



# Bio-organics Management: Novel Strategies to Manage Root-knot Nematode, *Meloidogyne incognita* Pest of Vegetable Crops

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## Abstract

Root-knot nematodes (*Meloidogyne* spp.) are sedentary endoparasites and soil-borne pathogens worldwide. *M. incognita* is one of the most devastating and dominant species among them causing economic yield losses in almost all vegetables and other agricultural crops in the world. Current management strategies against *M. incognita* are not sufficient. However, from the last decades, utilization of nematicides has been increasing to manage this pest due to which environmental and human health issues arises. Bio-organic approaches are the best alternatives to nematicides, including biological agents and organic matters. In bio agents both arbuscular mycorrhizal and nematophagous fungi have a potent ability to manage plant-parasitic nematodes by inducing systemic resistance and activation of pathogenesis related (PR) genes in inoculated plants against nematodes, whereas nematophagous fungi trap nematodes for their feeding and killing them. Soil application of organic matters *viz.*, botanical extract, oil cakes and agricultural wastes both *in vitro* and *in vivo* is also useful. Botanical extracts, oil cakes, kill nematodes by releasing secondary metabolites and inhibiting the movement of juveniles in the soil. Researchers from all over the world engage in evolving eco-friendly approaches that enhance and sustain the vegetable and agricultural production against this pest and keep it below the threshold level without affecting beneficial soil microbiota. In the future, such environment benign approaches have become an active field of research that adds new knowledge for their success against pest management, and enhancement of agricultural production for the human population.

**Keywords** *Meloidogyne incognita* · Arbuscular mycorrhizal · Nematophagus fungi · Induced systemic resistance · Pathogenesis related genes · Botanical extracts · Oil cakes

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## Biologisch-organische Bewirtschaftung: neue Strategien zur Bekämpfung des Wurzelgallennematoden *Meloidogyne incognita* als Schädling von Gemüsekulturen

### Zusammenfassung

Wurzelgallennematoden (*Meloidogyne* spp.) sind sesshafte Endoparasiten und bodenbürtige Krankheitserreger weltweit. *M. incognita* ist eine der verheerendsten und dominantesten Arten unter ihnen und verursacht wirtschaftliche Ertragseinbußen bei fast allen Gemüsearten und anderen landwirtschaftlichen Kulturen in der Welt. Die derzeitigen Strategien zur Bekämpfung von *M. incognita* sind nicht ausreichend. In den letzten Jahrzehnten wurden jedoch immer mehr Nematizide zur Bekämpfung dieses Schädlings eingesetzt, was zu Problemen für die Umwelt und die menschliche Gesundheit führte. Bio-organische Ansätze sind die beste Alternative zu Nematiziden, einschließlich biologischer Wirkstoffe und organischer Stoffe. Bei den biologischen Wirkstoffen haben sowohl arbuskuläre Mykorrhizapilze als auch nematophage Pilze die Fähigkeit, pflanzenparasitäre Nematoden zu bekämpfen, indem sie eine systemische Resistenz und die Aktivierung von PR-Genen (*pathogenesis related*) in den beimpften Pflanzen gegen Nematoden induzieren, während nematophage Pilze die Nematoden einfangen, um sie zu fressen und zu töten. Der Einsatz von organischen Stoffen im Boden, d.h. Pflanzenextrakten, Ölkuchen und landwirtschaftlichen Abfällen, ist sowohl *in vitro* als auch *in vivo* nützlich. Pflanzenextrakte und Ölkuchen töten Nematoden ab, indem sie sekundäre Metaboliten freisetzen und die Bewegung von Jungtieren im Boden hemmen. Forscher aus der ganzen Welt arbeiten an der Entwicklung umweltfreundlicher Ansätze, die die Gemüse- und Agrarproduktion gegen diesen Schädling verbessern und aufrechterhalten, ohne die nützliche Bodenmikrobiota zu beeinträchtigen. In der Zukunft werden solche umweltfreundlichen Ansätze ein aktives Forschungsgebiet sein, das neue Erkenntnisse über den Erfolg bei der Schädlingsbekämpfung und der Verbesserung der landwirtschaftlichen Produktion für die menschliche Bevölkerung liefert.

**Schlüsselwörter** *Meloidogyne incognita* · Arbuskuläre Mykorrhizapilze · Nematophage Pilze · Induzierte systemische Resistenz · Mit der Pathogenese verbundene Gene · Pflanzenextrakte · Ölkuchen

### Abbreviations

GalNac D-galactosamine N-acetyl  
GCs Giant cells  
J2s Second stage juveniles  
MAMPs Microbe-associated molecular pattern  
MTI MAMPs triggered immunity  
PPNs Plant parasitic nematodes

*lenchus* spp.), cyst nematodes (*Heterodera* and *Globodera*), burrowing nematode (*Radopholus similis*), pine wilt nematode (*Bursaphelenchus xylophilus*), stem and bulb nematode (*Ditylenchus dipsaci*), reniform nematode (*Rotylenchulus reniformis*), rice white tip nematode (*Aphelenchoides besseyi*), false root-knot nematode (*Nacobbus aberrans*) and dagger nematode (*Xiphinema index*-the virus vector nematode) (Jones et al. 2013). Among these, root-knot nematodes (*Meloidogyne* spp.) are the most dangerous and economically important.

### Introduction

The rhizosphere has numerous soil-borne microorganisms interacting with plant roots either antagonistically or synergistically and with other associated microbes. Few of them are helpful to plants and the rhizosphere, whereas some are harmful, i.e., act as biotic stressors. Plant-parasitic nematodes (PPNs) are the most critical and common soil-borne pathogens that affect the global agricultural industry (Kenney and Eleftherianos 2016). At present, about 4100 species of PPNS have been identified, which exhibit a negative impact on the agricultural industry by deteriorating numerous vegetable crops, including eggplant, okra, tomato, chilli, carrot, spinach, cabbage, cauliflower, etc. (Decraemer and Hunt 2013; Chariou and Steinmetz 2017). Numerous nematologists categorized top 10 PPNS that have a global economic impact; these are root-knot nematodes (*Meloidogyne* spp.), root lesion nematode (*Praty-*

### *Meloidogyne incognita* and Its Status On Vegetable Crops

Root-knot nematodes (*Meloidogyne* spp.) belonging to the family, Heteroderidae Order, Tylenchida are considered as highly adaptive, widespread and sedentary obligate endoparasites among all PPNS that completely depend on the host for their survival and reproduction (Khan 2008). Globally, >100 species of root-knot nematodes (*Meloidogyne* spp.) have been identified with more than 3000 host plants, including vegetables and fruits. Four species *viz.*, *M. incognita*, *M. javanica*, *M. arenaria* and *M. hapla* are major and more pathogenic to cause major losses to agricultural crops worldwide up to 90% and predispose the crops to other soil-borne pathogens (Hunt and Handoo 2009; Lunt et al. 2014).

According to Ghule et al. (2014), 14 species of root-knot nematodes have been identified from different areas of India. Out of different species of root-knot nematodes, *M. incognita* was the dominant species in agricultural fields that causes major loss and reduces the quality of vegetable crops viz., okra, eggplant, tomato, and spinach. However, the occurrence of root-knot disease in vegetable fields in different areas of India was predominant due to which vegetable qualities and production are affected. Other species viz., *M. javanica*, *M. arenaria* and *M. graminicola* are also common and pathogenic (Ghule et al. 2014). However, *M. hapla* is found in temperate/cooler areas (Escobar et al. 2015).

