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REVIEW

Root-knot nematodes (*Meloidogyne* spp.) a threat to agriculture in Mexico: biology, current control strategies, and perspectives

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Abstract

Root-knot nematodes (RKN) are sedentary parasites of the roots of plants and are considered some of the most damaging pests in agriculture. Since RKN target the root vascular system, they provoke host nutrient deprivation and defective water transport, causing above-ground symptoms of growth stunting, wilting, chlorosis, and reduced crop yields. In Mexico RKN infestations are primarily dealt with by treating with synthetic chemically based nematicides that are preferred by farmers over available bioproducts. However, due to environmental and human health concerns chemical control is increasingly restricted. Biological control of RKNs can help reduce the use of chemical nematicides as it is achieved with antagonistic organisms, mainly bacteria, fungi, other nematodes, or consortia of diverse microorganisms, which control nematodes directly by predation and parasitism at different stages: eggs, juveniles, or adults; or indirectly by the action of toxic diffusible inhibitory metabolites. The need to increase agricultural production and reduce negative environmental impact creates an opportunity for optimizing biological control agents to suppress nematode populations, but this endeavour remains challenging as researchers around the world try to understand diverse control mechanisms, nematode and microbe life cycles, ecology, metabolite production, predatory behaviours, molecular and biochemical interactions, in order to generate attractive products with the approval of local regulatory bodies. Here, we provide a brief review of the biology of the genus *Meloidogyne*, biological control strategies, and a comparison between chemical and bioproducts in the Mexican market, and guidelines emitted by national agencies to ensure safety and effectiveness of new developments.

Keywords Biological control · Economic impact · Nematophagous bacteria · Nematophagous fungi · Regulation of bioproducts · Root-knot nematode

Introduction

Nematodes are a diverse group of animals that inhabit all ecosystems; it is considered that as many as one million cosmopolitan species exist (Mitreva et al. 2005). Many are free-living, but others have developed parasitic lifestyles (Singh et al. 2021). It is estimated that all vertebrates (including humans) are parasitized at some point in their existence (Brooker 2010). Plants are also parasitized, with over 4100 nematode species described (Decraemer et al. 2006). Phytoparasitic nematodes are found in almost any agricultural crop throughout the world, reducing the production and quality of the crops and thus, causing important economic losses. According to the American Society of Phytopathology, it is estimated that worldwide economic impact due to nematode infestations reaches 14% of all crop yield losses, which is equivalent to almost 125 billion dollars annually (Chitwood

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2003). From an economic point of view, root-knot (*Meloidogyne* spp.) and cyst nematodes (*Heterodera* spp. and *Globodera* spp.) are the most important crop-damaging pest nematodes (Jones et al. 2013). They can also be vectors of viruses and affect beneficial plant microbiota (Khan 1993). Nematodes spread by infested seedlings and seedbeds, or by contaminated irrigation water, and the symptoms they produced are non-specific, typically manifesting as yellowing of the leaves, retarded development, and significantly low crop yields. Nematodes are also difficult to detect as they are colourless and microscopic (0.5 mm long by 20 µm wide), confounding producers who might not apply proper measures for their control (Siddique and Grundler 2018).

Meloidogyne is a genus of obligated plant parasites with species distributed worldwide, with an ability to infect almost every vascular plant, both under protected agriculture, greenhouses or in the field. Major *Meloidogyne* species are *M. arenaria*, *M. incognita*, *M. javanica,* and *M. hapla* (Wesemael et al. 2011; Jones et al. 2013; Coyne et al. 2018). Although it has a broad host crop selection, the most economically important are: soybean, cereals, tomato, potato and other solanaceous and tubercules (Trudgill and Blok 2001; Charchar et al. 2008; Wesemael et al. 2011; Sikandar et al. 2020).

Biology of the genus *Meloidogyne*

Meloidogyne is a genus of RKN listed number one on the top ten plant-parasitic nematodes by the scientific community in 2013 (Jones et al. 2013). Approximately, 100 species of RKN belong to *Meloidogyne*, which given its economic importance is also one of the most studied (Sikandar et al. 2020). Despite the challenges posed by its obligate biotrophic nature, *Meloidogyne* research encompasses all aspects of its existence: evolution, development, virulence, and plant responses to invasion (Curtis 2007; Ali et al. 2017; Ibrahim et al. 2019). Although transformation techniques have been so far unsuccessful, interference RNA and omics tools have shed light on *Meloidogyne* molecular mechanisms of its life cycle. Da Rocha et al. (2021), recently reported the parasitism regulatory landscape of *Meloidogyne* obtained by a thorough transcriptomic analysis at different developmental stages. *Meloidogyne* research has also benefited from our ample knowledge of *Caenorhabditis elegans* (a well-studied model organism). Although *Meloidogyne* and *C. elegans* diverged more than 500 million years ago, genome microsynteny between the two indicates shared developmental and biochemical pathways (Opperman et al. 2008). WormBase: a comprehensive resource for nematode research originally developed by Harris et al. (2010) for *C. elegans*, now contains information on parasitic nematodes, including more recent sequences of different *Meloidogyne* species (https://parasite.wormbase.org/index.html). Since *M. hapla* (54 Mb) and *M. incognita* (86 Mb) genomes were sequenced in 2008 (Abad et al. 2008; Opperman et al. 2008), another 19 genome drafts representing six species have been determined, allowing phylogenetic and genomic comparisons (https://www.ebi.ac.uk/ena/browser/view/PRJNA340324) (Mitreva et al. 2005; Lunt et al. 2014).

