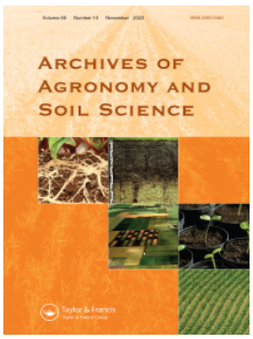

Archives of Agronomy and Soil Science

ISSN: 0365-0340 (Print) 1476-3567 (Online) Journal homepage: www.tandfonline.com/journals/gags20

Myco-ecological warfare with *Meloidogyne* species

Ndivhuwo Ramatsitsi, Alen Manyevere & Tuelo Motloba

To cite this article: Ndivhuwo Ramatsitsi, Alen Manyevere & Tuelo Motloba (2025) Myco-ecological warfare with *Meloidogyne* species, Archives of Agronomy and Soil Science, 71:1, 1-15, DOI: 10.1080/03650340.2025.2579892

To link to this article: https://doi.org/10.1080/03650340.2025.2579892

Published online: 31 Oct 2025.

ARCHIVES OF AGRONOMY AND SOIL SCIENCE
2025, VOL. 71, NO. 1, 1–15
https://doi.org/10.1080/03650340.2025.2579892

Taylor & Francis
Taylor & Francis Group

Myco-ecological warfare with *Meloidogyne* species

Ndivhuwo Ramatsitsi [a], Alen Manyevere [a] and Tuelo Motloba [a,b]

[a]Department of Agronomy, University of Fort Hare, Alice, South Africa; [b]Forestry and Agricultural Biotechnology Institute, University of Pretoria, Hatfield, South Africa

ABSTRACT

Root-knot nematodes (RKNs), *Meloidogyne*, are the most widely distributed plant-parasitic nematodes. This group of soil-borne pests represents one of the largest causes of plant biotic stress that are challenging to manage, deeming them economically important. Using fungal bio-control agents (BCAs) is considered economic and ecologically friendly. This review illuminates how fungal BCAs generally decrease the negative impacts of RKNs, i.e. either via antagonistic activities or by modifying effects on plant root morphology and physiology. Of the 38 reviewed BCAs, the most studied were *Arthrobotrys*, *Aspergillus*, *Lecanicillium*, *Purpureocillium*, *Trichoderma*, *Pochonia* and *Fusarium* endophytes. Of the several studied fungal BCAs, approximately 10 are globally marketed. Based on literature, an understanding of the intricate interactions between fungal BCAs and *Meloidogyne* is a prerequisite for carrying out an appropriate method for formulation of bio-control products. The major challenge in commercialising fungal BCAs has been attributed to inconsistency concerns under different conditions, incompatibilities of BCAs species and formulation procedures that result in reduced effectiveness.

ARTICLE HISTORY
Received 10 July 2025
Accepted 20 October 2025

KEYWORDS
Bio-control agents; fungi; nematophagous; root-knot nematodes; shelf life

Introduction

Nematodes are microscopic multicellular organisms classified within the large phylum, Nematoda, that encompasses unsegmented roundworms. Plant-parasitic nematodes (PPNs) are major pests of agricultural crops and are recognised as a serious threat to worldwide crop production (Kantor et al. 2024), with a projected 215 billion USD annual economic losses (Ferreira et al. 2019). Approximately 80% of the food we eat is produced by plants, and 40% of food crops are lost to agricultural pests including PPNs (Routray 2020). The most damaging PPNs are the root-knot nematodes (RKNs), *Meloidogyne* species (Khan MR and Quintanilla M 2023). *Meloidogyne* species, including *M. chitwoodi*, *M. enterolobii*, *M. incognita*, *M. javanica* and *M. hapla* reduce crop yield and quality of vegetable crops, field crops and fruit trees (Evlice et al. 2022; Sarir et al. 2022). This group of nematodes has been ranked as the most economically and scientifically important genus because of their wide host range, complex relationship with their host, level of damage caused by infestation and serious yield losses they cause (Sikora et al. 2018; Khan MR and Quintanilla M 2023). Nicol et al. (2011) report that *Meloidogyne* spp. are responsible for approximately 10% reduction of global crop production, with estimated economic losses of around 80 billion US dollars per year. A decade later, those losses had increased to a projected estimation of 15% annual yield losses of the world's crop production, which translates to around 157 billion US dollars (Sikora Rad and Molendijk 2021). *Meloidogyne* spp. have also been reported to cause 100% crop failure in highly susceptible crops (Onkendi et al. 2014). The entire degree of global crop losses due to *Meloidogyne* is likely to be underestimated since farmers are sometimes oblivious to their existence. This is primarily because, except for root galls, above ground symptoms induced on plants are often non-specific, resembling abiotic stress or other pathogenic pests, making it challenging to trace crop losses to *Meloidogyne* damage (Siddique and Grundler 2018).

Management of RKNs predominately relied on synthetic chemical nematicides that have been established to be highly effective (Sikora Rad and Molendijk 2021). However, attention towards environmental safety led to market withdrawal and usage restriction of several synthetic organophosphate- and carbamate-based chemical nematicides (Chen et al. 2020). Such restrictions resulted in severe crop-related economic losses and left a serious void in crop production and protection. Over the past years (Nicolopoulou-Stamati et al. 2016; Singh et al. 2019;

CONTACT Ndivhuwo Ramatsitsi nramatsitsi@ufh.ac.za Department of Agronomy, University of Fort Hare, Private Bag X1314, Alice 5700, South Africa

Forghani and Hajihassani 2020), it has become urgently necessary to manage RKNs in a sustainable and efficient approach. Current integrated pest management initiatives against RKNs are mostly restricted to generic strategies such crop rotation, soil sanitation and the use of tolerant/resistant cultivars (Mitiku 2018; Fourie and De Waele 2019; Sarir et al. 2022). These methods, however, can be ineffective, expensive and result in several unexpected ecological downsides (Sarir et al. 2022). For instance, crop rotation is not always effective on *Meloidogyne* infested fields as they thrive on a variety of crops (Khan A et al. 2023). Additionally, the use of resistant cultivars is not always a feasible option since many commercial cultivars have been established to be susceptible to *Meloidogyne* species (Ramatsitsi et al. 2024; Rusconi et al. 2025) and some *Meloidogyne* species have been established to break resistance in other crops (Ploeg et al. 2023). As a result, research, development and use of sustainable and economical sound fungal bio-control agents (BCAs) have been gaining attention for potential use in the management of RKNs (Molinari and Leonetti 2019; Sayed et al. 2019).

Review methodology

Search protocol

Following the worldwide shift towards conservation and climate-smart agriculture, the purpose of this review is to address the following questions: i) What are the mechanisms through which fungal BCAs parasitise *Meloidogyne* nematodes? ii) What are the most suitable fungal BCAs formulation methods to ensure optimum *Meloidogyne* suppression? and iii) How can fungi-nematode interactions be used to equip both researchers and farmers to reach the goal of sustainable yet profitable agriculture? The review further outlines challenges, research gaps and prospects with regards to implementing fungal BCAs for *Meloidogyne* management. The search questions were designed to access relevant information, after which a search protocol was developed. The objective of our non-systematic critical literature evaluation was to highlight the available empirical evidence and knowledge gaps in the broader subject matter of fungal BCAs in RKNs management. Addressing the BCAs mechanisms of parasitism, commercially available BCAs, formulations methods, the current work examined research conducted on fungal BCAs for suppression of *Meloidogyne* species. Challenges associated with fungal BCAs marketability were also examined because it has been demonstrated that the species used to manufacture these products could be incompatible with formulation procedures, hence raising concerns of their effectiveness. A thorough list of pertinent literature was gathered from Scopus (https://www.elsevier.com/products/scopus) as this is the largest database of peer-reviewed literature with the most indexed journals. Literature search was conducted using the following keywords: 'fungal bio-control agents', 'root-knot nematodes' '*Meloidogyne* nematodes', 'nematophagous fungi' and 'integrated pest management interventions'. To gather recent literature on BCAs mode of action on *Meloidogyne* spp., the search string was used, TITLE-ABS-KEY (('Meloidogyne' OR 'root-knot nematode') AND ('nematophagous fungi' OR 'biocontrol fungi') AND ('parasitize' OR 'trap' OR biocontrol OR 'nematicidal' OR 'egg parasite' OR 'ovicidal' OR 'female parasite' OR 'juvenile parasite' OR 'lytic enzyme' OR 'secondary metabolite' OR 'volatile organic compound' OR 'toxin' OR 'bioactive compound')) AND PUBYEAR > 2015 AND PUBYEAR < 2026 AND (EXCLUDE (DOCTYPE, 'review') AND EXCLUDE (DOCTYPE, 'chapter')). Following that, every source was categorised and grouped according to its applicability, and only those that were relevant to the current review study were chosen. After reviewing the abstracts, peer-reviewed articles, government publications, and policies were selected according to the inclusion criteria (Table 1). Further information was gathered by reviewing other sources, such as book chapters, thesis and webpages. The search was done in English, though there are several studies that are not published in English, and it is understood that this could have led to misinterpretation and a vernacular bias in the literature.

Table 1. The used inclusion and exclusion criteria for literature search and selection for review.