Annual vegetable losses reach up to 19.6%, whereas annual crop damage is up to the tune of Rs. 242.1 billion due to PPNs in India (Ahmad et al. 2021). Globally, an average of 10% annual yield loss is recorded in vegetables due to root-knot nematodes. However, much higher percentage losses have been recorded depending upon nematode species, and their population in the soil, locality, and crop species (Collange et al. 2011). Jain et al. (2007) reported yield losses up to 18.20%, 16.67%, 14.10%, 21.35%, 10.54%, and 27.21% in cucurbits, brinjal, okra, jute, rice, and tomato, respectively in India due to root-knot nematode, *M. incognita* (Table 1).

### Life Cycle of *M. incognita* On Vegetable Crops

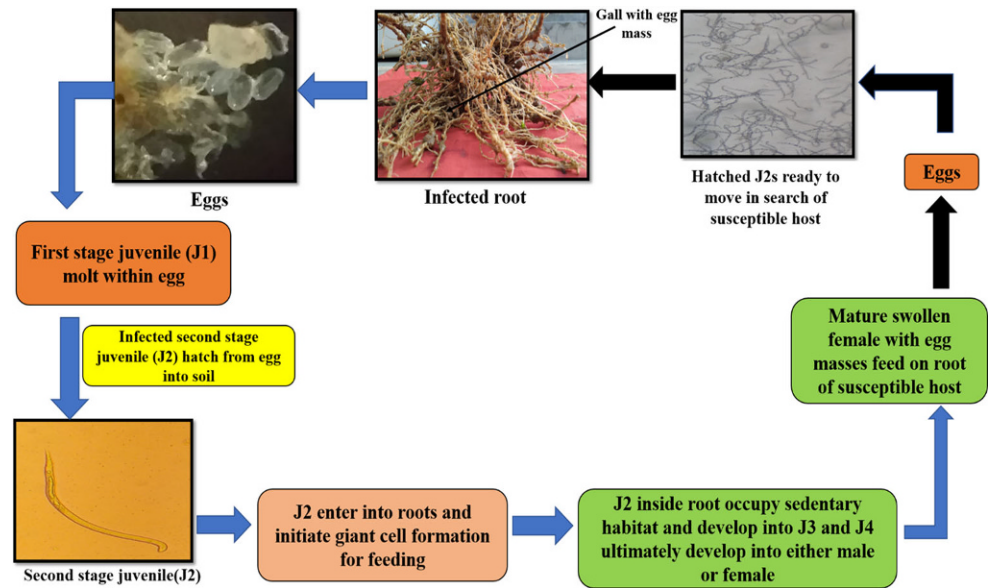
The life cycle of *M. incognita* i.e., from egg to mature female is completed in 25 days at 27°C, but this period is altered by the availability of suitable host, soil moisture (lesser extent), and soil temperature (widely) (Fig. 1). It

started with the hatching of second-stage juveniles (J2s), named to be an infective stage; a stage that initiates the process of infection into the host roots (Rawal 2020). However, CO<sub>2</sub> is a major root diffusate that plays a significant role in long-distance attractant for J2s of *M. incognita* and other PPNs (Robinson 2002). After attaching with the host roots, J2s secrete certain proteins or enzymes viz., endoxylanases, cellulases (endoglucanases), polygalacturonases and pectatelyases from their sub ventral glands into the roots (Davis et al. 2011; Wieczorek et al. 2014; Perry and Moens 2011). Some of these secreted enzymes change the components of the host plant's cell wall or inhibit the host cell cycle, increase degradation of host cell protein, and reduce defence and transcriptional regulation (Akker and Birch 2016). Some parasitic enzymes digest the cellular component of the host plant, establish the permanent feeding site of nematodes within the host roots and help in the formation of giant cells (GCs) (Shakeel et al. 2020). GCs become galls or knots by hypertrophy and hyperplasia and are source of mineral nutrients for nematodes till reproduction. The formation of galls in the roots (Fig. 2) damage the vascular system of the host plant and inhibits its ability to absorb essential mineral elements and water from the soil that ultimately leading to wilting and yellowing of plant (Gao et al. 2016; Lee and Kim, 2016; Jamal et al. 2017). Such infections on the plants also increase the plant's susceptibility to other soil-borne pathogens and form disease-complexes with other harmful soil microbes (Zhou et al. 2016).

**Table 1** Losses on vegetable crops due to various species of root-knot nematodes

Root-knot nematode species	Host crop	Losses (%)	Country	References
<i>Meloidogyne incognita</i>	Tomato	40%	India	Singh and Kumar (2015)
<i>Meloidogyne</i> spp	Chilli Radish	8–23% 8–20%	India	Gowda et al. (2017)
<i>Meloidogyne incognita</i>	Ivy gourd	35.09%	India	Basumatary et al. (2018)
<i>Meloidogyne incognita</i>	Cucumber	66.84% in poly house	India	Bhati and Baheti (2021)
<i>Meloidogyne</i> spp	Okra	480.00 million/annually approx	India	Jain et al. (2007)
<i>Meloidogyne</i> spp	Tomato	24–38%	Pakistan	Mukhtar (2018)
<i>Meloidogyne</i> spp	Tomato	30%	Nepal	Rawal (2020)
<i>Meloidogyne</i> spp	Tomato	80% approx	Turkey	Kaskavalci (2007)
<i>Meloidogyne incognita</i>	Tomato	2.3%	Ethiopia	Sikora and Fernandez (2005), Wesemael et al. (2011)
<i>Meloidogyne</i> spp	Potato	10%	Egypt	Shaloot (2001)
<i>Meloidogyne</i> spp	Carrot	45%	USA	Widmer et al. (1999)
<i>Meloidogyne</i> spp	Sponge gourd	Rs. 547.5 billion annually	India	Chandra et al. (2010), Jain et al. (2007)
<i>Meloidogyne incognita</i>	Bitter gourd	36.72%	India	Darekar and Mhase (1988)
<i>Meloidogyne incognita</i>	Pointed gourd	44%	India	Verma and Anwar (1996)

**Fig. 1** Life cycle of root-knot nematode *M. incognita*



**Fig. 2** Root samples of various vegetable crops infected with *M. incognita*, **a** Root of okra, **b** Beet root, **c** Spinach, **d** Cucurbita, **e** Tomato, and **f** Eggplant root



## Bio-organics Management

Continuous use of nematicides increases the environmental pollution and human health issues. Such issues enhance the utilisation of eco-friendly like bio-organic approaches that could be a grateful for managing *M. incognita* and sustain vegetables production. Although, cultural methods are traditional and facing more restrictions due to the wide host range of *M. incognita* and the existence of mixed populations of different species of genus, *Meloidogyne* in the field

(Xiang et al. 2018), uses of resistant cultivars have been also a successful management tool to protect the crop, but it has been found that certain new species of root-knot nematodes break this resistance viz., *M. enterolobii* (Xiang et al. 2018; Hajihassani et al. 2019). Bio-organics management as eco-friendly management included biotic, application of microbes in both *in vitro* and *in vivo* conditions and abiotic/organic approaches, uses of botanicals, oil cakes and agricultural wastes. Besides these, plants themselves also manage several types of soil-borne pathogens, including

*M. incognita*, by releasing various root exudates, namely amino acids, sugars, organic acids etc. (Bell et al. 2019).