Reproduction

Most *Meloidogyne* species reproduce asexually, and despite this being considered an evolutionary dead-end, *Meloidogyne* is a genus well-adapted to fluctuating environmental conditions, and thus, an attractive model for evolutionary analysis (Castagnone-Sereno et al. 2019). Asexual reproduction occurs either by miotic reduction and subsequent reestablishment of the chromosome number by fusion of the second polar nucleus with the egg pronucleus (for instance in *M. chitwoodi*, *M. exigua*, *M. fallax* and *M. hapla*), or by parthenogenesis (apomixis), for instance in *M. arenaria*, *M. incognita* and *M. javanica* (Castagnone-Sereno and Danchin 2014). Paradoxically, true asexuality correlates with the most successful evolution of *Meloidogyne* in terms of its global ubiquity and broad host range, infecting almost all Angiospermae. Asexual reproduction can however epigenetically produce males under stressing environmental conditions, but the sperm nucleus degrades upon female insemination (Baniya et al. 2021). A few minor *Meloidogyne* species (*M. carolinensis*, *M. megatyla*, *M. microtyla*, *M. pini*) are sexual with males fertilizing the eggs (Eisenback and Triantaphyllou 2020).

Meloidogyne life cycle

Females deposit ~ 500 eggs into a gelatinous matrix produced by 6 anal glands. The matrix is mainly composed of high and low molecular weight glycoproteins that protect the eggs and function as a temperature and humidity sensor for developmental progress, which is arrested by drought that reduces its volume and hardens the matrix. It also serves as an antimicrobial agent able to agglutinate invading soil microorganisms (Fig. 1). In order to create a canal through which egg masses are pushed outside an enlarged root (gall), it is thought that the plant cell wall is digested. Vieira et al. (2011) identified a carbohydrate binding domain (CBM) in the vulval secretion that might serve this purpose. The transitions from egg to adult throughout consecutive moults takes 25 to 30 days. The first moult occurs before hatching after vermiform stage-1 juveniles (J1) become stage-2 juveniles (J2). This second stage includes a pre-parasitic mobile phase (ppJ2) in the period between hatching, soil migration, root penetration, and establishing a feeding site within the host vasculature, where sedentarism commences,

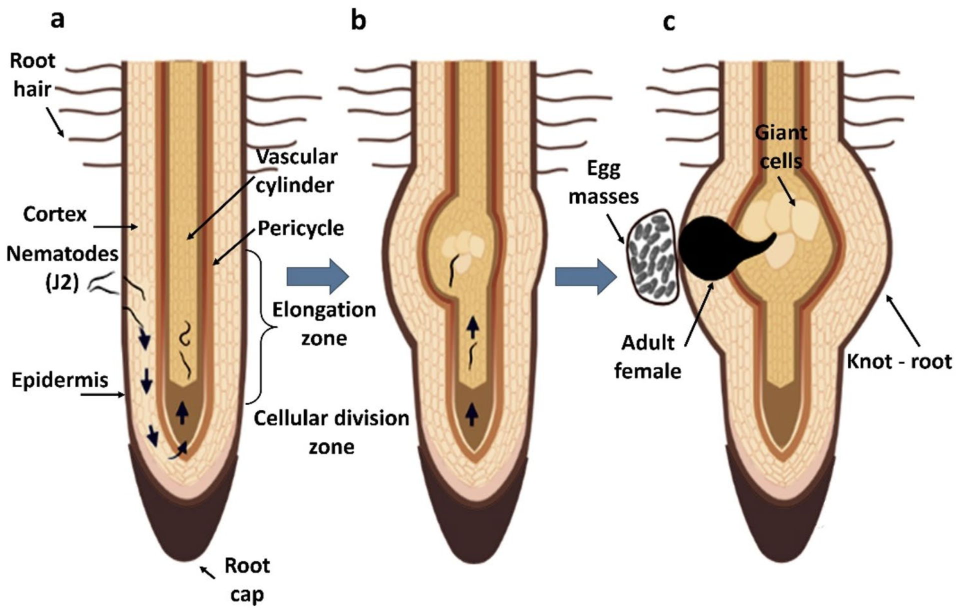

Fig. 1 Life cycle of *Meloidogyne*. **a** preparasitic stage-2 juveniles migrate in the soil following plant cues gradients (sugars, amino acids, pH, etcetera); once a susceptible host is found J2 mechanically enter the root moving downwards to avoid the Casparian strip and then up to the vascular cylinder, in which an unknown determinant indicates the establishment site. **b** Settlement of nematodes J3 to J4 and reprogramming of target cells that will enlarge becoming giant cells that will feed the nematode, one at a time. **c** As nematodes become adults, enlarged females produce egg masses on the root surface. Figure created with BioRender