Inclusion criteria	Exclusion criteria
English documents	Non-English documents
Peer-reviewed literature such as original papers, review papers, book chapters, government gazettes and policies, and technical notes	Grey literatures such as magazines, bulletins and newsletters
Bio-control agents of focus is fungal species	Bio-control agents of focus is not fungal species
Nematodes of focus is *Meloidogyne* species	Nematodes of focus is not *Meloidogyne* species

Results

Author keywords

The bibliometric analysis of keywords taken from the reviewed papers' titles and abstracts is shown in Figure 1. The node size, which represents the frequency of occurrence of the keywords, shows their coherence, while the connecting curves show how frequently they appear together. A higher correlation between respective terms is shown by shorter distances between nodes. The most common terms found were 'nematophagous fungi', 'root-knot nematode' and 'lycopersicon esculentum'.

Fungal bio-control agents

The studies covered were limited to fungal BCAs to suppress *Meloidogyne* species, a group of widely distributed pervasive plant-parasitic nematodes. A total of 24 fungal species, from 13 genera, that were reviewed are presented in Table 2. The most studied genera were *Trichoderma* and *Arthrobotrys* (six species each), followed by *Aspergillus* (four species), *Lecanicillium*, *Pochonia Fusarium* endophytes (three species each), *Fusarium* and *Purpureocillium* (each having two species). The seldom studied fungal BCAs genera were *Penicillium*, *Pochonia*, *Purpureocillium*, *Acremonia*, *Daldinia*, *Macrophomina*, *Phialemoniopsis* endophyte, *Dactylella* and *Muscodor*. Within the *Trichoderma* genus, the most common species were *T. harzianum* and *T. viride*. The *Trichoderma* genus has been deemed a prominent biocontrol group primarily because of its broad-spectrum and multiple parasitism activities (Mukhtar et al. 2018; Molinari and Leonetti 2019). While other studies focused on *in vitro* bioassays (Xu et al. 2021), others such as those by Silveira et al. (2001) and Mastan et al. (2019) focused on *in vivo* with known hosts of *Meloidogyne* species. According to the observed results, fungal BCAs exhibit diverse modes of parasitism including direct parasitism (Naz et al. 2021), secretion of nematicidal metabolites such as peroxidase, polyphenol oxidase, phenylalanine and ammonia lyase (Annapurna et al. 2018), as well as facilitating plant resistance (Mendoza-Mendoza et al. 2018).

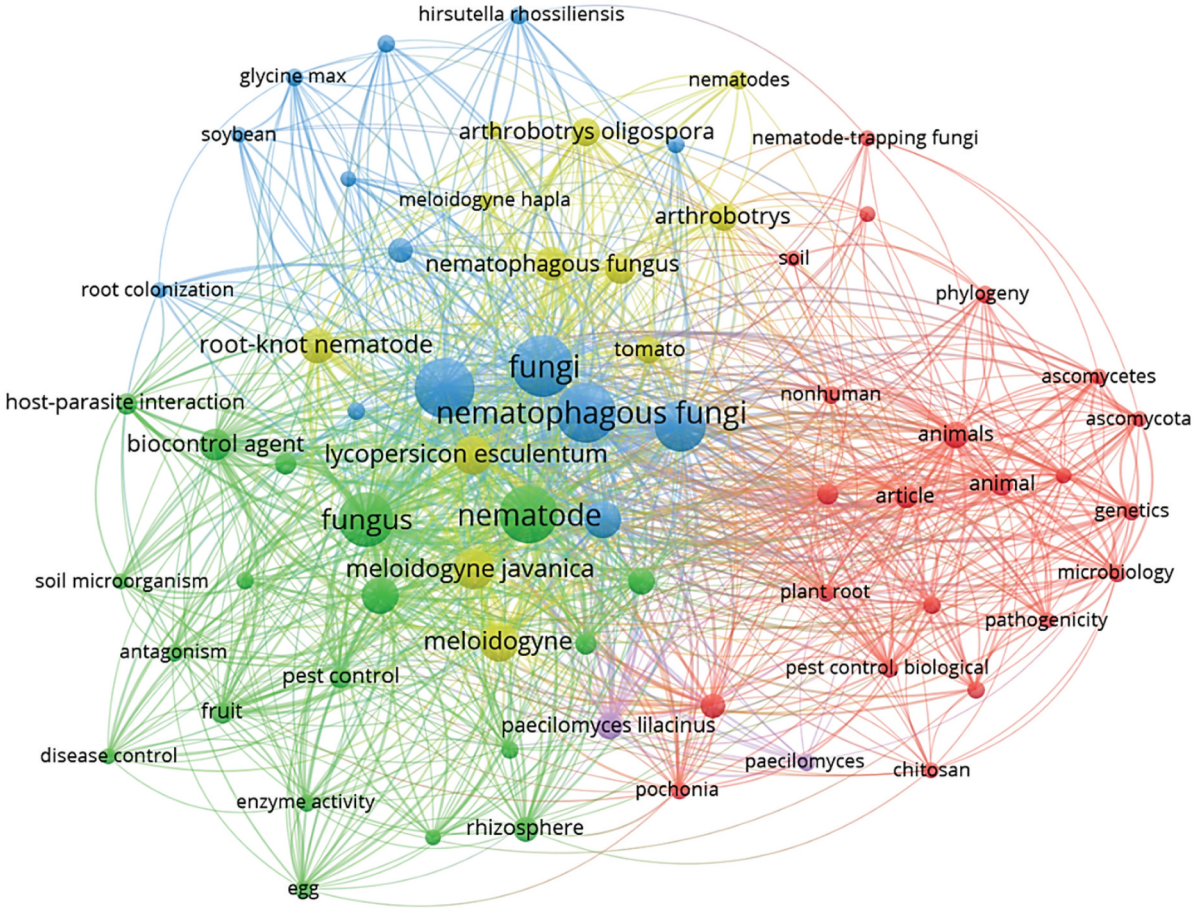

Figure 1. Keywords visualisation on abundance and composition of selected soil microbial species.

Table 2. Summary of different fungal bio-control agents' mode of parasitism against *Meloidogyne* species *in-vitro* and on various crops.

Fungal species	Nematode	Plant	Mode of parasitism	References
A. dactyloides, *A. oligospora*	*M. javanica*	*In vitro*, Sweet potato	Constricting hyphae ring trap formation leading to J2 capture and enzymatic digestion, reduced J2 recovery and reduced root galling on storage roots. Efficacy depends on prior soil conditioning and BCA duration.	Groves et al. (2025)
Arthrobotrys sp., *A. thaumasius*, *D. brochopaga*	*M. hapla*	*In vitro*	Predatory ring traps on J2s leading to mortality and population reduction over time.	Hastuti et al. (2023)
A. Thaumasius, *T. yunnnanense* J2	*M. hapla*	*In vitro*, Tomato	Combined action of secondary metabolites, physical constriction and induced resistance from fungal consortia reducing vermiform juvenile population and root knot numbers.	Hastuti et al. (2024)
A. superba, *A. oligospora* (Syn. *Orbilia oligospora*), *A. flagrans* (Syn. *Duddingtonia flagrans*)	*M. incognita*	*In vitro*	Chemotactic compounds attracting RKNs to sticky knobs and ring traps forming adhesive networks. J2 digestion by chitinases and proteases following predatory trapping leading to mortality.	Kanalbek et al. (2025)
A. flavus, *P. chrysogenum*, *P. chlamydosporia*	*M. incognita*	*In vitro*, cucumber	Direct parasitism and/or secretion of nematicidal metabolites including cyclosporin A and Glio-toxin.	Naz et al. (2021)
A. japonicus ZW1	*M. incognita*		Inhibit egg hatching and toxic to nematodes via nematicidal compound, 1,5-Dimethyl Citrate hydrochloride ester.	He et al. (2020)
A. oryzae, *L. psalliotae*, *P. Cyclothyroides*	*M. javanica*	*In vitro*, Tomato	Egg hatching inhibition. Spore concentration-dependent histological deformations on J2s, including constriction by hyphal traps, penetration by infective hypha, internal spore germination and hydrolytic enzyme production leading to increased mortality. Reduced root galling, eggs and J2s in roots.	Krif et al. (2024)
A. niger, *T. cystophila*	*M. enterolobii*	*In vitro*, tomato	Inhibition of egg hatching and complete J2 mortality by oxalic acid and citric acid production. Chitinase activity on egg shell and nematode cells. Vacuole formation within juvenile body.	Nishat et al. (2025)
A. niger, *A. terreus*, *T. longibrachiatum*	*M. incognita*	*In vitro*, tomato	Production of hydrolytic (cellulase, chitinase, xylanase, pectinase) and oxidative enzymes (polyphenol oxidase, peroxidase, catalase, proline), and plant growth promoters (IAA, siderophores, P solubilization) inducing ovicidal, female parasitic, J2 mortality, and induced resistance against RKN invasion.	Alhazmi et al. (2025)
T. harzianum, *T. viride*, *P. Chlamydosporia*, *P. lilacinum*	*M. incognita*	Tomato	Secretion of peroxidase, polyphenol oxidase, phenylalanine ammonia lyase and total phenol content.	Annapurna et al. (2018)
P. lilacinum	*M. incognita*	*In vitro*	Direct parasitism by mycelia. Degradation of eggshell by proteases, glycoside hydrolases, and carbohydrate esterases.	Xu et al. (2021)
A. implicatum endophyte	*M. incognita*	*In vitro*, tomato	Produce chitinase to parasitize *M. incognita* eggs, J2 and females.	Yao et al. (2015)
C. javanica	*Meloidogyne* spp.	Cucumber	Microsclerotial production of infective conidia that has ovicidal activity. Root know reduction on seedlings.	Li et al. (2025)
C. rosea	*M. incognita*	Tomato	Toxic metabolites disturbing embryonic developmental and impairing J2 motility. Inoculum concentration dependent reduction of J2 population densities and root galling.	Stucky et al. (2024)
D. cf. concentrica.	*M. javanica*	*In vitro*, tomato	Secrets biologically active volatile organic compounds (VOC) that inhibit egg hatching and J2 viability.	Liarzi et al. (2016)
D. haptotyla	*M. incognita*	*In vitro*, tomato	Concerted production of 2-furoic acid and synergistic secretion during nematode trapping, leading to life cyle disturbance and root gall reduction.	Lei et al. (2023)
G. intraradices, *G. mosseae*, *G. etunicatum*	*M. javanica*	Peach trees	Alter root morphology by increasing root growth and branching, as well as making the plants more competitive for nutrients and space.	Calvet et al. (2001)
F. oxysporum endophyte	*M. exigua*	Banana, coffee	Release nematicide metabolites that kill nematodes J2.	Aminuzzaman et al. (2013)
F. moniliforme endophyte	*M. graminicola*	Rice	Induce ISR from synthesis and release of chemical compounds, 4-hydroxybenzoicacid, indole-3-acetic acid (IAA) and gibepyrone D, that are also toxic nematodes.	Le et al. (2016)
F. redolens, *M. pseudophaseolina*, *P. cornearis*, endophytes	*M. incognita*.	Kaffir potato	Induce ISR by synthesising secondary metabolite, forskolin that enhance the expression of diterpene synthases, improving *Meloidogyne* species tolerance.	Mastan et al. (2019)
D. leptospora.	*M. incognita*	Tomato	Forms a non-constrictor ring and adhesive nodule.	Silveira et al. (2001)
H. rhossiliensis Endophyte	*M. incognita*	*Arabidopsis thaliana*	Strong J2 endoparasitism by conidial germination and infective hyphal germ tube penetration. Induction of plant defense and resistance.	Sun et al. (2024)