### Biotic Approaches Against *M. incognita*

In biotic approaches, application of living agents' viz., fungi (arbuscular and nematophagous fungi), bacteria or other microbes are considered. These bio agents consists of factors or substances that improve plant growth by inducing resistance gene and control PPNs is another best tool which replaces the chemicals in agriculture (Forghani and Hajihassani 2020). Several studies suggested that synthetic pesticides or chemicals create environmental issues. The excessive amount of chemicals in the soil reduces its fertility, builds soil disintegration, and has negative impacts on human health. Bio-agents will help the plants to control or reduce the harmful effects of soil-borne pathogens, including root-knot nematode, *M. incognita* by interacting with the roots of plants (Forghani and Hajihassani 2020). Other activities like facilitating the resources acquisition, production of plant hormones (gibberellins and cytokinin), lytic enzymes and antibiotics also are done by beneficial microbes within the soil (Glick 2012). Some of the mechanisms were involved to facilitate the endogenous defence at the gene level by activating the genes related to pathogenesis (PR-genes), PR-1, PR-1b, PR-3, 5, salicylic acid (SA)-dependent genes related to pathogenesis of the systemic acquired resistance (SAR) and other genes that kill *M. incognita*. Few enzymatic activities like endochitinase and glucanases were also increased against *M. incognita* in the roots of pre-treated inoculated plants (Molinari and Leonetti 2019).

### Arbuscular Mycorrhizal Fungi (AM Fungi) as Bio-control Agents Against *M. incognita*

Arbuscular mycorrhizal fungi (AM fungi) are found in greater than 80% of almost all soil plants species as obligate root symbionts. They increase uptake of mineral elements in their host plant in exchange of carbon, enhance plant growth and reduce stress in plants (biotic and abiotic stress) (Smith et al. 2010; Vos et al. 2012). These fungi also help plants to increase water uptake and reduce metal toxicity in the soil (Kerry and Hominick 2002). Several studies, *in vitro* and *in vivo* revealed the protective effects of AM fungi against root-knot nematodes in some plants viz., in tomato against *M. incognita*, in coffee against *M. exigua*, *M. coffeicola* and in banana against *X. index* (Vos et al. 2012; Koffi et al. 2013). AM fungi also facilitated the plants to produce certain compounds against PPNs and interfered in the secretion and production of root diffusates that attract PPNs (Teillet et al. 2013).

### Mechanisms of Action of AM Fungi Against *M. incognita*

#### Enhanced Plant Tolerance

**Increased Nutrients Uptake** AM fungi in their host plant facilitate the uptake of certain macro elements such as phosphorus, nitrogen, some micro element viz., zinc and water from the soil; in return, they take carbon from their host (Smith and Smith 2011; Baum et al. 2015). However, it has been found the plant that colonized by AM fungi showed higher phosphate uptake and less susceptibility to *M. incognita* in contrast to the plant that was not colonized by AM fungi. According to Pettigrew et al. (2005), higher nutrient uptake in cotton plant fields helped to reduce or control sedentary semi-endoparasitic nematode, *Rotylenchulus reniformis*.

**Changed Root Morphology** In addition, to increase nutrients uptake, AM fungi inoculated plants showed higher root branching, growth, and led to change in root morphology like tap root than fibrous root from which plant improve their nutrient acquisition and better biomass (Gutjahr and Paszkowski 2013; Yang et al. 2014). According to Vos et al. (2014), mycorrhizal treated plant shows better root growth and branching, leading to resistant against *M. incognita*. AM fungus *Funneliformis mosseae* protect the banana plant from migratory endoparasitic nematodes *Pratylenchus coffeae* and *Radopholus similis* by increasing or changing root morphology (Elsen et al. 2003b). However, it has been reported by some researchers that increased in root branching lead to an increase in infection sites that negatively affect host plant. Depending on the plant species and PPNs viz., root-knot nematode, *M. incognita* and cyst nematodes (*Heterodera* spp.), prefer lateral root formation sites and elongation zones, whereas *R. similis*, prefers primary roots due to presence of secretory substances in these zones (Curtis et al. 2009; Elsen et al. 2003a).

#### Challenges for Nutrients, Space and Infection Sites

Competition for space, host nutrients and infection sites is found among microbes which occupy the same habitat and have the same feeding requirements in an ecological niche when resources are limited such as carbon (C) (Vos et al. 2014). Competition for nutrients like carbon becomes the main mechanism for AM fungi-mediated bio-control (Jung et al. 2012). AM fungi treated plants do better photosynthesis in which carbon demand increase such higher carbon demand inhibits pathogen growth.

Competition for the available space suggested that high level of AM fungi colonization within the host roots resulted in a higher level of bio-control activity against

*M. incognita* (Vierheilig et al. 2008). However, a bio-control activity was observed when both AM fungi and *M. exigua* were inoculated in the coffee plants (Alban et al. 2013). Vigo et al. (2000) found that the AM fungi treated roots reduced the number of infection sites, revealing that more infections will be by pathogen infections.

### Effect of Induced Systemic Resistance

It has been found that inoculation of tomato plants with AM fungi increased the systemic resistance against *M. incognita* (De la Peña et al. 2006). Plants have a specialized pattern called microbe-associated molecular patterns (MAMPs) between harmful and beneficial fungi (Zamioudis and Pieterse 2012). Recognition receptors on MAMPs help to switch on the MAMPs triggered immunity (MTI) which initiate the defence in plant against further invasion by PPNs (Jones and Dangl 2006). Activation of MTI responses leads to hormonal and transcriptional changes in their host plant (Schouteden et al. 2015). Fiorilli et al. (2011) evaluated the changes in the transcriptome of tomato plants when colonized by AM fungi *F. mosseae*. They reported significant modification in genes both in shoots and roots, with the highest variations in both primary and secondary metabolism and defence response against biotic stimulus such as root-knot nematode, *M. incognita*. AM fungus *F. mosseae* was involved in the activation of the root-specific 9-lipoxygenase (9-LOX) and isoleucine conjugation of the jasmonic acid (JA-Ile) pathway. Activation of early MTI-response leads to the induction of jasmonate-linked 9-LOX-pathway that inhibit the development and growth of root-knot nematode. Expression of the 9-LOX gene (ZmLox3 gene) in maize plants was beneficial and enhanced protection against *M. incognita* (Gao et al. 2008). It has been observed that external JA-application and study of changes or mutants in the JA-pathway were found to initiate the resistance in host plant against PPNs (Fan et al. 2015; Fujimoto et al. 2011). Li et al. (2006) observed that the class III chitinase gene of *Glomus versiforme* in the roots of grapevine was activated during the infection

by *M. incognita*. Such report strongly recommends that AM fungi's class III chitinases gene provides resistance against the PPNs. Though the eggs with chitin are affected more by the chitinase enzymes, they also reduce the egg masses and number of the females of root-knot nematodes (Chan et al. 2015). However, future research should be focused on demonstrating the mechanism of action of chitinases against PPNs, with attention on the metabolome and proteome AM fungi-associated changes.