acquiring the parasitic stage (Fig. 1). The next two stages (J3 and J4) are identified by the number of the outer cuticles from previous moults and non-functional stylet; J4 is the stage at which sexual dimorphism distinguishes female and male nematodes. Sedentary mature females resume feeding and swell into a pear-shape and produce eggs. Differential gene expression accompanies these transitions: for instance, upregulated expression of sensory perception and cell wall degradation genes happens from eggs to ppJ2, whereas stress response genes (possibly for contending with plant defences) are upregulated between J2 to J3/J4 and sensory perception genes decrease their expression as the nematode becomes sedentary. Lipid metabolism-related genes are also upregulated at J3/J4 in preparation for the energetically costly adult phase. Mature females without the need for locomotion repress genes for this purpose. Gene regulation in the egg is dominated by developmental processes and includes membrane transport and DNA metabolism. Knowing the gene expression patterns of RNK provides strategies for the rational selection of target genes, and although variable results have been obtained, some genes have been identified through RNA silencing resulting in lower infestation levels (Iqbal et al. 2020).

Host selection and invasion

Host parasitism by *Meloidogyne* varies among species, with some infecting a broad range of vegetable crops, ornamental plants, and fruit trees (for instance *M. incognita*, *M. javanica* and *M. chitwoodi*); others grow in restricted geographical regions or are restricted to fewer hosts, such as *M. hispanica* that infects peach and tomato. In the soil, hatched ppJ2 swim randomly without feeding until they detect a susceptible root by following chemotactic gradients of plant exudates including amino acids, sugars, CO_2, and pH. Time of soil residence of ppJ2 juveniles is species-specific, and dependent on their lipid reserves, which when below 65% hinder invasion. When J2s reach the root tip of a suitable host, they access the region of root elongation near the meristematic region by mechanically perforating the least resistant site with their small and delicate stylet. To reach the stele, *Meloidogyne* first migrates down to the direction of the root tip to avoid the barrier imposed by the Casparian strip (composed of highly lignified and suberized endodermal cells), and moves up to the root differentiation zone where xylem elements are visible, in which they anchor to the central cylinder (von Mende 1997; Holbein et al. 2019). For their journey, *Meloidogyne* soften the middle lamella by secreting modifying enzymes (such as expansin-like proteins, cellulases, hemicellulases and pectinases) produced in the subventral glands (Vieira et al. 2011; Mitsumasu et al. 2015). This subset of enzymes is encoded by genes acquired laterally (LGT) from bacteria. *M. incognita* for instance contains more than 60 genes from six different protein families for the digestion of cell wall oligo- and polysaccharides (Abad et al. 2008). Paganini et al. (2012), estimated that up to 3.4% of the RKN genes might have been acquired via LGT, with pathogenic bacteria (*Ralstonia solanacearum*, *Xanthomonas campestris*), symbionts (*Sinorhizobium meliloti*) or rhizobacteria (*Burkholderia ambifaria*), likely being some of the donor organisms (Danchin et al. 2010; Paganini et al. 2012). Interestingly, intercellular migration causes limited tissue damage.

Feeding sites (giant cells)

Giant cells (GCs) are reprogramed cells induced by RKN effectors (reviewed by Haegeman et al. (2012)), which serve a nourishing function for the sedentary phase of the parasite. Molecular determinants of the selection of the feeding site remain unknown but must locate to the vascular cylinder at the differentiated region of the root, where five to eight parenchymal cells are selected. Through successive induction of mitosis and endoreplication in the absence of cytokinesis these cells enlarge. Each GC will feed, one at a time, the female in its progression from J2 to adult (Escobar et al. 2015). GCs are metabolically very active, with dense cytoplasm, a large number of organelles and expanded nuclei and nucleoli. Cell fate of GCs is epigenetically regulated by differential expression of host micro RNAs (Jaubert-Possamai et al. 2019), DNA hypomethylation (Atighi et al. 2020), and histone modification (Hassanaly-Goulamhoussen et al. 2021), which together establish a new balance of growth hormones (e.g. auxin/cytokinin), cell cycle progression, and suppression of jasmonic acid-dependent immune responses via gibberellin signalling (Hewezi 2020). Simultaneously, galls form around GCs by increased cell proliferation of the vascular system and hypertrophy of the endodermis and the cortex; galls along the root give the infection its common name of root-knots. Gall organogenesis involves root apical meristem reprogramming for transient pluripotency, quiescent centre identity and procambium-associated increase of genes and regulators in a nematode-dependent manner, which also brings about changes in the cell wall composition that consistent with the dedifferentiated state, they contain more galactose and less xylose (Ishida et al. 2020; Olmo et al. 2020).