(*Continued*)

Table 2. (Continued).

Fungal species	Nematode	Plant	Mode of parasitism	References
Lecanicillium sp.	*M. javanica*	*In vitro*	Egg shell disintegration, penetration, colonization and hatching inhibition. Proteomic activity (actin, hsp70-like, fumarate reductase/succinate dehydrogenase, and GTP-binding ypt1) involved in signalling and stress response.	Hajji-Hedfi et al. (2023)
L. saksenae	*M. incognita*	*In vitro*	Secretion of hydrolytic enzymes, chitinases and proteases. Hyphal attachment to gelatinous matrix. Egg disintegration.	Sreeja et al. (2025)
M. albus	*M. chitwoodi*, *M. hapla*	Tomato, potato, tobacco	Produce volatiles (synthetic mixture of key antimicrobial gases) that increase nematode mortality.	Riga et al. (2008)
M. carneum	*M. enterolobii*	*Tomato*	Egg shell penetration inhibiting hatching. Hydrolytic enzyme activity on J2s. Population density reductions on roots. Compatibility and synergy with Metam sodium.	López-Lima et al. (2023)
P. chrysogenum Snef1216	*M. incognita*	*In vitro*	Induced ovicidal and larvicidal activity.	Sikandar et al. (2020)
P. chlamydosporia	*M. enterolobii*	Potato, guava	Trap and colonise their sessile host eggs, J2 and females.	Muthulakshmi et al. (2012)
P. chlamydosporia	*M. enterolobii*	Tomato	Secondary metabolite effects on fecundity, affecting multiple embryogenic stages, and altering life cycle and expectancy.	Arunachalam et al. (2025)
P. chlamydosporia	*M. hapla*	Lacy phacelia	Additive modifications on the host transcriptome and metabolome, leading to partial upregulation of defense-related transcripts. Reduced fecundity.	Könker et al. (2025)
P. chlamydosporia	*M. incognita*	*In vitro*	Production of resorcylic acid lactones with strong ovicidal and female parasitism.	Li Z et al. (2024)
P. chlamydosporia	*M. javanica*	Tomato	Grow hyphae that penetrate eggs and trap J2.	Escudero and Lopez-Llorca (2012)
P. lavendulum	*M. incognita*	Tomato	Ovicidal and J2 parasitism through the production of toxic enzymes. Rhizospheric persistence in Cd contaminated soils.	Li X et al. (2024)
P. lilacinus	*Meloidogyne*	Tomato	Release nematicide metabolites that kill nematodes.	Oclarit and Cumagun (2009)
P. lilacinum	*M. incognita*	Tomato	Strong ovicidal effects and reduced reproductive potential.	Ali et al. (2024)
P. lilacinum	*M. incognita*	Tomato	Spore adhesion to egg shell or juvenile followed by infective hypha penetration through egg shell or cuticle inducing embryonic mortality. Compatibility and synergy with Dazomet.	Nie et al. (2023)
P. lilacinum	*M. incognita*	Tomato	Egg shell penetration by conidial infective hypha promoting hatching inhibition by chitinase and protease activity. Enhanced suppression of population densities in roots.	Niño-Arteaga et al. (2023)
T. harzianum, P. chlamydosporia	*M. incognita*	Tomato	Induce ISR through priming defences regulated by SA, which prevents root invasion by J2.	Molinari and Leonetti (2019)
T. harzianum, *T. hamatum*, *T. asperellum*	*M. javanica*, *M. incognita*	Tomato	Hydrolytic enzymes such as chitinase and β-1,3-glucanase are activated to degrade the nematodes' cell wall.	Vos et al. (2012); Geraldine et al. (2013)
T. asperelloides	*M. incognita*	Tomato	Produce chitinase enzyme that inhibit egg hatching and J2 vitality.	Sayed et al. (2019)
T. harzianum, *T. viride*	*M. incognita*	Tomato	Produce conidia that can attach to different nematode stages.	Mukhtar et al. (2018)
T. harzianum	*Meloidogyne*	Tomato	Stimulates faster SA-mediated defence responses, to protect the roots against nematode invasion.	Mendoza-Mendoza et al. (2018)
T. astroviride, *T. virens*	*M. incognita*	Maize	Activates expression of JA and SA-mediated defences.	Contreras-Cornejo et al. (2016)
T. longibrachiatum strain 40,418	*M. incognita*	Tomato	Induced systemic resistance activated by production of peptaibols, trilongin AIVa and trilongin BI. SA and JA signalling affecting juvenile functionality.	Luo et al. (2024)

Discussion

Nematophagous fungi mode of parasitism

Antibiosis

Antibiosis in nematophagous fungi involves the production of *Meloidogyne*-toxic compounds by the fungi (Poveda et al. 2020). These toxic compounds include metabolites and enzymes, such as xylanase, pectinase, and glucanase (Vos et al. 2012). During antibiosis, hydrolytic enzymes such as chitinase and β-1,3-glucanase are activated to degrade the RKNs cuticle (Geraldine et al. 2013). An *in vitro* study by Molinari and Leonetti (2019) showed that such enzymes can degrade nematode eggshell and cuticle, allowing the BCAs to subsequently absorb nematode nutrients. *Trichoderma* species secrete cellular enzymes such as cellulase, xylanase, pectinase, lipase, amylase, arabinase and protease, volatile metabolites such as 6-n-pentyl-2 H-pyran-2-one (6-PAP), trichodermin, trichodermol, gliovirin, gliotoxin, viridin, herzianolide, pyrones, peptaibols to degrade nematode cell walls (Aminuzzaman et al. 2013; Bansal et al. 2021). *Meloidogyne incognita* second-stage juvenile (J2) was killed by the filtrates of *Paecilomyces lilacinum*, *Fusarium moniliforme* and *F. oxysporum* endophyte, whereas the nematode egg hatching was restricted by *A. flavus*, *Cylindrocarpon magnusianum* and *Mortierella* species (Aminuzzaman et al. 2013). *Aspergillus* and *Pochonia* are two more of the fungi genera that produce *Meloidogyne*-toxic metabolites, such as cyclosporin A, Glio-toxin and 1,5-Dimethyl Citrate hydrochloride ester (He et al. 2020; Naz et al. 2021).

Parasitism

Meloidogyne parasitism by nematophagous fungi involves the fungal BCAs making physical contact with the nematode eggs or J2 (Poveda et al. 2020). Successful parasitism is facilitated by physical penetration of the nematophagous fungi into the body of the host via development of specialised organs such as haustoria and appressoria and secretion of various enzymes such as proteases, chitinases and lipases (Sayed et al. 2019; Naz et al. 2021). Parasitism by fungal BCAs has been classified into three groups, (i) nematode-trapping/predators, (ii) opportunistic or ovicidal and (iii) endoparasites (Liu et al. 2009; Soares et al. 2018). For example, *Aspergillus* genus consists of nematode-trapping fungal species. The nature of parasitism of *Aspergillus* species could be explained by the various nematode hunting strategies used by different genera. *Aspergillus flavus* is a constricting ring-forming fungus that is known to construct conidial traps (Naz et al. 2021). When a nematode enters the constricting ring, the ring cells begin to constrict it by raising cell volume up to three times its usual size, rendering the J2 immobile (Xu et al. 2021). Another adhesive network-forming fungus, *P. lilacinum*, functions as a facultative nematode catcher that only captures sources of nitrogen and it breaks down organic materials to produce carbon and energy (Xu et al. 2021). Using traps/enzymes, egg-parasitic fungi prey and feed on RKNs, thereby preventing eggs from hatching. *Acremonium implicatum* is an endophytic fungus with bio-control potential against *M. incognita* due to its opportunistic egg parasitism capacity. In a study by Yao et al. (2015), findings demonstrated that *A. implicatum* hyphae colonised *M. incognita* eggs by destroying the integrity of the eggs through penetration of the eggshells. Conidia stuck to the eggshells, encircled the infected eggs and evolved into trophic hyphae. Likewise, *T. harzianum* hyphae successfully penetrated egg mass matrix of *M. incognita* and significantly decreased egg hatching (Mukhtar et al. 2018).