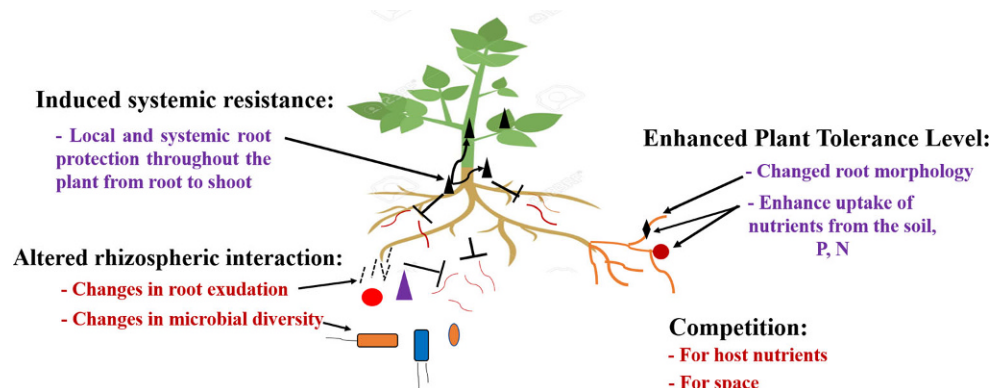
### Altered Rhizospheric Interactions

Alteration in the release of root exudates affects the microbial community in the vicinity of roots and affects interactions between pathogen and plant (Lioussanne 2010). Some reports suggested that the colonization of a plant by AM fungi increased the diversity of beneficial microbes like *Streptomyces* species, fluorescent pseudomonads, chitinase-producing actinomycetes, and facultative anaerobic bacteria (Nuccio et al. 2013; Miransari 2011). These microbes showed antagonistic activity against root-knot nematodes and other PPNs, either by egg-parasitizing fungal activity or nematode-trapping activity or also by induction of the plant defence (Zamioudis and Pieterse 2012). Secretory substances from the roots of mycorrhizal plants were involved in the activation of the beneficial fungus *Trichoderma* spp. having bio-control activity against root-knot nematodes and attraction of plant growth-promoting bacteria *Pseudomonas fluorescense* (Druzhinina et al. 2011; Sikora et al. 2008) (Fig. 3).

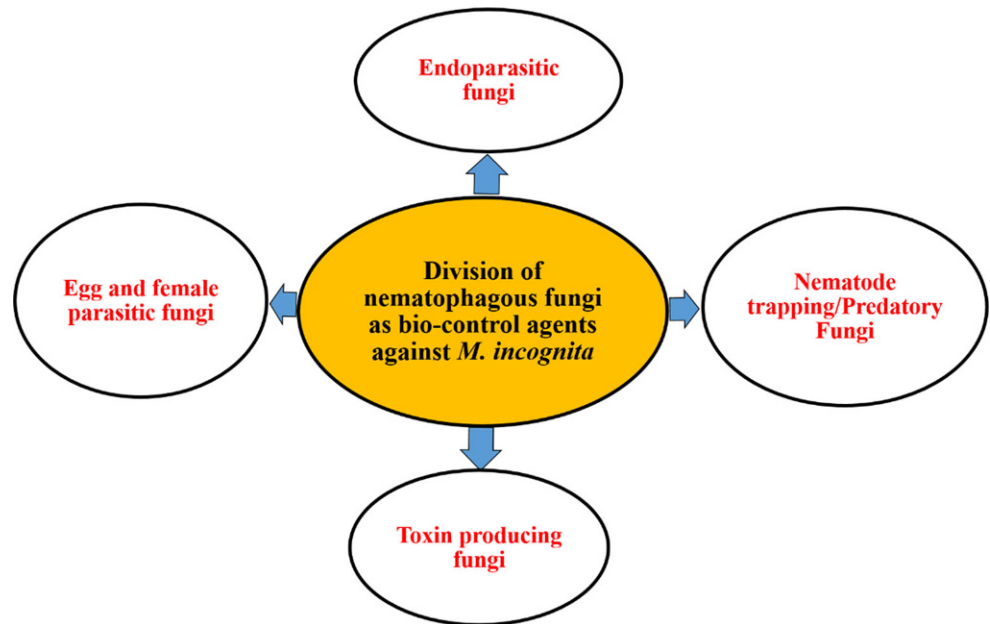
### Nematophagous Fungi as Bio-control Agents Against *M. incognita*

“Nematophagous fungi” are referred to a various group of fungi that feed and colonize on the nematodes. Some fungi parasitize nematodes are obligatory, whereas most of them are as facultative saprophytes of nematodes (Lopez-Llorca et al. 2008). These fungi belong to various phylogenetic groups, Zygomycota, Chytridiomycota, Ascomycota

**Fig. 3** Mechanisms of action of arbuscular mycorrhizal fungi as bio agents against root-knot nematode, *M. incognita*



**Fig. 4** Division of nematophagous fungi as bio-agents against root-knot nematode, *M. incognita* in vegetable crops



and Basidiomycota. The fungi of zygomycetes group are entirely dependent on water and encircle soil particles in searching of nematode hosts by their swimming zoospores. Based on the mechanisms of action against nematodes, nematophagous fungi can be classified into four major groups: (I) nematode-trapping fungi (predatory fungi), (II) endoparasitic fungi, (III) egg-parasitic fungi and (IV) toxin-producing fungi (Fig. 4; Table 2).

#### Predatory/nematode Trapping Fungi

Fungi of this group are soil-borne that trap moving stages of *M. incognita* with the help of various trapping structures of different size and shapes as shown in Table 2. The predatory nature of these fungi exists in the presence of nematodes prey and produces various types of trapping devices such as adhesive network, knobs, and columns, non-constricting and constricting rings through which they capture nematodes (Zhang and Hyde 2014). It was found that trapping fungi also have the capability to release certain compounds as antimicrobial and nematocidal properties, pleurotin (*Nematoctonus robustus*, *N. concurrens*) or linoleic acid (*Arthrobotrys oligospora* and *A. conoides*) viz., *A. superba* secrete a compound for trapping J2s of *M. incognita* (Hallmann et al. 2009). However, soil applications of various substances like organic compounds (chopped leaves, oil cakes) and glucose increases the trapping ability of nematode-trapping fungi (Duddington 1962; Cooke 1962). Nematode trapping ability of *Drechslerella stenobrocha* strain AS6.1 was enhanced by soil application of abscisic acid (ABA) and inhibited by nitric oxide (NO) (Xu et al. 2011). It has been found that *A. dactyloides* efficiently trapped pathogenic juveniles of *M. graminicola* compared

to *Dactylella brochopaga* and *Monacrosporium eudermatum* (Hallmann et al. 2009).

#### Endoparasitic Fungi

Endoparasitic fungi infect *M. incognita* using their spores (conidia or zoospores) and complete their vegetative phase inside nematode (Lopez-Llorca et al. 2008). However, as compared to trapping fungi, endoparasitic fungi consist of either a limited saprophytic phase or no saprophytic phase (Moosavi and Zare 2012). The conidia of endoparasitic fungi adhere to the nematode cuticle with the help of hyphae and kill them. Other endoparasitic fungi like *Nematoctonus* spp., *Drechmeria coniospora* and *Haptocillium balanoides*, are extensively studied and have a potent practical approach for controlling PPNs such as *Meloidogyne* spp. compared to nematode trapping fungi of which *D. coniospora* is the most studied against root-knot nematode (Viaene et al. 2006). However, *in-vitro* studies showed that *Hirsutella rhossiliensis* caused the death of *M. incognita* J2s in 2 days, whereas *Ditylenchus dipsaci* in 4 days (Cayrol et al. 1986).