Strategies of nematode control

A wide variety of chemical pesticides and other management tools are available for crop growers to control phytoparasitic nematodes, but none is efficient in the sense of efficacy against new nematode biotypes, nematode resistance and adaptability, high cost and expense, and environmental safety (Chitwood 2003). As current options become non-sustainable, new environmentally friendly and sustainable strategies for nematode control must be developed, as this is a key component for sustainable food safety and enhancing the quality of life in a growing world population (Barker et al. 1994). The activity of bioactive agents (microorganisms) contributes to the suppression of populations of phytopathogenic nematodes, whether through: (i) antibiosis or competition for rhizosphere colonization by the production of toxic compounds. Two examples are: hydro-soluble compounds fervenulin, avermectin and nemadectin isolated from different strains and species of *Streptomyces* with activity against *M. incognita* [preprint by Hu et al. (2021)], and iturin, surfactin, and fengycin produced by *Bacillus* strains (Ramyabharathi et al. 2020). (ii) Plant growth promotion and plant induced resistance (IR). Plant resistance to infection by RKN involves treatment with inducing agents (microorganisms or metabolites) that prepare the plant for a prospective RKN infection, during which defence responses would be expected to occur faster or at a higher level compared to non-treated crops (Walters et al. 2005; Hilker and Schmülling 2019). Upon RKN detection plant responses include a burst of reactive oxygen species (ROS), cell signalling through the salicylic acid (SA), ethylene (ET) and jasmonic acid (JA) pathways, upregulation of pathogenesis-related protein genes (*PR*), and defensin and antimicrobial peptide coding genes (Przybylska and Obrępalska-Stęplowska 2020). (iii) Predation and parasitism, which is carried out by natural enemies of nematodes, including bacteria, fungi, mites, and other predatory nematodes (Khan and Kim 2007; Yang et al. 2020). All mechanisms are illustrated in Fig. 2, and examples of particular cases from the abundant literature on this topic are provided in the following section.

Biological control

Control of nematodes by bacteria

Plant growth-promoting bacteria (PGPB) establish close associations with plants and can enhance plant growth and protection from disease and abiotic stress (de Souza et al. 2015; Gupta et al. 2015). The biological control potential of PGPB against phytoparasitic nematodes has been analysed in species belonging to *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Clostridium*, *Desulfovibrio*, *Pasteuria*, *Serratia*, *Burkholderia*, *Azospirillum*, *Bacillus*, *Chromobacterium*, *Pseudomonas*, and *Corynebacterium* (Jatala 1986; Migunova and Sasanelli 2021). *Bacillus* and *Pseudomonas* are of particular interest, as these widely occur in natural environments, are currently used and commercialized, and in the last two decades they have shown the highest efficacy for biological control (Berlitz et al. 2014; Meena 2014; Dehghanian et al. 2020; Migunova and Sasanelli 2021).

The use of strains belonging to the genus *Bacillus* as biological control agents is increasing, as this is a widely occurring genus, abundant in the rhizosphere. Beneficial activity of some *Bacillus* strains has been well studied, and various molecular mechanisms of nematode control have been described (Ongena and Jacques 2008; Lugtenberg and Kamilova 2009; Sivasakthi et al. 2014). The potential of *Bacillus* as bionematicides is based on the production of nematocidal proteases and chitinases, antibiotics, crystal