Systemic resistance

Plants have an inherent ability to avert pathogens, also referred to as resistance. This is formed by genes that detect and initiate immune responses against the invading pathogen (Birkenbihl et al. 2017). While some plants have evolved to efficiently utilise this ability and even amplify their resistance, other plants lack these genes against particular pathogens and therefore display susceptibility (Lorang et al. 2007). Apart from direct mechanisms of attack on RKNs, fungal BCAs have plant-modifying effects that indirectly affect RKNs. Colonisation of plant roots by beneficial endophytic and mycorrhizal fungi can protect plants against a wide range of RKNs through inducing host resistance. Two different types of systemic resistance can be conferred to host plants by beneficial fungal species, namely induced systemic resistance (ISR) and systemic acquired resistance (SAR) (Birkenbihl et al. 2017). The two are distinguished according to the biochemical pathways involved. The ISR is salicylic acid (SA) -independent, whereas SAR is a salicylic acid-dependent pathway. For example, *T. harzianum* fungus can induce jasmonic acid (JA)- and SA-regulated defence

pathways in tomato (*Solanum lycopersicum* L.) plants, causing resistance to the RKNs. Other studies have shown that, by colonising the plant roots, *Trichoderma* stimulates their defence mechanisms against numerous plant-pathogenic micro-organisms, including *Meloidogyne* nematodes (Leonetti et al. 2014; Mendoza-Mendoza et al. 2018). Sahebani and Hadavi (2008) reported that under greenhouse conditions, the inoculation of tomato seeds with *T. harzianum* caused resistance-related enzymes, such as peroxidase, polyphenol oxidase and phenylalanine ammonia lyase, to rise dramatically. In addition to inducing systemic resistance to *M. javanica*, ISR induced by *T. atroviride* has been shown to become heritable to subsequent generations (Contreras-Cornejo et al. 2016).

Chemoreception disruption of nematode chemotaxis

The ability of *Meloidogyne* spp. to detect the presence of a host and locate it depends on their sensory organs positioned around the mouth area of the head (Eisenback and Hunt 2009). The two organs in particular are the amphids and inner labial papillae (Jansson 1994). These enable J2 to hatch from the egg after perceiving environmental cues such as soil temperature, moisture, pH and carbon dioxide (Lu et al. 2022). In the same manner that olfactory organs allow other organisms to have direction, RKNs would not be able to navigate a host without these organs.

Chemoreception takes place when messenger signals from the host bind to RKNs sensory organs. Jansson and Lopez-Llorca (2004) showed that carbohydrate moieties in these organs are primarily responsible for reception. These glycoproteins bind to volatile and water-soluble substances such as exudates from the host promoting variable-distance chemotaxis to the host or other food sources (Halloran and Burnell 2006). Conidia from the nematophagous fungus *Drechmeria coniospora* has been shown to adhere to these sensory organs (Jansson 1993, 1994). Proteins on the conidia sticky buds bind to the glycoproteins of PPNs sensory organs which block reception, ultimately decreasing PPNs chemotaxis (Jansson 1993). A dual mechanism by this fungus is shown in its ability to not only block reception but also further parasitise the nematode (Jansson and Lopez-Llorca 2004). This mechanism of nematode confusion has been tested on other species such as the free-living nematode, *Caenorhabditis elegans* and not yet on *Meloidogyne* species. To date, studies on nematode chemoreception disruption have largely used *C. elegans* as a model organism. This is because *C. elegans* is genetically well characterised, has a short life cycle, and is amenable to laboratory manipulation, making it an ideal system for fundamental neurobiological and sensory research (Halloran and Burnell 2006). In contrast, equivalent studies on *Meloidogyne* species are lacking. This discrepancy likely reflects both the technical difficulties of maintaining obligate PPNs *in vitro* and the relative scarcity of genetic tools available for *Meloidogyne*. As such, while the nematode confusion mechanism has been demonstrated in *C. elegans*, further research is required to determine whether this strategy is effective in disrupting host-finding behaviour in RKNs under realistic agricultural conditions.

Formulation methods of bio-control fungi products

Liquid-based substrates

The components of liquid formulations include stabilisers, colourants, surfactants, and supplementary nutrients in combination with whole cultures or cell suspensions that optimise the longevity of the product (Bejarano and Puopolo 2020) and boost the BCAs adhesion, surfactant, and dispersion capabilities. Combining processed cultures with emulsifiers, surfactants, and/or mineral or vegetable oils that facilitate their subsequent dispersion in water is what constitutes an oil-based formulation. Liquid-based formulated bionematicides may be water- or oil-soluble polymer structures to keep the encapsulated BCAs propagules hydrated (Martinez et al. 2023). For such products, animals, humans, plants, or microorganisms should not become poisoned by the oils or gels that are utilised. Oil- or gel-based formulations have been suggested to be ideal for foliar sprays under dry ambient settings due to their protective properties, which are meant to supplement the BCAs (Brar et al. 2006). The increased water activity in liquid-based formulations, as compared to dry formulations, makes it considerably more challenging to prolong product shelf life because of imbibition damage over time brought on by extended exposure to water or spontaneous germination (Gervais et al. 1988).

Items in the liquid or gel condition are more vulnerable to bacterial contamination, necessitating a higher level of sterile processing. For these reasons, dry formulations tend to dominate the market for currently

available marketed items. Nevertheless, despite these drawbacks, liquid and gel-based formulations are quickly gaining traction for industrial use due to improved manufacturing processes and the straightforward administration of such formulations. This has resulted in studies (Swarnakumari et al. 2020) concentrating on methods and modification procedures for creating formulations that support propagule viability during extended storage times. Biocontrol propagules in oil, either alone or in combination with water, make up oil-based products. Mineral-based oil, which is produced from crude oil, or vegetable-based oil, which is extracted from plant seeds, can be used (Peng and Xia 2011). (Mbarga et al. 2014). developed oil dispersion including conidia of *T. asperellum*, soybean oil, an emulsifying-dispersing agent, a structural agent and glucose.

Solid-based substrates

Different solid-based substrates including grains, organic matter and agricultural waste have been successfully used to culture and store fungal BCAs (Mulatu et al. 2021; Bulgari et al. 2023). Solid-based substrates may be powdered or grain formulations made with soil, organic or inorganic carriers. The two primarily differ from one another by their particle sizes. Powdered formulations have a few hundred mm particle size, on the other hand, grain formulations have particle sizes ranging from 0.1 to 2.5 mm (microgranules, 100–600 µm, fine granules, 0.3–2.5 mm). Larger grains (up to 6 mm) might, however, be manufactured (Bejarano and Puopolo 2020). To manufacture powdered formulations, either the granules themselves are crushed into a fine powder, or the bio-agents are mechanically blended with a milled carrier and adjuvants until a homogeneous combination is obtained. Using milling equipment, manufacturing can be accomplished mechanically or manually. Furthermore, lyophilisation and spray drying can be used to create powders (Stephan et al. 2016).

In what is regarded as a significantly moderate dehydration process, cells are first embedded in a matrix that shields them from destruction throughout the freezing and drying processes. In spray-drying, a liquid matrix is atomised into a drying chamber with hot air flow, causing the water to evaporate quickly and forming dry particles (Yánez-Mendizábal et al. 2012). Naeimi et al. (2020) established that mass production of *T. harzianum* AS12-2 on solid substrates, *vis*. rice straw, rice husk, and broom sorghum grain, preserved viability and efficacy of the strain's spores for a year. Furthermore, the outcomes of the greenhouse assay demonstrated that no discernible variations existed among the substrates and that all bioformulations were successful in managing the pathogen. In a study by Mulatu et al. (2021), it was feasible to sustain conidial viability for wettable powder formulations of *T. longibrachiatum* and *T. asperellum* for eight months at room temperature (25 °C) on organic substrates. Ideally, the best growth media would be one that does not diminish the productivity/viability and virulence of the cultured fungi (Martinez et al. 2023). Table 3 shows current commercial fungal BCAs of *Meloidogyne* nematodes.

Overall, both liquid- and solid-based substrates provide distinct advantages and limitations for formulating fungal bio-control products. Liquid formulations are advantageous for their ease of application, uniform distribution, and compatibility with spray equipment; however, they often face challenges related to contamination, storage stability, and reduced shelf life. In contrast, solid-based formulations offer longer persistence, greater stability during storage, and in some cases enhanced protection of fungal propagules under field conditions, though they may be more labour-intensive to produce and slower to disperse. The choice between the two therefore depends on the intended application environment, the target cropping system, and the balance between production costs and field performance.

Challenges, research gaps and prospects

The use of fungal BCAs in managing RKNs is continuously becoming adopted across the world. Even though some of these fungal BCAs have been successfully commercialised, such as *A. niger*, *P. chlamydosporia*, *P. lilacinus* and *T. harzianum*, their application is not without challenges (Tranier et al. 2014; Askary 2015). Fungal BCAs might be incompatible with the formulation and application process or have reduced effectiveness in the environment where they would be applied. The same is true for mass production of microbial agents, storage, conservation, and potential negative effects on non-target organisms (Bamisile et al. 2021). Despite numerous studies to identify effective RKNs antagonists, challenges related to scaling up production and formulation studies have prevented several

Table 3. Environmental Protection Agency approved commercial fungal biocontrol agents for *Meloidogyne* nematodes.

