. and Ciancio, A. (2012): Root-Knot nematodes from asparagus and associated biological antagonists in Peru. Nematropica, 42: 57- 62.

Nega, A. (2014): Review on Nematode Molecular Diagnostics: From Bands to Barcodes. Journal of Biology, Agriculture and Healthcare, 4(27): 129- 153.

Nicol, J.M.; Turner, S.J.; Coyne, D.L.; Nijs, L.; Hockland, S. and Maafi, Z.T. (2011): Current Nematode Threats to World Agriculture. In: Jones, J.; Gheysenm, G. and Fenoll, C. (eds) Genomics and Molecular Genetics of Plant-Nematode Interactions. Springer, Dordrecht, Pp. 21- 43. https://doi.org/10.1007/978-94-007-0434-3_2

Nitao, J.K.; Meyer, S.L.F.; Schmidt,W.F.; Fettinger, J.C. and Chitwood, D.J. (2001): Nematode-antagonistic trichothecenes from *Fusarium equiseti*. Journal of Chemical Ecology, 27: 859- 869.

Nwadiaro, P.; Ogbonna, A.; Ponchang, W. and Adekojo, D. (2015): Keratinolytic activity of *Cladosporium* and *Trichoderma* species isolated from barbers' landfill. Int. J. Biosci., 6: 104–115.

Ongena, M.; Jacques, P.; Touré, Y.; Destain, J.; Jabrane, A. and Thonart, P. (2005): Involvement of fengycin-type lipopeptides in the multifaceted biocontrol potential of *Bacillus subtilis*. Applied Microbiology and Biotechnology, 69: 29-38. https://doi.org/10.1007/s00253-005-1940-3

Onkendi, E.M.; Kariuki, G.M.; Marais, M. and Moleleki, L.N. (2014): The threat of Root-Knot nematodes (*Meloidogyne* spp.) in Africa: a review. Plant Pathology, 63(4): 727- 737. http: //hdl.handle.net/2263/41425

Onkendi, M. and Moleleki, L.N. (2013a): Distribution and genetic diversity of root-knot nematodes (*Meloidogyne* spp.) in potatoes from South Africa. Plant Pathology, 62(5): 118 4-1192. https://doi.org/10.1111/ppa.12035

Onkendi, M. and Moleleki, L.N. (2013b): Detection of *Meloidogyne enterolobii* in potatoes in South Africa and phylogenetic analysis based on intergenic region and the mitochondrial DNA sequences. European Journal of Plant Pathology, 136(1): 1-5. http://hdl.handle.net/2 263/39617

Pal, K.K. and Gardener, B.M. (2006): Biological control of plant pathogens. Plant Health Instruct., 2: 1117– 1142. doi:10.1094/PHI-A-2006-1117-0

Park, H.G.; Managbanag, J.R.; Stamenova, E.K. and Jong, S.C. (2004): Comparative analysis of common indoor *Cladosporium* species based on molecular data and conidial characters. Mycotaxon, 89 (2): 441- 451.

https://www.cabidigitallibrary.org/doi/full/10.5555/200431 25893

Peiris, P.U.S.; Li, Y.; Brown, P. and Xu, C. (2020): Fungal biocontrol against *Meloidogyne* spp. in agricultural crops: A systematic review and meta-analysis. Biological Control, 144: 104235. https://doi.org/10.1016/j.biocontrol.2020.104235

Pereira, P.T.; de Carvalho, M.M.; Gírio, F.M.; Roseiro, J.C. and Amaral-Collaço, M.T. (2002): Diversity of microfungi in the phylloplane of plants growing in a Mediterranean ecosystem. Journal of Basic Microbiology, 42 (6): 396-407. https://doi.org/10.1002/1521-4028(200212)42:6<396::AID-JOBM396>3.0.CO;2-L

Powers, T.O. and Harris, T.S. (1993): A polymerase chain reaction method for identification of five major *Meloidogyne* species. Journal of Nematology, 25(1): 1-6. PMCID: PMC2619349PMID: 19279734