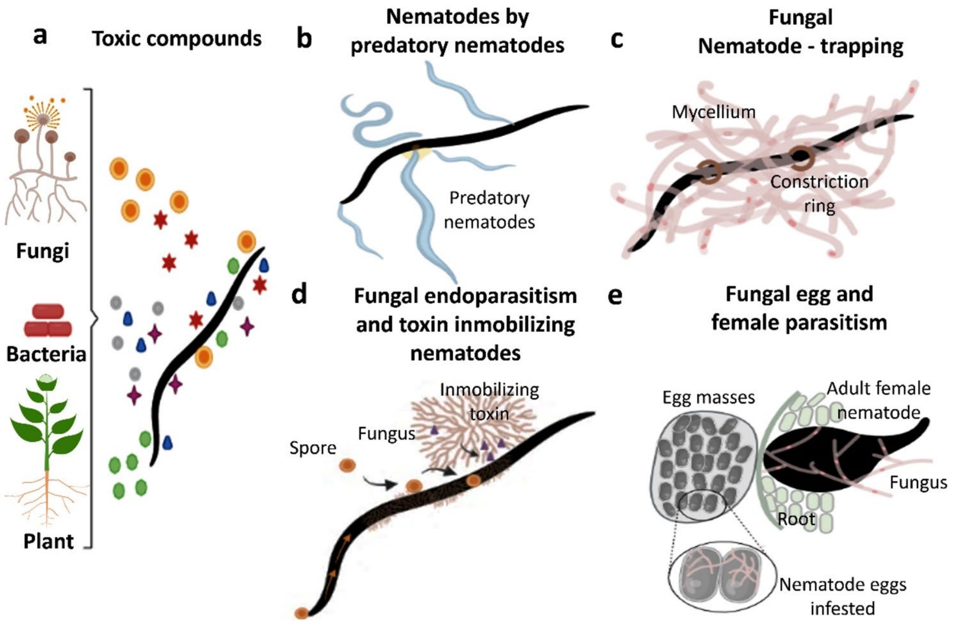

Fig. 2 Biocontrol strategies against RKN by different organisms. **a** Attack by spores and various toxic and lethal metabolites (represented as symbols around the nematode) released by fungi, bacteria, and plants. **b** Predatory nematodes feeding on parts of the body of RNKs. **c** Nematodes that become entangled in a sticky web of mycelium and fungal constrictor rings. **d** Immobilized nematodes by fungal toxins and colonized with ingested or attached fungal spores that germinate and invade the interior and exterior of the nematode. **e** Fungi that parasitize adult females in the reproductive stage or eggs of nematodes. Figure created with BioRender

proteins, secondary metabolites, and the induction of plant systemic resistance (Engelbrecht et al. 2018).

For example *Bacillus cereus* produces C16 sphingosine and phytosphingosine, two nematocidal compounds that induce reactive oxygen species (ROS) in *M. incognita*, destroying its genital area, and thus, inhibiting nematode reproduction (Gao et al. 2016). Sphingosine is safe for the environment, humans, and animals, but it is very toxic to nematodes with a nematocidal LC_{50} of 0.64 µg/ml, making it a safe and effective agent. Gao et al. (2016), also analyzed the plant defense-related enzymes phenylalanine ammonia-lyase (PAL), polyphenol oxidase (PPO), and peroxidase (POD) in tomato treated with *B. cereus* S2, and found increases of 43.8%, 51.8%, and 86.2%, respectively, when compared to the untreated control. This indicates that *B. cereus* also activates plant defence systems for controlling *M. incognita.* Additionally, Geng et al. (2016) identified multiple potential nematocidal factors from the genome of *B. firmus* DS-1, but focused on a peptidase S8 superfamily protein Sep1 (*sep1*). Authors demonstrated that *B. firmus* DS-1 is toxic against *C. elegans* and *M. incognita* due to serine protease activity and degradation of the nematode intestinal tissues. Another report detected genes associated with nematocidal activity in *B. subtilis* OKB105, since it controls *M. javanica* through the activity of the *purL* gene (phosphoribosylformylglycinamidine synthase, FGAM synthase). Nematocidal activity was lost by disruption of the *purL* gene and restored when complemented with either plasmid pMA5-*purL* or pUC18-*purL*, demonstrating a role for this gene in mediating nematocidal activity (Xia et al. 2011). *Bacillus thuringiensis* is a well-known biocontrol agent, characterized by the production of crystal proteins, encoded by *cry* genes. These toxins have insecticidal and nematocidal activity. Several studies have identified that *B. thuringiensis* Cry toxins (e.g., Cry6A, Cry5B, Cry1Ea11, Cry1Ab, Cry14Ab) can control a wide spectrum of nematodes, among them *Meloidogyne* spp., *Bursaphelenchus xylophilus, Heterodera glycines,* and *C. elegans* by inhibiting egg hatching and killing stage-2 juveniles (Khan et al. 1995; Höss et al. 2008; Radhakrishnan et al. 2017; Huang et al. 2018; Kahn et al. 2021; Migunova and Sasanelli 2021). *Bacillus nematocida* has a peculiar nematocidal mechanism, luring nematodes to their death using a "Trojan horse" strategy. The attraction is mediated by potent volatile organic compounds such as benzaldehyde and 2-heptanone, which makes this species more attractive to worms than other dietary bacteria (Niu et al. 2010). Once the bacterium is consumed by nematodes, it secretes extracellular proteases, such as alkaline serine protease Bace16 (*bace16* gene), to attack the host intestinal tissues, eventually killing it (Niu et al. 2010). *B. megaterium* strain YMF3.25 is an efficient biocontrol agent against *M. incognita*. Huang et al. (2010) identified nematocidal volatile metabolites produced by this bacterium (benzeneacetaldehyde, 2-nonanone, decanal, 2-undecanone, and dimethyl disulphide) that are active against both, juveniles and eggs at 0.5 mmol. Finally, secondary metabolites (such as lipopeptides) produced by *Bacillus* are of great interest. These are low-molecular-weight amphipathic compounds with antimicrobial properties (Ongena and Jacques 2008). Strains of *B. subtilis* were tested for their nematocidal activity against *M. incognita*, and strain Bs5, with biosynthetic capability for surfactin and iturin, was promising in reducing hatching of *M. incognita* eggs. Crude antibiotics extracted from strain Bs5 exerted lethal effects on eggs and juveniles