Fungal biocontrol agents	Commercial name	Formulation	References
Paecilomyces lilacinus strain 251	BioAct(r)	Water-dispersible granule, BioAct(r)/ MeloCon can be applied through the irrigation system.	Brand et al. (2010)
Beauveria bassiana	Botanigard(r) ES or Botanigard(r)22WP	Liquid-formulated	Liu et al. (2008)
Purpureocillium lilacinum	BIOSTAT(r)		
Consortium of *Ascophyllum nodosum*, *Bacillus amyloliquefaciens*, and *Trichoderma harzianum*	GA sol+	Granules	Krif et al. (2022)
Verticillium lecanii	MYCOTAL(r)	Wettable powder	Meyer (1999)
T. harzianum T-22	TRIANUM®		González et al. (2012)
Consortium of *Bacillus subtilis, Trichoderma* spp., *Paecilomyces* spp.	Nemaxxion Biol(r)	Liquid-formulated large-spectra	Tranier et al. (2014)
Consortium of *Arthrobotrys* spp, *Dactyllela* spp., *Paecilomyces* spp., Mycorrhiza (*Glomus* spp.), and bacteria (*B*. spp., *Pseudomonas* spp.)	REM G(r)	Liquid-formulated	Tranier et al. (2014)
Pochonia Chlamydosporia	RIZO-TURBO or PC-ATTACK or PC-GUARD or RIZOTEC	Liquid-formulated and granules	Machado (2022)
Paecilomyces lilacinus	Purpureonyd FR 25 or Nettus* or BN40.001/19* or Nemat or ATIALY	Liquid-formulated and granules	Machado (2022)

promising fungi from progressing through further research and commercialising (Ganeshan et al. 2021; Lahlali et al. 2022). Many factors can influence the efficacy of a specific fungal BCAs against RKNs, including environmental factors, time of treatment, season, method and frequency of application. The same fungal BCAs may perform differently *in vitro* and *in vivo*, i.e. under laboratory, greenhouse, glass house, shade/net house and field conditions. There have been reports on the inconsistency of these products in managing RKNs (Agbenin and Agbenin NO 2012; Huang et al. 2016). Such inconsistencies could be due to both biotic and abiotic factors across different exposure conditions. In a study by Jaffee (Jaffee et al. 1992), fungal nematode-parasitism was 100% under *in vitro* conditions but dropped to almost 0% with the same nematode population densities under *in vivo* conditions. Martinelli et al. (2012) studied the survival ability of five nematophagous fungi, *A. robusta, A. oligospora, A. musiformis, D. leptospora* and *M. eudermatum*, after their field application. Six months after application, only *D. leptospora* was still active, while the rest were no longer active.

Nematophagous fungi of the genera *Aspergillus*, *Talaromyces* and *Trichoderma* are promising BCAs that have demonstrated effective antagonistic effects against a wide range of PPNs (Abd-Elgawad and Askary 2018). Recent findings further confirm this potential, as *A. terreus*, *T. minioluteus, T. sayulitensis, T. ghanense* and *T. viride* exhibited strong ovicidal and nematicidal activity against M. enterolobii under both *in vitro* and *in vivo* conditions (Ramatsitsi et al. 2025). However, because soil is a dynamic matrix, the extent of RKNs mitigation can be influenced by a variety of circumstances. The efficacy of fungal BCAs *in vivo* may be affected by temperature, moisture, soil texture and structure, nematode density, and proliferation. As a result, the BCAs is deemed ineffective since it is incapable of adapting to rapidly changing environmental conditions. Indigenous fungal species, on the other hand, would have significant advantages over introduced/exotic ones because they may be more virulent against local nematode populations, compete more successfully with indigenous microflora, and be more adapted to environmental conditions. Further studies should be carried out to establish the types and proportions of metabolites/enzymes produced by isolates from a certain location, particularly how they differ from those secreted by foreign/introduced species, to achieve better nematode control. Given the high economic impact that RKNs continue to impose, a better and detailed understanding of the rhizosphere interactions serves as prerequisites to appropriately improve the efficacy of fungal BCAs in sustainable agriculture. Further research on identifying more fungal species with the potential to parasitise RKNs is also important since their threat to agricultural production is an ongoing worldwide crisis.

Since BCAs would become part of the ecosystem and directly affect the environment (Akter et al. 2025), we must be ready for, or at least envisage, any possible risks that may arise from their use. Therefore, before

using BCAs, a comprehensive analysis of the advantages and potential hazards should be conducted in order to give stakeholders the knowledge they need for effective, secure, and long-term pest management and optimum production (Ehlers 2011). Higher population of BCAs with a declining population of pests, means shortage of food for the BCAs, thus potential for BCAs to turn into pests. This means that coupled with ensuring effectiveness, BCAs conservation practices should also be implemented. It is also imperative to test each nematophagous fungi because species from the same genera may be both parasitic and beneficial. For instance, while *A. tubingensis* is an endophytic nematophagous fungus (Sikandar et al. 2023), *A. flavus* is nematophagous and pathogenic to plants (Lohmar et al. 2019). Another study by Ramatsitsi et al. (2023) elucidated that though *A. terreus* resulted in enhanced seed germination, *A. flavus* caused seed rot and poor germination of different commercial seeds. Before becoming available on the market, BCAs and biopesticides must successfully complete and pass an approval procedure. This procedure ensures that the product that is brought to the market is safe for both people and the environment (Chaudhary et al. 2024). Government authorities across countries oversee establishing guidelines for the use of these agro products that interact with the food chain. Organisations including Organic Materials Review Institute, the United States Environmental Protection Agency, Canada Pest Management Regulatory Agency, Southern Africa Biopesticides Project and French Ministry of Agriculture & Fishing are in charge of evaluating the dangers associated with the products used in food crops (Tranier et al. 2014). While all these procedures are rightfully necessary, it takes a long time and money, which could prove unaffordable, especially in developing countries, resulting in a prolonged shift from agro synthetic to biochemical. This is evidenced by continued use of synthetic chemicals in crop production (Pathak et al. 2022).

Furthermore, the multi-step process from initial identification of potential BCAs, *in vitro* and *in vivo* evaluation, mass liquid or solid-based production and registration of BCAs present several challenges that call for substantial collaboration from governmental organisations, the business community and academia. This is also evidenced by the marked disproportion between the number of nematophagous fungi studied experimentally and those that have successfully reached commercialisation, highlighting the gap between research potential and market realisation. The disparities in registration requirements across three continents (Europe, North and South America) (Huang et al. 2016) highlight the real-world challenges in evaluating and promoting novel BCAs marketable products. Selling BCAs products is a challenging endeavour since significant evidence must be given to regulators and farmers alike to reassure them that the new product can offer the same level of effectiveness, if not more, than current products in a way that is both economic and safe. The molecular foundations of nematode-microbe relationships have come into more prominence over the years. Studying biochemical processes behind these relationships is fundamental to understanding how nematodes respond to BCAs and vice versa, as well as how the host plant responds to this relationship. To completely understand the scope of these interactions and take advantage of nematophagous fungi, biological control should thus constantly take an evolutionary viewpoint, considering the inherent genetic, phenotypic, and behavioural variety of BCAs and their targets.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The work was supported by the Potatoes South Africa.

ORCID

Ndivhuwo Ramatsitsi http://orcid.org/0000-0001-7779-3764
Alen Manyevere http://orcid.org/0000-0002-4756-0895
Tuelo Motloba http://orcid.org/0000-0003-1135-4704

Data availability statement

Data sharing is not applicable to this article as no new data were created or analysed in this study.

References

Abd-Elgawad MMM, Askary TH. 2018. Fungal and bacterial nematicides in integrated nematode management strategies. Egypt J Biol Pest Control. 28(1):74. https://doi.org/10.1186/s41938-018-0080-x

Agbenin NO. 2012. Biological control of plant parasitic nematodes: prospects and challenges for the poor Africa farmer. Plant Prot Sci. 47(2):62–67. https://doi.org/10.17221/46/2010-PPS

Akter S, Mahmud U, Shoumik BAA, Khan MZ. 2025. Although invisible, fungi are recognised as the engines of a microbial powerhouse that drives soil ecosystem services. Arch Microbiol. 207(4):79. https://doi.org/10.1007/s00203-025-04285-4

Alhazmi N, Ibrahim D, Moussa TAA. 2025. Evaluation of nematicidal and plant growth promotion properties of some soil nematophagous fungi against root-knot nematode *Meloidogyne incognita: in vitro* and greenhouse studies. Egypt J Bot. 65(3):589–600. https://doi.org/10.21608/ejbo.2025.368405.3226

Ali AAI et al. 2024. Utilising endophytic plant growth-promoting bacteria and the nematophagous fungus *Purpureocillium lilacinum* as biocontrol agents against the root-knot nematode (*Meloidogyne incognita*) on tomato plants. Eur J Plant Pathol. 170(2):417–436. https://doi.org/10.1007/s10658-024-02907-z

Aminuzzaman FM, Xie HY, Duan WJ, Sun BD, Liu XZ. 2013. Isolation of nematophagous fungi from eggs and females of *Meloidogyne* spp. and evaluation of their biological control potential. Biocontrol Sci Technol. 23(2):170–182. https://doi.org/10.1080/09583157.2012.745484

Annapurna M, Bhagawati B, Kurulkar U. 2018. Biochemical mechanism of native fungal bioagents in the management of root-knot nematode Meloidogyne incognita on tomato. Int J Curr Microbiol Appl Sci. 7(11):380–395. https://doi.org/10.20546/ijcmas.2018.711.047

Arunachalam A et al. 2025. Unfastening sublethal effects of the nematophagus fungus *Pochonia chlamydosporia* [TNAU pc-001] on the biotic potentials of *Meloidogyne enterolobii* (Yang & Eisenback, 1983) (Tylenchida: meloidogynidae). J Crop Health. 77(3):1–12. https://doi.org/10.1007/s10343-025-01149-1

Askary TH. 2015. Nematophagous fungi as biocontrol agents of phytonematodes. In: Askary T, Martinelli P, editors. Biocontrol agents of phytonematodes. CAB International; pp 81–125.