Powers, T.O.; Mullin, P.G; Harris, T.S.; Sutton, L.A. and Higgins, R.S. (2005): Incorporating molecular identification of *Meloidogyne* spp. into a large-scale regional nematode survey. Journal of Nematology, 37(2): 226-235. PMCID: PMC2620951 PMID: 19262865

Quintanilla, M. and Fazlabadi, R.Y. (2023): Methods of sustainable management of plant nematodes, limitation, and challenges for crop growers. In: Khan, M.R. and Quintanilla, M. (eds) Nematode Diseases of Crops and their Sustainable Management. Elsevier, London, UK, Pp. 55- 63. https://doi.org/10.1016/B978-0-323-91226-6.00028-6

Qureshi, S.A.; Ruqqia, S.V.; Ara, J. and Ehteshamul-Haque, S. (2012): Nematicidal potential of culture filtrates of soil fungi associated with rhizosphere and rhizoplane of cultivated and wild plants. Pak. J. Bot., 44: 1041-1046.

Rashidifard, M.; Fourie, H.; Véronneau, P.V.; Marais, M.; Daneel, M.S. and Mimee, B. (2018): Genetic diversity and phylogeny of South African *Meloidogyne* populations using genotyping by sequencing. Scientific Reports, 8: 13816. https://doi.org/10.1038/s41598-018-31963-9

Răut, I.; Călin, M.; Capră, L.; Gurban, A.; Doni, M.; Radu, N. and Jecu, L. (2021): *Cladosporium* sp. isolate as fungal plant growth promoting agent. Agronomy, 11 (2): 392. https://doi.org/10.3390/agronomy11020392

Sahebani, N. and Hadavi, N. (2008): Biological control of the Root-Knot nematode Meloidogyne javanica by Trichoderma harzianum. Soil Biol. Biochem., 40: 2016-2020. https://doi.org /10.1016/j.soilbio.2008.03.011

Sasser, J. N. and Freckman, D. (1987): A world perspective on nematology: The role of the society. In J. A. Veech and D. W. Dickson, eds. Vistas on nematology, Hyattsville, Maryland, 7-20.

Sasser, J.N. (1980): Root-Knot nematodes a global menace to crop production. Plant Disease, 64: 36-41.

Seesao, Y.; Gay, M.; Merlin, S.; Viscogliosi, E.; Aliouat-Denis, C.M. and Audebert, C. (2017): A review of methods for nematode identification. Journal of Microbiological Methods, 138: 37–49. https://doi.org/10.1016/j.mimet.2016.05.030

Segarra, G.; Casanova, E.; Bellido, D.; Odena, M.A.; Oliveira, E. and Trillas, I. (2007): Proteome,

salicylic acid, and jasmonic acid changes in cucumber plants inoculated with *Trichoderma asperellum* strain T34. Proteomics and Systems Biology, 7: 3943-3952. https://doi.org/10.1002/pmic.20070 0173

Sharma, R.R.; Singh, D. and Singh, R. (2009): Biological control of postharvest diseases of fruits and vegetables by microbial antagonists: A review. Biological Control, 50(3): 205-221. https://doi.org/10.1016/j.biocontrol. 2009.05.001

Sharon, E.; Bar-Eyal, M.; Chet, I.; Herrera-Estrella, A.; Kleifeld, O. and Spiegel, Y. (2001): Biological control of the Root-Knot nematode *Meloidogyne javanica* by *Trichoderma harzianum*. Phytopathology, 91: 687– 693. doi: 10.1094/PHYTO.2001.91.7.687

Sidhu, R.K.; Sharma, S. and Parshad, V.R. (2014): Scanning electron microscopy of parasitic association of soil fungus *Trichoderma* sp. with Root-Knot nematode *Meloidogyne incognita*. Afr. J. Microbiol. Res., 8 (45): 3770-3774. https://doi.org/10.5897/AJMR 2013.6538