(Kavitha et al. 2012). Similarly, *B. subtilis* strain Bbv57 also produced surfactin and iturin, and the presence of the *ItuD*, *srfA,* and *sfp* genes was experimentally confirmed by PCR and chromatography of the products. Application of crude antibiotics obtained from bacterial cultures at concentrations of 25, 50, and 100% in in vitro assays to egg masses of *M. incognita* or stage-2 juveniles, showed that at the highest concentration egg hatching was 92% reduced and juveniles mortality increased by 87% in comparison with untreated controls (Ramyabharathi et al. 2018). Beneficial microorganisms can trigger resistance in plants, and this is well studied for several *Bacillus* spp. (Shafi et al. 2017).

Fluorescent pseudomonads (*Pseudomonas fluorescens*, *P. putida*, *P. aeruginosa,* and *P. aureofaciens*) are effective against certain insects and nematodes. Molecular mechanisms of some *Pseudomonas* strains to reduce nematode populations include production of metabolites and induction of plant systemic resistance (Meena 2014). Cronin et al. (1997) evaluated strain *Pseudomonas fluorescens* F113 as a biological control agent against the potato cyst nematode *Globodera rostochiensis,* and found that it controlled mobile nematode juveniles by producing secondary metabolites such as 2,4-diacetylphloroglucinol (DAPG). Dehghanian et al. (2020) examined the induction of tomato resistance against *M. javanica*, as well as changes in the expression of plant defense gene *PR1* that codes for protein PR1 (involved in the protection towards pathogenic fungi and oomycetes) after applying salicylic acid (SA) and *P. fluorescens* strain CHA0. The combined treatment slightly improved plant growth, and reduced egg-masses by 92% and the reproduction factor of *M. javanica* by 11-fold compared to the untreated controls. Meanwhile *PR1* gene showed a two-fold increase in relative expression after the combined treatment of *P. fluorescens* + SA and nematode addition to the pots; however, *PR1* increased expression was transitory returning to basal levels 48 h after nematode inoculation.

The *Pasteuria* genus is of particular interest as these are obligate, mycelial, endospore-forming bacterial parasites of phytoparasitic nematodes (Tian et al. 2007). The spores of *Pasteuria* spp. attach to the cuticles of stage-2 juveniles of RKNs and germinate after entering the roots and begin feeding. Germ tubes can penetrate the cuticle, and vegetative microcolonies then form and proliferate inside the body of the developing female; due to reproductive system degeneration, the adult female is almost devoid of eggs (Jatala 1986; Gowen et al. 2007; Tian et al. 2007). Bhuiyan et al. (2018) established an experiment where sugarcane was grown in pasteurized sand containing different concentrations of endospores of *P. penetrans* for the control of *M. javanica* showing that the severity of root galling and the number of nematode eggs decreased as the endospore concentration increased: at the highest endospore level, egg numbers decreased 96%. Other studied bacteria include *Serratia proteamaculans* Sneb 851 that has shown high nematocidal potential against *M. incognita* with 99% and 61% mortalities for stage-2 juveniles and eggs, respectively (Zhao et al. 2018). Commercial products containing *Serratia* sp. were tested (Nemaless = *S. marcescens* and Nemafree = *Serratia* sp.) against RKN *M. incognita*, and results showed a reduction in the number of stage-2 juveniles, egg masses, egg numbers, and low reproduction factor (Raddy et al. 2013). Additionally, *Rhizobium etli* G12 suppresses early infection of *Globodera pallida* and *M. incognita* (Hallmann et al. 2001). Other bacteria-based products include Nortica (*B. firmus*), Econem (species of *Pasteuria*) and Sudozone (*P. flourescens* Schroeter) (Abd-Elgawad and Vagelas 2015).