Bamisile BS, Siddiqui JA, Akutse KS, Ramos Aguila LC, Xu Y. 2021. General limitations to endophytic entomopathogenic fungi use as plant growth promoters, pests and pathogens biocontrol agents. Plants. 10(10):2119. https://doi.org/10.3390/plants10102119

Bansal R et al. 2021. Dual role of a dedicated GAPDH in the biosynthesis of volatile and non-volatile metabolites- novel insights into the regulation of secondary metabolism in *Trichoderma virens*. Microbiol Res. 253:126862. https://doi.org/10.1016/j.micres.2021.126862

Bejarano A, Puopolo G. 2020. Bioformulation of microbial biocontrol agents for a sustainable agriculture. In: De Cal A, Melgarejo P, Magan N, editors. How research can stimulate the development of commercial biological control against plant diseases. Springer International Publishing; pp 275–293.

Birkenbihl RP, Liu S, Somssich IE. 2017. Transcriptional events defining plant immune responses. Curr Opin Plant Biol. 38:1–9. https://doi.org/10.1016/j.pbi.2017.04.004

Brand D, Soccol CR, Sabu A, Roussos S. 2010. Production of fungal biological control agents through solid state fermentation: a case study on *Paecilomyces lilacinus* against root-knot nematodes. Micol Apl Int. 22(1):31–48.

Brar SK, Verma M, Tyagi R, Valéro J. 2006. Recent advances in downstream processing and formulations of *Bacillus thuringiensis* based biopesticides. Process Biochem. 41(2):323–342. https://doi.org/10.1016/j.procbio.2005.07.015

Bulgari D et al. 2023. Solid-state fermentation of *Trichoderma* spp.: a new way to valorize the agricultural digestate and produce value-added bioproducts. J Agric Food Chem. 71(9):3994–4004. https://doi.org/10.1021/acs.jafc.2c07388

Calvet C, Pinochet J, Hernández-Dorrego A, Estaún V, Camprubí A. 2001. Field microplot performance of the peach-almond hybrid GF-677 after inoculation with arbuscular mycorrhizal fungi in a replant soil infested with root-knot nematodes. Mycorrhiza. 10(6):295–300. https://doi.org/10.1007/PL00009998

Chaudhary R et al. 2024. Microbial bio-control agents: a comprehensive analysis on sustainable pest management in agriculture. J Agric Food Res. 18(4):101421. https://doi.org/10.1016/j.jafr.2024.101421

Chen J, Li Q, Song B. 2020. Chemical nematicides: recent research progress and outlook. J Agric Food Chem. 68 (44):12175–12188. https://doi.org/10.1021/acs.jafc.0c02871

Contreras-Cornejo HA, Macías-Rodríguez L, Del-Val E, Larsen J. 2016. Ecological functions of *Trichoderma* spp. and their secondary metabolites in the rhizosphere: interactions with plants. FEMS Microbiol Ecol. 92(4):fiw036. https://doi.org/10.1093/femsec/fiw036

Ehlers RU. 2011. Cost-benefit, risk and trade-off analysis of regulation. In: Ehlers R, editor. Regulation of biological control agents. Springer; pp 139–153.

Eisenback JD, Hunt D. 2009. Root-knot nematodes. In: Perry R, Moen M, Starr J, editors. General morphology. CABI Publishing; pp 18–54.

Escudero N, Lopez-Llorca LV. 2012. Effects on plant growth and root-knot nematode infection of an endophytic GFP transformant of the nematophagous fungus *Pochonia chlamydosporia*. Symbiosis. 57(1):33–42. https://doi.org/10.1007/s13199-012-0173-3

Evlice E, Toktay H, Yatkın G, Erdoğuş FD, İmren M. 2022. Population fluctuations of root-knot nematodes *Meloidogyne chitwoodi* and *M. hapla* under field conditions. Phytoparasitica. 50(3):233–242. https://doi.org/10.1007/s12600-021-00939-3

Ferreira JM, Carreira DN, Braga FR, Soares FEDF. 2019. First report of the nematicidal activity of *Flammulina velutipes*, its spent mushroom compost and metabolites. 3 Biotech. 9(11):1–6. https://doi.org/10.1007/s13205-019-1951-x

Forghani F, Hajihassani A. 2020. Recent advances in the development of environmentally benign treatments to control root-knot nematodes. Front Plant Sci. 11:1125. https://doi.org/10.3389/fpls.2020.01125

Fourie H, De Waele D. 2019. Integrated pest management (IPM) of nematodes. In: Fourie H, De Waele D, editors. Integrated management of insect pests. ed.1st ed. Burleigh Dodds Science Publishing; pp 771–840.

Ganeshan S, Kim SH, Vujanovic V. 2021. Scaling-up production of plant endophytes in bioreactors: concepts, challenges and perspectives. Bioresour Bioprocess. 8(1):63. https://doi.org/10.1186/s40643-021-00417-y

Geraldine AM et al. 2013. Cell wall-degrading enzymes and parasitism of sclerotia are key factors on field biocontrol of white mold by *Trichoderma* spp. BioControl. 67(3):308–316. https://doi.org/10.1016/j.biocontrol.2013.09.013

Gervais P, Fasquel J-P, Molin P. 1988. Water relations of fungal spore germination. Appl Microbiol Biotechnol. 29 (6):586–592. https://doi.org/10.1007/BF00260989

González I et al. 2012. Induction of chitinases and glucanases in *Trichoderma* spp. strains intended for biological control. Biotecnología Apl. 29(1):12–16.

Groves K, Li Y, Peiris PUS, Brown PH. 2025. Efficacy of nematophagous fungi (*Arthrobotrys dactyloides* and *A. oligospora*) as biocontrol agents against root-knot nematode (*Meloidogyne javanica*) in sweetpotato. BioControl. 70(1):95–106. https://doi.org/10.1007/s10526-024-10289-8

Hajji-Hedfi L et al. 2023. Biological and proteomic analysis of a new isolate of the nematophagous fungus *Lecanicillium* sp. BMC Microbiol. 23(1):108. https://doi.org/10.1186/s12866-023-02855-4

Halloran FD, Burnell A. 2006. The chemosensory system of *Caenorhabditis elegans* and other nematodes. In: Marcel D, Willem T, editors. Chemical ecology: from gene to ecosystem. Springer; pp 71–88.

Hastuti L et al. 2023. Nematophagous fungi isolated from municipal waste-contaminated soil in Medan city, North Sumatera: morphological identification, phylogeny analysis and assessment as root-knot nematodes biocontrol. YYU J Agr Sci. 33(4):522–533. https://doi.org/10.29133/yyutbd.1230261

Hastuti LDS, Putri TQA, Priyani N, Kesuma SI. 2024. Efficacy of fungal bioconsortia comprising *Trichoderma yunnnanense* and *Arthrobotrys thaumasius* in the management of *Meloidogyne hapla* infestations in tomato cultivation. Int J Agric Biol. 32(5):461–467. https://doi.org/10.17957/IJAB/15.2224

He Q, Wang D, Li B, Maqsood A, Wu H. 2020. Nematicidal evaluation and active compounds isolation of *Aspergillus japonicus* ZW1 against root-knot nematodes *Meloidogyne incognita*. Agron. 10(9):1222. https://doi.org/10.3390/agronomy10091222

Huang WK et al. 2016. Testing various biocontrol agents against the root-knot nematode (*Meloidogyne incognita*) in cucumber plants identifies a combination of *Syncephalastrum racemosum* and *Paecilomyces lilacinus* as being most effective. Bio Control. 92:31–37. https://doi.org/10.1016/j.biocontrol.2015.09.008

Jaffee BA, Muldoon AE, Tedford EC. 1992. Trap production by nematophagous fungi growing from parasitised nematodes. Ecol Epidol. 82(6):615–620. https://doi.org/10.1094/Phyto-82-615

Jansson HB. 1993. Adhesion to nematodes of conidia from the nematophagous fungus *drechmeria coniospora*. Microbiol. 139(8):1899–1906. https://doi.org/10.1099/00221287-139-8-1899

Jansson HB. 1994. Adhesion of conidia of *drechmeria coniospora* to *Caenorhabditis elegans* wild type and mutants. J Nematol. 26(4):430–435.

Jansson HB, Lopez-Llorca LV. 2004. Control of nematodes by fungi. In: Dekker M, editor. Fungal biotechnology in agricultural, food, and environmental applications. Marcel Dekker; pp 205–215.