#### Egg Parasitic Fungi

Fungi parasitizing eggs, female and other stages of PPNs, attracted more attention due to their potent approach in controlling economically important nematodes viz., root-knot nematode, *M. incognita* and cyst nematodes (*Heterodera* spp.). These fungi infect their host nematodes with the help of specialized structures called zoospores, appressoria, lateral mycelial branches and penetration peg (Lopez-Llorca et al. 2008). *Paecilomyces lilacinus*, *Pochonia chlamydosporia* and *Lecanicillium psalliotae* are the

**Table 2** Classification of nematophagous fungi according to their mode of action against different stages of plant-parasitic nematodes (Li et al. 2015; Moosavi and Zare 2012)

Phylum	Name of fungi	Fungal group	Infective structures against PPNs
Ascomycota fungi	<i>Drechslerella stenobrocha</i>	Nematode-trapping fungi	Constricting rings
	<i>Arthrobotrys oligospora</i> , <i>Arthrobotrys conoides</i> , <i>Arthrobotrys musiformis</i> , <i>Arthrobotrys superba</i>	Nematode-trapping fungi	Adhesive networks
	<i>Dactylellina haptotyla</i>	Nematode-trapping fungi	Adhesive knobs and/or Non-constricting rings
	<i>Hirsutella minnesotensis</i>	Endoparasitic fungi	Adhesive conidia
	<i>Drechmeria coniospora</i>	Endoparasitic fungi	Adhesive conidia
	<i>Harposporium cerberi</i>	Endoparasitic fungi	Ingested conidia
	<i>Pochonia chlamydosporia</i>	Egg- and female-parasitic fungi	Appressoria
	<i>Lecanicillium psalliotae</i> , <i>Lecanicillium lecanii</i>	Egg- and female-parasitic fungi	Appressoria
	<i>Paecilomyces lilacinus</i>	Egg- and female-parasitic fungi	Appressoria
	Basidiomycota fungi	<i>Pleurotus ostreatus</i>	Toxin-producing fungi
<i>Coprinus comatus</i>		Toxin-producing fungi	Toxin, spiny structures
<i>Nematoctonus haptocladus</i>		Endoparasitic fungi	Adhesive spores
<i>Nematophthora gynophila</i>		Egg- and female-parasitic fungi	Zoospores
Oomycota fungi	<i>Myzocytiopsis enticularis</i> , <i>M. humicola</i>	Endoparasitic fungi	Zoospores
	<i>Haptoglossa heterospora</i>	Endoparasitic fungi	Gun cell, injection
	<i>Stylopaga hadra</i>	Nematode-trapping fungi	Adhesive hyphae
Zygomycota fungi	<i>Cystopage cladospora</i>	Nematode-trapping fungi	Adhesive hyphae

most frequently isolated and promising bio-control agents against *M. incognita* among all egg parasitic fungi (Li et al. 2015). The egg shell layer of *M. incognita* consists of chitin and protein organized in an amorphous and microfibrillar structure degraded by several hydrolytic enzymes like proteases and chitinases of egg parasitic fungi (Yang et al. 2007a).

### Toxin Producing Fungi

The toxin-producing fungi are the most prominent and more potent against PPNs. These fungi release toxins that show nematocidal properties and paralyse the nematodes before penetration of fungal hyphae through nematode cuticle (Lopez-Llorca et al. 2008). Fungus, *Pleurotus ostreatus* released a potent toxin named trans-2-decenedioic acid, showing both *in vivo* and *in vitro* nematocidal properties and quickly paralysed the PPNs (Luo et al. 2004).

Besides the four groups of nematophagous fungi, some other fungal species of genus, *Trichoderma* is considered a good bio-control agent that produces a variety of enzymes against *M. incognita*, and secretes plant growth-promoting compounds (Agrawal and Kotasthane 2012). *Trichoderma* spp. secrete extracellular hydrolytic enzymes *viz.*, serine protease (SprT), trypsin like protease (PRA1) and

chitinolytic (chi18-5 and chi18-12) that can parasitize nematode larva and eggs (Szabo et al. 2012). Comparative evaluation of protease enzyme expression in *T. harzianum* revealed that 13 peptidase encoding genes with the addition of aspartic protease genes P6281 and P9438, acidic serine protease gene PRA1, sedolisin protease gene P5216 and metalloendopeptidase gene P7455, all these genes play a major role in parasitising *M. incognita* eggs (Szabo et al. 2013). *Trichoderma* spp. were also involved in the release of some other nematocidal compounds like  $\beta$ -vinylcyclopentane-1 $\alpha$ , 3 $\alpha$ -diol, 6-pentyl-2H-pyran 2-one, trichodermin, and 4-(2-hydroxyethyl) phenol (Yang et al. 2012). However, the hatching of *Meloidogyne* spp. eggs were also inhibited by the cultural filtrates of *Trichoderma* isolates. This inhibition was directly proportional to the cultural filtrate concentration and the time of exposure (Rompalli et al. 2016).

### Mechanisms of Action of Nematophagous Fungi Against *M. incognita*

The methods by which nematophagous fungi infects/kill root-knot nematode, *M. incognita* takes place by the process like attraction/recognition, adhesion, penetration and digestion through enzymatic action (Dong and Zhang 2006).



## Attraction and Recognition of Nematodes

Attraction and recognition is the initial stage during the mechanism of nematodes infection by nematophagous fungi, during such process cell-cell communication and involvement of a range of interactions *viz.*, physiological, biochemical or morphological taking place between fungi and *M. incognita*. The process of attraction and recognition were facilitated by certain volatile organic compounds (VOCs) secreted by the nematophagous fungi (Wang et al. 2010). Various VOCs include terpenoid (camphor), monoterpenes ( $\alpha$ -pinene and  $\beta$ -pinene) released from the pine tree during the infection by pinewood nematode, *Bursaphelenchus xylophilus*. However, it has been found that endoparasitic fungus, *Esteya vermicola* mimics the scent of such VOCs that released from the pine tree infected by pinewood nematode (Lin et al. 2013). Although it has been found that nematode, *Neoaplectana glaseri* released a putative morphogenic signal (nemin) that induces trap formation in *A. conoides*, a compound ascaroside was also involved to induce of trap formation and adhesive network against nematodes in *A. oligospora* (Hsueh et al. 2013). According to Li et al. (2007), G proteins are the major proteins that act as sensors, inducing the pathogenesis, response to environmental signals and constricting-ring formation in *A. dactyloides*.

## Adhesion to Nematodes Shell or Cuticle Through Adhesive Proteins

Adhesive proteins in nematophagous fungi are the polymer of extracellular fibrils and present on the spores or outer surface of traps of fungi and play major role for those fungi that adhered to the cuticle or shell of the root-knot nematode (Tunlid et al. 1991).