Control of RKN by nematophagous fungi

Most research on different biological control agents against phytoparasitic nematodes is focused on nematophagous fungi (Bilgrami et al. 2008). Some species of the genus *Trichoderma* (Sharon et al. 2001; Al-Hazmi and TariqJaveed 2016; Fan et al. 2020) have been studied for these purposes, but other genera have also shown high nematocidal activity, for example *Dactylella, Arthrobotrys*, *Nematoctonus*, *Aspergillus*, *Penicillium, Pochonia*, *Paecilomyces*, *Metarhizium* and *Verticillium* (Sánchez Portillo et al. 2016; Thongkaewyuan and Chairin 2018; Peiris et al. 2020; Naz et al. 2021). Nematophagous fungi employ diverse mechanisms to control nematode populations, such as: (i) nematode-trapping (predatory) fungi produce extensive hyphal networks and constricting rings as trapping devices to catch nematodes; (ii) endoparasitic fungi are obligate parasites that infect nematodes by either adhering to their surface or through direct ingestion followed by germination, growth, and nematode killing; (iii) egg-and female-parasitic fungi, which as facultative parasites grow on and parasitise the sedentary stages of nematodes such as eggs and cysts; and (iv) production of toxins that immobilise the nematodes before hyphal penetration through the nematode cuticle (Jatala 1986; Lopez-Llorca et al. 2007; Zhang et al. 2020). Most of these fungi are facultative saprotrophs, meaning that in the absence of nematodes, they feed on decomposing organic matter, and therefore soils rich in organic matter promote their persistence (Lopez-Llorca et al. 2007). Representative species of nematophagous fungi from diverse taxa, are *Arthrobotrys oligospora* and *Drechslerella* sp. (nematode-trapping fungi); *Metacordyceps chlamydosporia* (≡*Pochonia chlamydosporia*), *P. rubescens* and *Purpureocillium lilacinum* (≡*Paecilomyces lilacinus*; egg- and female-parasitic fungi); *Drechmeria coniospora* (endoparasitic fungus); and *Pleurotus ostreatus* (toxin-producing fungus) (Lopez-Llorca et al. 2007; Zhang et al. 2020).

Arthrobotrys oligospora is one of the most extensively studied nematophagous fungi and it is considered as the model of the nematode-trapping group (Peiris et al. 2020; Soliman et al. 2021). This fungus acts as a facultative nematode-trapper for nitrogen, but it also decomposes organic matter as a saprophyte as the source of carbon and energy (Cooke 1963; Jaffee 2004). In vitro experiments have demonstrated high efficacy of the fungus in capturing and suppressing *M. incognita* stage-2 juveniles, and microscopic observations showed that it traps prey with adhesive loops of hyphae; *A. oligospora* also significantly suppressed root-knot in tomato plants showing 74% predatory activity towards *M. incognita* in comparison to 36% of the control (Soliman et al. 2021).

Pochonia chlamydosporia is a facultative parasite that first colonizes the rhizosphere as a saprotroph but which, upon encounter with cyst nematode (CN) and RKN, it infects the nematodes eggs, as these are its main target, although stage-2 juveniles of *Meloidogyne* within egg masses can be colonized and parasitized, and consequently, *P. chlamydosporia* has been isolated from the nematodes (Manzanilla-López et al. 2013; Peiris et al. 2020). Some isolates of *P. chlamydosporia* also induce plant resistance against *M. incognita* by up-regulation of the salicylic acid pathway in tomatoes inoculated with both fungus and nematode. This was assessed in a co-inoculation experiment to determine the expression of genes related to the salicylic acid and jasmonic acid pathways through the study of pathogenesis-related protein 1, *PR1,* and lipoxygenase, *LoxD,* respectively. For the experiment, the soil was inoculated with chlamydospores just before transplanting, and with stage-2 juveniles of *M. incognita* 1 week later. *PR1* expression in roots treated with *P. chlamydosporia* was upregulated at 0, 7, and 42 days after nematode inoculation compared to control plants, and the *LoxD* gene was upregulated only 7 days after nematode inoculation (Ghahremani et al. 2019). *P. lilacinus* is another egg nematode parasite currently used as a biological control agent against various nematodes (Khan et al. 2006). Commercial *P. lilacinus* strain 251 (PL251) was evaluated for its potential to control *M. incognita* in tomatoes, showing reduction of root galling by 66%, number of egg masses by 74%, and final nematode population by 71% compared to the non-inoculated control (Kiewnick and Sikora 2006). The main mechanism of action of *P. lilacinus* is direct infection of sedentary stages, in particular the egg stage, through the production of leucinotoxins, chitinases, proteases, and acetic acid (Djian et al. 1991; Khan et al. 2004).

The endoparasitic fungus *D. coniospora* is an obligate parasite and mostly exists as conidia in the environment. This species infects nematodes via the adhesion of conidia to the host cuticle, which upon germination produces an appressorium to pierce the cuticle and extend hyphae into the nematode epidermis (Lebrigand et al. 2016). Conidia of *D. coniospora* adhere to different phytoparasitic nematode species, such as *Ditylenchus* spp., *Pratylenchus penetrans*, *Cephalenchus* sp. and *Heterodera schachtii*, but conidial attachment to a particular nematode species does not always lead to infection, as specific recognition signals are required (Jansson 1993; Lebrigand et al. 2016; Zhang et al. 2020).