Kanalbek G et al. 2025. Isolation, morphological and molecular–phenological identification of nematophagous fungi inhabiting the soils of agricultural lands in southern Kazakhstan. J Fungi. 11(1):42. https://doi.org/10.3390/jof11010042

Kantor C, Eisenback JD, Kantor M. 2024. Biosecurity risks to human food supply associated with plant-parasitic nematodes. Front Plant Sci. 15:15. https://doi.org/10.3389/fpls.2024.1404335

Khan A, Khan A, Ali A, Fatima S, Siddiqui MA. 2023. Root-knot nematodes (*Meloidogyne* spp.): biology, plant-nematode interactions and their environmentally benign management strategies. Protein Expr Purif. 32(2):210–220. https://doi.org/10.1016/j.pep.2003.07.007

Khan MR, Quintanilla M. 2023. Nematode diseases of crops and their sustainable management. 1st ed. Academic Press, Elsevier.

Könker J, Zenker S, Meierhenrich A, Patel A, Dietz KJ. 2025. *Pochonia chlamydosporia* synergistically supports systemic plant defense response in *Phacelia tanacetifolia* against *Meloidogyne hapla*. Front Plant Sci. 15:1497575. https://doi.org/10.3389/fpls.2024.1497575

Krif G et al. 2022. Efficacy of authentic bio-nematicides against the root-knot nematode, *Meloidogyne javanica* infecting tomato under greenhouse conditions. Physiol Mol Plant Pathol. 118:101803. https://doi.org/10.1016/j.pmpp.2022.101803

Krif G et al. 2024. Potential effects of nematophagous fungi against *Meloidogyne javanica* infection of tomato plants under *in vitro* and *in vivo* conditions. J Crop Health. 76(4):829–839. https://doi.org/10.1007/s10343-024-00989-7
Lahlali R et al. 2022. Biological control of plant pathogens: a global perspective. Microorganisms. 10(3):596. https://doi.org/10.3390/microorganisms10030596
Le H, Padgham J, Hagemann M, Sikora R, Schouten A. 2016. Developmental and behavioural effects of the endophytic *Fusarium moniliforme* Fe14 towards *Meloidogyne graminicola* in rice. Ann Appl Biol. 169(1):134–143. https://doi.org/10.1111/aab.12287
Lei HM et al. 2023. 2-furoic acid associated with the infection of nematodes by *Dactylellina haptotyla* and its biocontrol potential on plant root-knot nematodes. Microbiol Spectr. 11(5):e01896–01823. https://doi.org/10.1128/spectrum.01896-23
Leonetti P, Costanza A, Zonno MC, Molinari S, Altomare C. 2014. How fungi interact with nematode to activate the plant defence response to tomato plants. Commun Agric Appl Biol Sci. 79(3):357–363.
Li X et al. 2024. Eco-friendly management of Meloidogyne incognita in cadmium-contaminated soil by using nematophagous fungus *Purpureocillium lavendulum* YM 1. 683: efficacy and mechanism. Environ Res. 244:117930. https://doi.org/10.1016/j.envres.2023.117930
Li Y et al. 2025. Microsclerotia formation of the biocontrol fungus *Cordyceps javanica* IF-1106 and evaluation of its stress tolerance and pathogenicity. Front Microbiol. 16:1583850. https://doi.org/10.3389/fmicb.2025.1583850
Li Z et al. 2024. Nematicidal glycosylated resorcylic acid lactones from the fungus *Pochonia chlamydosporia* PC-170 and their key biosynthetic genes. Front Microbiol. 15:1385255. https://doi.org/10.3389/fmicb.2024.1385255
Liarzi O, Bucki P, Braun Miyara S, Ezra D. 2016. Bioactive volatiles from an endophytic Daldinia cf. concentrica isolate affect the viability of the plant parasitic nematode *Meloidogyne javanica*. PLOS ONE. 11(12):e0168437. https://doi.org/10.1371/journal.pone.0168437
Liu T, Wang L, Duan Y-X, Wang X. 2008. Nematicidal activity of culture filtrate of Beauveria bassiana against *Meloidogyne hapla*. World J Microbiol Biotechnol. 24(1):113–118. https://doi.org/10.1007/s11274-007-9446-z
Liu X, Xiang M, Che Y. 2009. The living strategy of nematophagous fungi. Mycoscience. 50(1):20–25. https://doi.org/10.1007/S10267-008-0451-3
Lohmar JM, Puel O, Cary JW, Calvo AM. 2019. The *Aspergillus flavus* rtfA gene regulates plant and animal pathogenesis and secondary metabolism. Appl Environ Microbiol. 85(6). https://doi.org/10.1128/aem.02446-18
López-Lima D, Alarcón-Utrera D, Ordáz-Meléndez JÁ, Villain L, Carrión G. 2023. *Metarhizium carneum* formulations: a promising new biological control to be incorporated in the integrated management of *Meloidogyne enterolobii* on tomato plants. Plants. 12(19):3431. https://doi.org/10.3390/plants12193431
Lorang JM, Sweat TA, Wolpert TJ. 2007. Plant disease susceptibility conferred by a "resistance" gene. Proc Natl Acad Sci USA. 104(37):14861–14866. https://doi.org/10.1073/pnas.0702572104
Lu CJ et al. 2022. Survival and infectivity of second-stage root-knot nematode *Meloidogyne incognita* juveniles depend on lysosome-mediated lipolysis. J Biol Chem. 298(3):101637. https://doi.org/10.1016/j.jbc.2022.101637
Luo N et al. 2024. Synergistic effect of two peptaibols from biocontrol fungus *Trichoderma longibrachiatum* strain 40418 on co-induced plant resistance. J Agric Food Chem. 72(38):20763–20774. https://doi.org/10.1021/acs.jafc.4c01952
Machado A. 2022. Bionematicides in Brazil: an emerging and challenging market. RAPP. https://doi.org/10.31976/0104-038321v280002
Martinelli PRP, Santos JM, Soares P. 2012. Survival of nematophagous fungi establishment of applied in the field for the control of key citrus nematodes in Brazil. Biosci J. 28:696–675.
Martinez Y, Ribera J, Schwarze F, De France K. 2023. Biotechnological development of *Trichoderma*-based formulations for biological control. Appl Microbiol Biotechnol. 107(18):5595–5612. https://doi.org/10.1007/s00253-023-12687-x
Mastan A, Bharadwaj R, Kushwaha RK, Vivek Babu CS. 2019. Functional fungal endophytes in *coleus forskohlii* regulate labdane diterpene biosynthesis for elevated forskolin accumulation in roots. Microb Ecol. 78(4):914–926. https://doi.org/10.1007/s00248-019-01376-w
Mbarga JB et al. 2014. A new oil-based formulation of *Trichoderma asperellum* for the biological control of cacao black pod disease caused by *Phytophthora megakarya*. BioControl. 77:15–22. https://doi.org/10.1016/j.biocontrol.2014.06.004
Mendoza-Mendoza A et al. 2018. Molecular dialogues between *Trichoderma* and roots: role of the fungal secretome. Fungal Biol Rev. 32(2):62–85. https://doi.org/10.1016/j.fbr.2017.12.001
Meyer SLF. 1999. Efficacy of the fungus *verticillium lecanii* for suppressing root-knot nematode egg numbers on cantaloupe roots. Hort Tech. 9(3):443–447. https://doi.org/10.21273/horttech.9.3.443
Mitiku M. 2018. Plant-parasitic nematodes and their management: a review. Agric Res Technol. 16(2). https://doi.org/10.19080/ARTOAJ.2018.16.55580
Molinari S, Leonetti P. 2019. Bio-control agents activate plant immune response and prime susceptible tomato against root-knot nematodes. PLOS ONE. 14(12):e0213230. https://doi.org/10.1371/journal.pone.0213230
Mukhtar T, Jabbar A, Raja M, Javed H. 2018. Management of root-knot nematode, *Meloidogyne incognita*, in tomato with two *Trichoderma* species. Pak J Zool. 50(4):1589–1592. https://doi.org/10.17582/journal.pjz/2018.50.4.sc15
Mulatu A, Alemu T, Megersa N, Vetukuri RR. 2021. Optimisation of culture conditions and production of bio-fungicides from *Trichoderma* species under solid-state fermentation using mathematical modeling. Microorganisms. 9(8):1674. https://doi.org/10.3390/microorganisms9081675

Muthulakshmi M, Kumar S, Subramanian S, Anita B. 2012. Compatibility of *Pochonia chlamydosporia* with other biocontrol agents and carbofuran. J Biopest. 5243–245. https://doi.org/10.57182/jbiopestic.5.0.243-245

Naeimi S, Khosravi V, Varga A, Vágvölgyi C, Kredics L. 2020. Screening of organic substrates for solid-state fermentation, viability and bioefficacy of *Trichoderma harzianum* AS12-2, a biocontrol strain against rice sheath blight disease. Agron. 10(9):1258. https://doi.org/10.1007/s12600-021-00950-8

Naz I et al. 2021. Biological control of root knot nematode. Meloidogyne incognita, in vitro, greenhouse and field in cucumber. Biocontrol. 152:104429. https://doi.org/10.1016/j.biocontrol.2020.104429

Nicol JM et al. 2011. Genomics and molecular genetics of plant-nematode interactions. In: Jones G, Fenoll C, editors. Current nematode threats to world agriculture. Springer; pp 21–43.