Lectins are considered as adhesive proteins that isolated from adhesive traps of nematophagous fungi, it functions as recognition of root-knot nematodes due to the presence of different glycosyls, like D-glucose, D-mannose and N-acetyl-D-galactosamine (GalNAc) (Nordbring-hertz and Mattiasson 1979). Balogh et al. (2003) noticed that deletion of a gene code for lectin protein (AOL\_s00080g288) from *A. oligospora* did not affect its pathogenicity against PPNs. Two lectin genes (fucose-binding lectin gene and GalNAc-binding lectin gene) occurred in the nematophagous fungus, *D. stenobrocha* genome, enhancing the pathogenicity of fungus against PPNs (Liu et al. 2014). Few other genes that code for potent fungal adhesion protein are also occurred in the nematophagous fungal genome along with lectins for example, 12, 17, and 26 CFEM containing proteins are found in *A. oligospora*, *D. stenobrocha*, and *D. haptotyla*, respectively (Meerupati et al. 2013). Similarly, the occurrence of 6, 6, and 28 GLEYA-containing

proteins that function like lectins was also suggested by Meerupati et al. (2013). Quantitative Polymerase chain reaction analyses of 17 adhesion proteins in *A. oligospora* having five genes, AOL\_s00076g567, AOL\_s00043g50, AOL\_s00007g5, AOL\_s00210g231, and AOL\_s00076g207 were changed or coded for trap formation mechanism in *A. oligospora* against *M. incognita* (Yang et al. 2011).

## Enzymatic Action of Nematophagous Fungi Against *M. incognita*

Extracellular enzymes, such as collagenases, serine proteases, and chitinases, causes breaking of nematode eggshells and cuticles facilitating fungal penetration and colonization (Yang et al. 2013).

**Collagen Degrading Enzyme (Collagenases)** Such enzymes cause the degradation of collagen protein of nematodes. According to Tosi et al. (2002), almost all species under *Arthrobotrys* release collagenase enzymes. Other enzymes like glycoside hydrolases (GHs) are also played an important role in degradation of hemicellulose, cellulose, xylans, lignocellulose and other cellular constituents of PPNs including root-knot nematode (Gibson 2012).

**Cuticle Degrading Protease (Serine Proteases)** Serine proteases are the most studied extracellular enzymes released by nematophagous fungi. Approximately 20 serine proteases were identified from various nematophagous fungi in which P32 serine protease was first discovered from the fungus, *Pochonia rubescens* (*Verticillium suchlasporia*) (Yang et al. 2007b). The phylogenetic study suggested that serine protease belongs to two lineages, (I) neutral protease from nematode-trapping fungi, (II) alkaline proteases from nematode-parasitic fungi (Li et al. 2010). Both of the proteases differ in electrostatic surface potential distributions, the flexibility of substrate-binding sites and catalytic and nematocidal activities (Liang et al. 2011). Although pathogenicity of nematophagous fungus, *A. oligospora* against PPNs was improved by its genetic changes, *i.e.*, by inserting an additional copy of cuticle-degrading protease (PII) into its genome (Ahman et al. 2002).

**Chitin Degrading Enzymes (Chitinases)** Egg shells of PPNs have a structural component known as chitin (40% w/w). Enzyme chitinases found in egg parasitic fungi were used to penetrate the egg shell of nematodes. The first chitinase Chi43 enzyme was isolated from two nematode eating fungi, *P. rubescens* and *P. chlamydosporia* (Tikhonov et al. 2002). Although 16 important genes that code for GH18 chitinases analysed from nematophagous fungi, *A. oligospora* and *D. stenobrocha* genomes respectively,

provide nematicidal activities (Liu et al. 2014) (Fig. 5; Table 3).

### Abiotic Approaches Against *M. incognita*

Various abiotic approaches were considered against *M. incognita* and farmers evaluated them to utilise as organics in their fields. Fortunately, they have been involved in controlling or keeping the PPNs population below the threshold level. Several researchers have reported the various organic products of plant origin, viz., botanicals, oil cakes, agriculture and industrial wastes have potent nematicidal and plant growth promoting properties after amending to the soil. Addition of these compounds to the soil enhance the releases of various metabolites from the plant such as alkaloids, terpenes, diterpenes, sesquiterpenes, fatty acid, glucosinolates, phenols and polyacetylenes which provide a defence to plants against pathogens including *M. incognita* (Thoden et al. 2011).

### Mechanisms of Action of Various Organics Against *M. incognita*

**Botanical Extracts Against *M. incognita*** Plant extracts have nematicidal properties, and they reduce not only the population of nematodes, but also stimulate the growth of the plant (Olabiya and Ayeni 2016). More than 100 species

of plants have been utilized for their antinemic activities. Few of them showed promising results in killing root-knot nematodes viz., *Euphorbia caducifolia*, *Azadirachta indica*, *Calotropis procera* and *Nerium oleander*. They also exhibited inhibitory effects against J2s of root-knot nematodes (Laquale et al. 2015). According to Yuhui et al. (2018), crude root extract of *Fumaria parviflora* contains nematicidal compounds like alkaloids, sterol and alcohol. These compounds reduced root galls and killed J2s of *M. incognita* and alcoholic containing compounds from *F. parviflora* like 23 $\alpha$ -Homostigmast-en-3 $\beta$ -ol, and Nonacosane-10-ol showed synergistic effects on J2s of *M. incognita* on tomato. Wen et al. (2019) tested *in vitro* aqueous extract of two plants *Paenonia rockii* and *Camellia oleifera* against *M. incognita*, extract of *P. rockii* at 5 mg/ml caused 100% mortality or inactivation of J2s of *M. incognita*. *In vivo* experiment by using aqueous extracts of chinaberry fruits (*Melia azedarach*), researchers got success in the management of *M. incognita* and *M. javanica* and improved soil biological activity (Ntalli et al. 2018). Aqueous extract of garlic contains compound allicin (diallyl thiosulfinate), tested *in vitro* against root-knot nematode, *M. incognita*. *In vitro* study of allicin showed inhibitory effect against *M. incognita*. However, *in vivo* study of allicin showed that it enhanced tomato yield and reduced the population of *M. incognita* by increasing enzymatic activities like peroxidase, catalase and superoxide dismutase in tomato leaves