Sikandar, A.; Zhang, M.Y.; Wang, Y.Y.; Zhu, X.F.; Liu, X.Y.; Fan, H.Y.; Xuan, Y.H.; Chen, L.J. and Duan, Y.X. (2020): Review article: *Meloidogyne* incognita (Root-Knot nematode) a risk to agriculture. Appl. Ecol. Environ. Res., 18: 1679–1690. http://dx.doi.org/10.156 66/aeer/1801_16791690

Singh, U.B.; Singh, S.; Khan, W.; Malviya, D.; Sahu, P.K.; Chaurasia, R.; Sharma, S.K. and Saxena, A.K. (2019): *Drechslerella dactyloides* and *Dactylaria brochopaga* mediated induction of defense related mediator molecules in tomato plants pre-challenged with *Meloidogyne incognita*. India Phytopathology, 72: 309-320. https://doi.org/10.1007/ s42360-019-00132-x

Smits, T.H.; Rezzonico, F.; Kamber, T.; Goesmann, A.; Ishimaru, C.A.; Stockwell, V.O.; Frey, J.E. and Duffy, B. (2010): Genome sequence of the biocontrol agent *Pantoea vagans* strain C9-1. Journal of Bacteriology, 192(24): 6486- 6487. https://doi.org/10.1128/jb.01 1 22-10

Spadaro, D., and Gullino, M.L. (2004): State of the art and future prospects of the biological control of postharvest fruit diseases. International Journal of Food Microbiology, 91(2): 185-194. https://doi.org/10.1016/S0168-1605(03)00380-5

Spadaro, D., and Gullino, M.L. (2005): Improving the efficacy of biocontrol agents against soilborne pathogens. Crop Prot., 24: 601–613. https://doi.org/10.1016/j.cropro.200 4. 11.003

Stockwell, V.O.; Johnson, K.B.; Sugar, D. and Loper, J.E. (2011): Mechanistically compatible mixtures of bacterial antagonists improve biological control of fire blight of pear. Phytopathology, 101: 113–123. doi: 10.1094/PHYTO-03-10-0098

Sweeney, M.J. and Dobson, D.W. (1998): Mycotoxin production by *Aspergillus*, *Fusarium* and *Penicillium* species. Int. J. Food Microbiol., 43: 141–158.

Takaya, N.; Yamazaki, D.; Horiuchi, H.; Ohta, A. and Takagi, M. (1998): Cloning and characterization of a chitinase-encoding gene (chiA) from *Aspergillus nidulans*, disruption of which decreases germination frequency and hyphal growth. Bioscience, Biotechnology, and Biochemistry, 62: 60– 65, https://doi.org/10.1271/bbb.62.60

Tasic, S. and Tasic, N.M. (2007): Cladosporium spp. cause of opportunistic mycoses. Acta. Fac. Med. Naiss., 24(1): 15-19.

Tigano, M.; De Siqueira, K.; Castagnone-Sereno, P.; Mulet, K.; Queiroz, P.; Dos Santos, M.; Teixeira, .C; Ahmeida, M.; Silva, J. and Carneiro, R. (2010): Genetic diversity of the root-knot nematode *Meloidogyne enterolobii* and development of a SCAR marker for this guava-damaging species. Plant Pathology, 59(6): 1054-1061. https://doi.org/10.1111/j.13 65-3059.2010. 02350.x

Tikhonov, V.E.; Lopez-Llorca, L.V.; Salinas, J. and Jansson, H. (2002): Purification and characterization of chitinases from the nematophagous fungi *Verticillium chladosporium* and *V. suchlasporium*. Fungal Genetics and Biology, 35: 67-78. https://doi. org/10.1006 /fgbi.2001.1312

van Elsas, J.D. and Migheli, Q. (1999): Evaluation of risks related to the release of biocontrol agents active against plant pathogens. In: Albajes, R.; Lodovica-Gullino, M.; van Lenteren, J.C. and Elad, Y. (eds.) Integrated pest and disease management in greenhouse crops. Kluwer, The Netherlands, pp. 377–393. https://doi.org/10.1007/0-306-47585-5_27