Nicolopoulou-Stamati P, Maipas S, Kotampasi C, Stamatis P, Hens L. 2016. Chemical pesticides and human health: the urgent need for a new concept in agriculture. Front Public Health. 4:148. https://doi.org/10.3389/fpubh.2016.00148

Nie H, Lv B, Sun M, Zhong Z, Li S. 2023. Pre-treatment with Dazomet enhances the biocontrol efficacy of *Purpureocillium lilacinum* to *Meloidogyne incognita*. BMC Microbiol. 23(1):244. https://doi.org/10.1186/s12866-023-02978-8

Niño-Arteaga DM et al. 2023. Biocontrol of the root-knot nematode *Meloidogyne incognita* with *Purporeocillum lilacinum* and liquid bio-formulates in tomato (*Solanum lycopersicum*). Not Bot Horti Agrobot Cluj-Na. 51(1):13010–13010. https://doi.org/10.15835/nbha51113010

Nishat Y, Chen Q, Lan D, Sikandar A, Wu HY. 2025. Co-fermentation of nematode-antagonistic fungi. Aspergillus niger, and Talaromyces cystophila, with a plant homogenate of Rehmannia glutinosa Libosch to manage Meloidogyne enterolobii in tomato. Crop Protection. 198:107368. https://doi.org/10.1016/j.cropro.2025.107368

Oclarit E, Cumagun C. 2009. Evaluation of efficacy of *Paecilomyces lilacinus* as biological control agent of *Meloidogyne incognita* attacking tomato. J Plant Prot Res. 49(4):337–340. https://doi.org/10.2478/v10045-009-0053-x

Onkendi EM, Kariuki GM, Marais M, Moleleki LN. 2014. The threat of root-knot nematodes (*Meloidogyne* spp.) in Africa: a review. Plant Pathol. 63(4):727–737. https://doi.org/10.1111/ppa.12202

Pathak VM et al. 2022. Current status of pesticide effects on environment, human health and it's eco-friendly management as bioremediation: a comprehensive review. Front Microbiol. 13:962619. https://doi.org/10.3389/fmicb.2022.962619

Peng G, Xia Y. 2011. The mechanism of the mycoinsecticide diluent on the efficacy of the oil formulation of insecticidal fungus. BioControl. 56(6):893–902. https://doi.org/10.1007/s10526-011-9360-z

Ploeg AT et al. 2023. Tomato mi-gene resistance-breaking populations of *Meloidogyne* show variable reproduction on susceptible and resistant crop cultivars. J Nematol. 55(1):20230043. https://doi.org/10.2478/jofnem-2023-0043

Poveda J, Abril-Urias P, Escobar C. 2020. Biological control of plant-parasitic nematodes by filamentous fungi inducers of resistance: *Trichoderma*, mycorrhizal and endophytic fungi. Front Microbiol. 11:992. https://doi.org/10.3389/fmicb.2020.00992

Ramatsitsi MN, Khosa MC, Mashamaite CV, Ramachela K. 2023. *In vitro* assessment of eight selected indigenous fungal isolates tolerance to various abiotic stresses and their effects on seed germination. Curr Microbiol. 80(12):386. https://doi.org/10.1007/s00284-023-03507-6

Ramatsitsi MN, Nxumalo S, Ramachela K, Khosa MC. 2024. Host response of five potato cultivars to *Meloidogyne* nematodes. J Plant Dis Prot. 131(3):891–898. https://doi.org/10.1007/s41348-023-00851-4

Ramatsitsi N, Dube ZP, Ramachela K, Motloba T. 2025. Bio-control efficacy of selected indigenous nematophagous fungi against *Meloidogyne enterolobii in vitro* and on dry bean (*Phaseolus vulgaris* L.). Int Microbiol. 28(1):151–160. https://doi.org/10.1007/s10123-024-00571-1

Riga E, Lacey LA, Guerra N. 2008. Muscodor albus, a potential biocontrol agent against plant-parasitic nematodes of economically important vegetable crops in Washington state, USA. BioControl. 45(3):380–385. https://doi.org/10.1016/j.biocontrol.2008.01.002

Routray S. 2020. International year of plant health 2020. Biotica Res Today. 2:142–145.

Rusconi JM et al. 2025. A survey of root-knot and false root-knot nematodes at commercial vegetable farms under protected cultivation in La Plata Green Belt, Argentina. Nematol. 27(2):167–179. https://doi.org/10.1163/15685411-bja10380

Sahebani N, Hadavi N. 2008. Biological control of the root-knot nematode *Meloidogyne javanica* by *Trichoderma harzianum*. Soil Biol Biochem. 40(8):2016–2020. https://doi.org/10.1016/j.soilbio.2008.03.011

Sarir A, Mehrab K, Ikram U. 2022. Integrated root-knot nematodes (*Meloidogyne*) management approaches. In: Jorge MM, Victor Hugo Del RA, Romel HB, editors. Parasitic helminths and zoonoses. IntechOpen; p Ch. 13.

Sayed M, Abdel-Rahman T, Ragab A, Abdellatif A. 2019. Biocontrol of root-knot nematode *Meloidogyne incognita* by chitinolytic *Trichoderma* spp. Egypt J Agronematology. 18(1):30–47. https://doi.org/10.21608/ejaj.2019.52842

Siddique S, Grundler FMW. 2018. Parasitic nematodes manipulate plant development to establish feeding sites. Curr Opin Microbiol. 46:102–108. https://doi.org/10.1016/j.mib.2018.09.004

Sikandar A et al. 2020. Review article: *Meloidogyne incognita* (root-knot nematode) a risk to agriculture. Appl Ecol Environ Res. 18(1):1679–1690. https://doi.org/10.15666/aeer/1801_16791690

Sikandar A et al. 2023. Efficacy of *Aspergillus tubingensis* GX3' fermentation against *Meloidogyne enterolobii* in tomato (*Solanum lycopersicum*. L.). Plants. 12(14):2724. https://doi.org/10.3390/plants12142724

Sikora RA, Coyne D, Hallmann J, Timper P. 2018. Reflections and challenges: nematology in subtropical and tropical agriculture. In: Rac S, Hallmann D, Timper J, editors. Plant parasitic nematodes in subtropical and tropical agriculture. ed.3rd ed. CABI Publishing; pp 1–19.

Sikora Rad J, Molendijk L. 2021. Integrated nematode management: state-of-the-art and visions for the future. CABI Publishing.

Silveira A et al. 2001. Scanning electron microscopy of the predatory ability of agents of the biocontrol of nematodes. Sem Ci Agr. 22(1):113–120. https://doi.org/10.5433/1679-0359.2001v22n1p113

Singh A, Sharma P, Kumari A, Kumar R, Pathak D. 2019. Management of root-knot nematode in different crops using microorganisms. In: Varma A, Tripathi S, Prasad R, editors. Plant biotic interactions. Springer; pp 85–99.

Soares FEDF, Sufiate BL, de Queiroz JH. 2018. Nematophagous fungi: far beyond the endoparasite, predator and ovicidal groups. Agr Nat Resour. 52(1):1–8. https://doi.org/10.1016/j.anres.2018.05.010

Sreeja P, Rani OPR, Chellappan M. 2025. *Lecanicillium saksenae*: a novel nematophagous fungus against root knot nematode, *Meloidogyne incognita* (Kofoid & White, 1919) from Kerala, India. J Asia Pac Entomol. 28(2):102416. https://doi.org/10.1016/j.aspen.2025.102416

Stephan D, Da Silva A-P, Bisutti IL. 2016. Optimization of a freeze-drying process for the biocontrol agent *pseudomonas* spp. and its influence on viability, storability and efficacy. Biol Control. 94:74–81. https://doi.org/10.1016/j.biocontrol.2015.12.004

Stucky T et al. 2024. Control of the plant-parasitic nematode *Meloidogyne incognita* in soil and on tomato roots by *Clonostachys rosea*. J Appl Microbiol. 135(5):lxae111. https://doi.org/10.1093/jambio/lxae111

Sun X et al. 2024. Parasitism of Hirsutella rhossiliensis on different nematodes and its endophytism promoting plant growth and resistance against root-knot nematodes. J Fungi. 10(1):68. https://doi.org/10.3390/jof10010068

Swarnakumari N, Sindhu R, Thiribhuvanamala G, Rajaswaminathan V. 2020. Evaluation of oil dispersion formulation of nematophagus fungus, *Pochonia chlamydosporia* against root-knot nematode, *Meloidogyne incognita* in cucumber. J Asia Pac Entomol. 23(4):1283–1287. https://doi.org/10.1016/j.aspen.2020.10.008

Tranier M-S et al. 2014. Commercial biological control agents targeted against plant-parasitic root-knot nematodes. Braz Arch Biol Technol. 57(6):831–841. https://doi.org/10.1590/S1516-8913201402540

Vos C et al. 2012. Arbuscular mycorrhizal fungi affect both penetration and further life stage development of root-knot nematodes in tomato. Mycorrhiza. 22(2):157–163. https://doi.org/10.1007/s00572-011-0422-y

Xu WF et al. 2021. Understanding the transcriptional changes during infection of *Meloidogyne incognita* eggs by the egg-parasitic fungus *Purpureocillium lilacinum*. Front Microbiol. 12. https://doi.org/10.3389/fmicb.2021.617710

Yánez-Mendizábal V et al. 2012. Formulation development of the biocontrol agent *Bacillus subtilis* strain CPA-8 by spray-drying. J Appl Microbiol. 112(2):954–965. https://doi.org/10.1111/j.1365-2672.2012.05258.x

Yao YR et al. 2015. Transformation of the endophytic fungus *acremonium implicatum* with GFP and evaluation of its biocontrol effect against *Meloidogyne incognita*. World J Microbiol Biotechnol. 31(4):549–556. https://doi.org/10.1007/s11274-014-1781-2