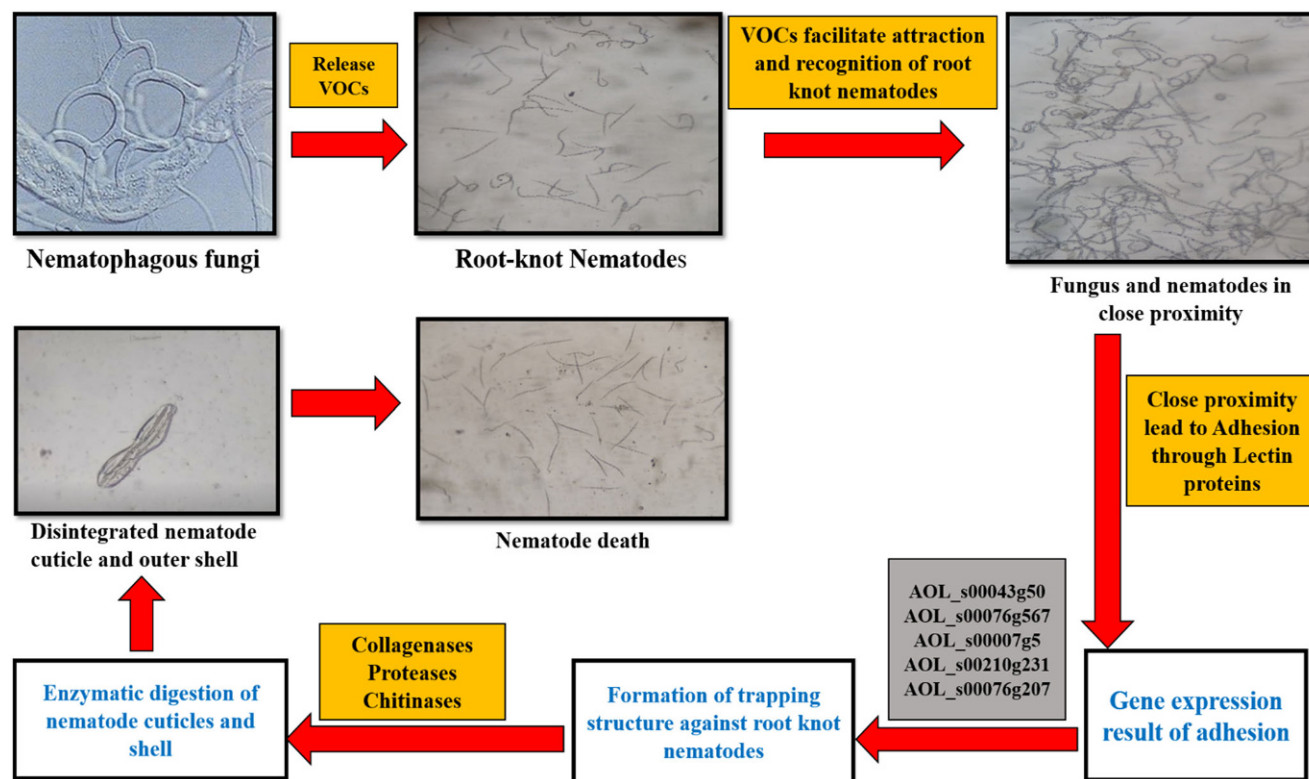


Fig. 5 Mechanisms of action of nematophagous fungi as bio agents against root-knot nematode, *M. incognita* in vegetable crops

**Table 3** Application of biotic agents tested against various species of root-knot nematodes on vegetable crops

Fungal species	Root-knot nematode species	Vegetable crops	Type of study	References
<i>Trichoderma longibrachiatum</i>	<i>Meloidogyne incognita</i>	Cucumber	<i>In vitro, in vivo</i>	Zhang et al. (2015)
<i>Lecanicillium muscarium</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vitro, in vivo</i>	Hussain et al. (2018)
<i>Trichoderma viridae</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vivo</i>	Mukhtar (2018)
<i>Trichoderma herzianum</i>				
<i>Penicillium chrysogenum</i>	<i>Meloidogyne incognita</i>	Cucumber	<i>In vivo</i>	Sikandar et al. (2019)
<i>Arthrotrichy oligospora</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vitro, in vivo</i>	Soliman et al. (2021)
<i>Purpureocillium lilacinum</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vivo</i>	Hore et al. (2018)
<i>Paecilomyces lilacinus</i>	<i>Meloidogyne incognita</i>	Egg plant	<i>In vivo</i>	Nisha and Sheela (2016)
<i>Trichoderma harzianum</i>	<i>Meloidogyne incognita</i>	Pea	<i>In vivo</i>	Brahma and Borah (2016)
<i>Penicillium chrysogenum</i>	<i>Meloidogyne incognita</i>	Cucumber	<i>In vitro, in vivo</i>	Naz et al. (2021)
<i>Pochonia chlamydosporia</i>				
<i>Trichoderma spp</i>	<i>Meloidogyne incognita</i>	Pepper	<i>In vivo</i>	Herrera-Parra et al. (2017)
<i>Pochonia chlamydosporia</i>	<i>Meloidogyne incognita</i> <i>Meloidogyne enterolobii</i>	Tomato/ Banana	<i>In vitro, in vivo</i>	Silva et al. (2017)
<i>Xylaria grammica</i>	<i>Meloidogyne incognita</i>	Tomato/ Melon	<i>In vitro, in vivo</i>	Kim et al. (2018)
<i>Pochonia chlamydosporia</i>	<i>Meloidogyne incognita</i>	Carrot	<i>In vivo</i>	Bontempo et al. (2017)
<i>Paecilomyces lilacinus</i>	<i>Meloidogyne javanica</i>	Tomato	<i>In vivo</i>	Hanawi (2016)

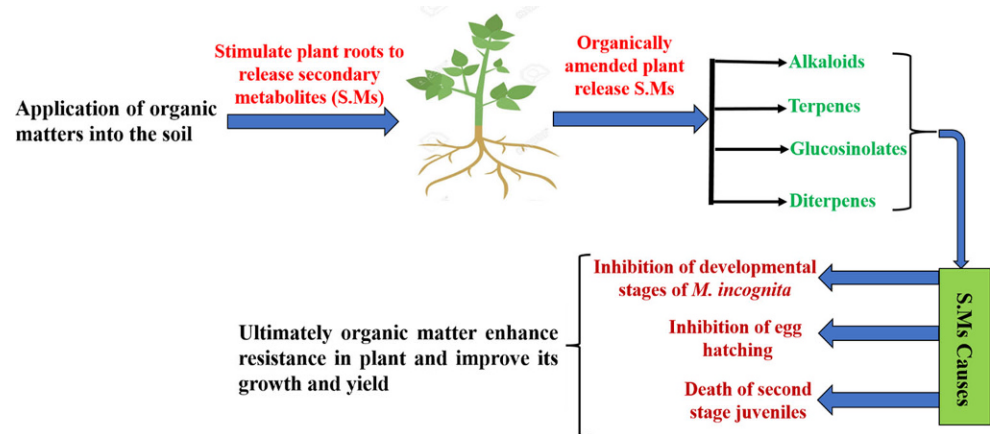
compared to untreated control (Ji et al. 2019). Thus, allicin may be a potent alternative of chemical nematicides for the management of root-knot nematodes. Water extracts of fruits and leaves of *Coccinia grandis* and *Ageratum conyzoides* showed the mortality of J2s and inhibition of egg hatchability of *M. incognita in vitro* (Asif et al. 2017). According to Ntalli et al. (2020), lemon thyme powder (*Thymus Citriodorus*) enhanced the growth of tomato plants in a dose-response manner. When it was applied in the soil at 1 g kg<sup>-1</sup>, it exhibited nematicidal activity at a 95% level on *M. incognita*. D'Addabbo et al. (2020) tested *in vitro* aqueous extract of *Medicago* spp. (*M. hybrid*, *M. murex*, *M. heyneana*, *M. lupulina*, and *M. truncatula*) which have bioactive compounds, saponins that killed the J2s and inhibited egg hatching of *M. incognita*.

**Plant Oil Cakes Against *M. incognita*** Oil cakes are an effective source of phosphorus, nitrogen and potassium (NPK) that improve the chemical, physical and biological activity of soil and inhibit the development of root-knot nematodes. Soil amended with different types of oil cakes which took about 10–14 days for decomposition after that releases nutrients for plant growth and eventually caused inhibition of the population of PPNs. Amendment of oil cakes in moist soil is more effective compared to dry soil. Amendment of mustard and neem cake into the soil was found to be effective against the multiplication of root-knot nematode. However, oil cakes from *Jatropha* sp. flax (*Linum usitatissimum*), mahua (*Madhoca indica*), sesame (*Sesamum indicum*), castor (*Ricinus communis*) and groundnut (*Arachis hypogea*) have been found effective in reducing the multiplication of

root-knot nematodes (Rehman et al. 2015). Neem cake reduced the egg hatching, killing *M. incognita* J2s and also enhanced tomato growth and yield (Kumar and Khanna 2008). The application of neem cake effectively suppressed root-knot nematode, and increased the growth and yield parameters of cucumber (Devi and Das 2016).