Vinale, F.; Nigro, M.; Sivasithamparam, K.; Flematti, G.; Ghisalberti, E.L.; Ruocco, M.; Varlese, R.; Marra, R.; Lanzuise, S.; Eid, A.; Woo, S.L. and Lorito, M. (2013): Harzianic acid: a novel siderophore from *Trichoderma harzianum*. FEMS Microbiol. Letters, 347(2): 123- 9. doi: 10.1111/1574-6968.12231

Walsh, U.F.; Morrissey, J.P. and O'Gara, F. (2001): *Pseudomonas* for biocontrol of phytopathogens: from functional genomics to commercial exploitation. Current Opin. Biotechnol., 12: 289–295. doi: 10.1016/s0958-1669(00)00212-3

Welsh, D.T. and Herbert, R.A. (1999): Osmotically induced intracellular trehalose, but not glycine betaine accumulation promotes desiccation tolerance in *Escherichia coli*. FEMS Microbiol. Lett., 174: 57– 63. doi: 10.1111/j.1574-6968. 1999.tb13549.x

Wendimu, G.Y. (2021): Biology, taxonomy, and management of the Root-Knot nematode (*Meloidogyne incognita*) in sweet potato. Advances in Agriculture, 8820211. https://doi. org/10.1155/2021/8820211

Wright, S.A.; Zumoff, C.H.; Schneider, L. and Beer, S.V. (2001): *Pantoea agglomerans* strain EH318 produces two antibiotics that inhibit *Erwinia amylovora* in vitro. Applied and Environmental Microbiology, 67(1): 284- 292. https://doi.org/10.1128/AEM.67.1.284-292.2001

Yew, S.; Chan, C.; Ngeow, Y.; Toh, Y.F.; Na, S.L.; Lee, K.W.; Hoh, C.; Yee, W.; Ng, K.P. and Kuan, C.S. (2016): Insight into different environmental niches adaptation and allergenicity from the *Cladosporium sphaerospermum* genome, a common human allergy-eliciting Dothideomycetes. Scientific Reports, 6: 27008. https://doi.org/10.1038/srep27008

Yu, Z.; Mo, M.; Zhang, Y. and Zhang, K.Q. (2014): Taxonomy of Nematode-Trapping Fungi from Orbiliaceae, Ascomycota. In: Zhang, K.Q. and Hyde, K. (eds) Nematode-Trapping Fungi. Fungal Diversity Research Series, Vol 23. Springer, Dordrecht Pp. 64-183. https: // oi.org/10.1007/978-94-017-8730-7_3

Zeng, Y.; Ye, W. and Kerns, J. (2014): First report and morphological and molecular characterization of *Meloidogyne incognita* from Radermachera sinica in China. Nematropica., 44(2): 118-129.

Zhang, K.Q. and Hyde, K.D. (2014): Nematode-trapping fungi 1st ED., Springer, the Netherlands, Berlin.

Zhang, S.; Gan, Y. and Xu, B. (2015): Biocontrol potential of a native species of *Trichoderma longibrachiatum* against *Meloidogyne incognita*. Appl. Soil. Ecol., 94: 21- 29. http://dx.doi.org/10.1016/j.apsoil.2015.04.010

Zijlstra, C. (2000): Identification of *Meloidogyne chitwoodi, M. fallax* and *M. hapla* based on SCAR-PCR: a powerful way of enabling reliable identification of populations or individuals that share common traits. European Journal of Plant Pathology, 106(3): 283- 290. https://doi.org/10.1023/A:1008765303364

Zin, N.A. and Badaluddin, N.A. (2020): Biological function of *Trichoderma* spp. for agriculture applications. Ann. Agri. Sci., 65: 168-178. https://doi.org/10.1016/j.aoas.2020.09.003