**Agriculture and Industrial Wastes Against *M. incognita*** Agricultural wastes can be characterised as plant parts or pieces that remain in the field after crop harvesting. These wastes may vary in their decomposition rate or properties like antinemic (Lal 2005). It improves soil's chemical, physical and biological properties and manages root-knot nematodes after their proper and complete decomposition. Application of agricultural wastes like saw dust and rice husk into the soil inhibited the population of root-knot nematodes (*Meloidogyne* spp.) and enhanced growth and yield of tomato crop (Prakash and Singh 2014). Due to global industrialization and mass crop cultivation, it is important to invent a new method or process for changing industrial wastes into value-added products that could be utilized in controlling soil-borne pathogens like root-knot nematodes. Brito et al. (2020) were considering some agro-industrial waste viz., sugarcane bagasse, orange bagasse, poultry litter, and some other wastes to manage *M. javanica* in pots. Several wastes like soybean hulls, orange bagasse and others are most efficient in the control of root-knot nematodes up to 55–100%. Cassava (*Manihot esculenta*), starch industry releases a liquid residue known as Manipueira as good source of cyanogenic glycosides. It showed nematicidal

**Fig. 6** Mechanisms of action of organic matter against root-knot nematode, *M. incognita*



**Table 4** Application of abiotic agents tested against various species of root-knot nematodes on vegetable crops

Type of abiotic substances	Root-knot nematode species	Vegetable crops	Type of study	References
Root extract of <i>Fumaria parviflora</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vitro, in vivo</i>	Yuhui et al. (2018)
Aquas extract of Peganum (Peganum harmala L.)	<i>Meloidogyne incognita</i>	Egg plant	<i>In vivo</i>	Bakr and Ketta (2018)
Aquas extract from fruits of <i>Melia azedarach</i>	<i>Meloidogyne incognita</i> , <i>Meloidogyne javanica</i>	Tomato	<i>In vivo</i>	Ntalli et al. (2018)
Essential oil from garlic	<i>Meloidogyne incognita</i>	Tomato	<i>In vitro, in vivo</i>	Jardim et al. (2020)
Leaves of <i>Phyllanthus amarus</i>	<i>Meloidogyne incognita</i>	Carrot	<i>In vitro, in vivo</i>	Khan et al. (2019)
Green manure from <i>Fumaria parviflora</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vivo</i>	Naz et al. (2015)
Extract of Aloe vera	<i>Meloidogyne incognita</i>	Tomato	<i>In vivo</i>	Abdulrahman et al. (2019)
Lemon thyme powder	<i>Meloidogyne incognita</i>	Tomato	<i>In vivo</i>	Ntalli et al. (2020)
Chopped fresh leaves of neem and madar	<i>Meloidogyne incognita</i>	Bottle gourd	<i>In vivo</i>	Singh and Patel (2015)
Manipueira industrial waste	<i>Meloidogyne incognita</i>	Tomato	<i>In vivo</i>	Nasu et al. (2015)
Castor cake	<i>Meloidogyne incognita</i>	Okra	<i>In vivo</i>	Archana and Goswami (2017)
Essential oil from <i>Dysphania ambrosioides</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vitro, in vivo</i>	Barros et al. (2019a)
Neem leaf powder	<i>Meloidogyne</i> spp	Chilli pepper	<i>In vivo</i>	Kankam and Sowley (2016)
Neem cake	<i>Meloidogyne incognita</i>	Cucumber	<i>In vivo</i>	Devi and Das (2016)
Sisal liquid residue industrial waste	<i>Meloidogyne javanica</i>	Tomato	<i>In vitro, in vivo</i>	Damasceno et al. (2015)
Neem, karanj and mustard cake	<i>Meloidogyne incognita</i>	Okra	<i>In vivo</i>	Baheti et al. (2019)
Aquas sesame seed extract	<i>Meloidogyne</i> spp	Okra	<i>In vivo</i>	Kankam et al. (2015)
Essential oil from <i>Piptadenia viridiflora</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vitro, in vivo</i>	Barros et al. (2019b)
Essential oil from <i>Artemisia nilagrica</i>	<i>Meloidogyne incognita</i>	Tomato	<i>In vivo</i>	Kalaiselvi et al. (2019)

effects against *M. incognita* by reducing galls or killing J2s and improved tomato yield (Nasu et al. 2015).

**Essential Oils (EOs) Against *M. incognita*** Researchers and industrialist engage in the evaluation of essential oils (EOs) as bio-nematicides for the root-knot nematodes. EOs and other secondary metabolites extracted from plants were directly affected the root-knot nematodes, especially on the J2s and egg hatchability (El-Nagdi et al. 2017). *In vitro* testing of EOs from true myrtle (*Myrtus communis*) showed nemati-

cidal activity against *M. incognita* (Ardakani et al. 2013). According to Onkendi et al. (2014), EOs from plants belonging to the family Asteraceae were utilized as management for root-knot nematodes. *In vitro* experiment showed that EOs were considered as soil bio fumigants for reducing galls or killing *M. incognita* J2s on tomato and enhancing its yield (Laquale et al. 2015). EOs from Mexican tea (*Dysphania ambrosioides*) have 99.08% of total oil with nematicidal activities, i.e., inhibited egg hatching by 100% and galls by 99.5%, further chromatography, mass spec-

trometry studies showed that oil from *D. ambrosioides* was composed of *p*-cymene (3.35%), (*Z*)-ascaridole (87.28%) and *E*-ascaridole (8.45%). EOs from three Brazilian plants (*Hyptis suaveolens*, *Astronium graveolens* and *Piptadenia viridiflora*) were tested both *in vitro* and *in vivo* against *M. incognita*. Among them, *Piptadenia viridiflora* showed inhibitory effect against *M. incognita* due to the presence of major component, benzaldehyde. These component was able to inhibit egg hatching up to 65% and its oxime compounds were able to reduce galls up to 84% and egg hatching up to 89% on tomato plant (Barros et al. 2019b) (Fig. 6; Table 4).

## Conclusion

When examining the significance of monetary damage due to root-knot nematode, *M. incognita* and the fact of the limitations by the government for the utilization of pesticides, it is important to researchers that there is a demand for the evolving new novel eco-friendly approaches against *M. incognita*. Several scientists are concerned about the excessive utilization of pesticides for controlling the crop pests by the farmers, and they pressurize the farmers to minimize the use of pesticides to overcome the environment pollution issues. This review mainly focused on the bio-organic management as eco-friendly for controlling of *M. incognita*. Biological agents and organic matters are the alternative for pesticides that do not only manage *M. incognita* as eco-friendly, but also improve growth and yield of vegetables. In biological agents, nematophagous fungi manage root-knot nematodes by cuticle penetration, absorption and digestion of nematode cuticle and AM fungi colonizes the rhizosphere, induced resistance in plants and compete with nematode and killing them. Organic soil amendments prompt the development of beneficial soil microbe's population and reduce the population of nematodes or plant diseases as well as boost soil fertility, water holding capacity, physical properties of soil, and plant growth. Both soil amendments and the bio-control agents have been studied to some extent against root-knot nematodes. Still, with advancements in technology recently, there should be more profound studies on how these two approaches can synergistically affect nematodes and kill them. Whatever methods/strategies are invented, in future the focus is on the essential aspects like green approaches which manage root-knot nematodes without affecting environment and human health.

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**Conflict of interest** A. Khan, G. Ahmad, M. Haris and A.A. Khan declare that they have no competing interests.

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