Toxin-producing nematophagous fungi have nematode-immobilizing activity that can also kill their hosts. A particular example of this predatory mechanism is represented by the basidiomycete oyster mushroom *P. ostreatus* that preys on nematodes to supplement nitrogen intake under nutrient-limiting conditions. Recent studies have shown that *P. ostreatus* triggers a massive calcium influx and rapid cell necrosis in the neuromuscular system of *C. elegans* via nematode sensory cilia; it was also effective in paralyzing a diversity of other species of the genera *Diploscapter*, *Oscheius*, *Rhabditis*, *Pristionchus*, *Panagrellus*, *Acrobeloides*, *Cephalobus*, *Mesorhabditis*, and *Pelodera*, which after immobilisation, hyphal growth and penetration, the nematodes were subsequently digested (Satou et al. 2008; Lee et al. 2020). Fewer studies have been conducted with oyster mushrooms as a biological control agent of phytoparasitic nematodes, but they have shown potential for controlling sugar beet nematode *Heterodera schachtii* and the *M. incognita* in cowpea (Palizi et al. 2009; Youssef and El-Nagdi 2021).

Control of nematodes by predatory nematodes

As biological control agents against phytoparasitic nematodes, predatory nematodes can be applied, but this is challenging because their biology, behaviour, feeding preferences, prey relationships, and other ecological parameters are important to consider for evaluation of their potential. Predatory nematodes belong to the orders Mononchida, Diplogasterida, Rhabditida, Aphelenchida; superfamilies Dorylaimoidea, Nygolaimoidea, Actinolaimoidea; and families Ironidae, Oncholaimidae, Monohysteridae, and Thalassogeneridae. They have different types of feeding apparatus, modes of searching and catching prey, and feeding mechanisms (Bilgrami 2008; Roy and Borah 2020), which serve for classification in three categories: (i) some feed by cutting the prey body and sucking its contents, as they are unable to engulf intact prey (Diplogasterida); (ii) others feed by a combined action of cutting and sucking and occasionally engulfing a whole prey (Mononchida); and, (iii) those which feed only by puncturing the prey cuticle and sucking out the body contents (suborders Dorylaimina, Aphelenchida, and Nygolaimina) (Roy and Borah 2020).

From the biological control application perspective Diplogasterid predatory nematodes have some advantages over other predatory nematodes. As reported by Siddiqi et al. (2004) and Bilgrami et al. (2005) diplogasterid predators are easy to culture in vitro, have high rates of reproduction and predation, have short life cycles, and can detect and respond to prey attractants (showing rare cannibalism), while juveniles possess great tolerance to unfavourable environmental conditions. The first field release of a diplogasterid predator *Mononchoides gaugleri* was performed to determine its effect on existing parasitic nematode populations in turfgrass fields, with a 24.3% reduction of the phytoparasitic nematode population, although unfortunately the rate of predator persistence was low (Bilgrami et al. 2008).

Members of Mononchida have probably received the most attention as possible candidates for control of phytoparasitic nematodes (Jatala 1986), but these are non-specific predators and exert only partial control (Bilgrami 2008). On the other hand, *Iotoncus kherai* preys on phytoparasitic nematodes *M. incognita*, *Hirschmanniella oryzae,* and *Rotylenchulus reniformis* (Mohandas and Prabhoo 1980). Small, (1979) reported that predatory nematodes *Prionchulus punctatus* had a significant influence on the *M. incognita*-induced galling, reducing the number of females. *P. punctatus* was also effective in the reduction of populations of *G. rostochiensis* and stage-3 juveniles of *Rotylenchus fallorobustus* (Small and Grootaert 1983; Bilgrami 2008).

In addition to nematodes, predators *Dorylaimina*, *Aphelenchina* and *Nygolaimina* switch to feeding on bacteria and fungi, which presumably enhances their survival when prey nematodes are scarce (Bilgrami 2008). A comparative study of the predation by *Allodarylaimus americanus* and *Discolaimus silvicolus* on different species of phytoparasitic nematodes showed that both species preferred stage-2 juveniles of *M. incognita*, *Anguina tritici*, *Hetherodera mothi*, and *Tylenchulus semipenetrans* over other nematodes (Khan et al. 1995).

Control of nematodes by microbial consortia

As mentioned before, biological control agents against phytoparasitic nematodes possess a wide range of mechanisms and modes to exert control, combining different strategies by consortia for effective and optimal bioactivity. Synergistic interactions and results at least similar to the most effective control agent used individually, are expected with consortia containing different mechanisms of control (Xu and Jeger 2013). The application of a consortium that includes bacterial and fungal nematode-antagonists is one of the most promising methods. Combined applications of *Fusarium oxysporum* non-pathogenic strain 162, egg pathogen *P. lilacinus* 251, and antagonistic bacteria *B. firmus* were evaluated to assess control of *Radopholus similis* in banana plants; mixtures of *F. oxysporum* and *P. lilacinus* caused a 68.5% reduction in nematode density and combined application of *F. oxysporum* and *B. firmus* was the most effective treatment in controlling *R. similis* on banana (86.2%) compared to the control treatment (Mendoza and Sikora 2009). Similarly, a combination of fungal strains can effectively control a wide range of phytoparasitic nematodes. *P. lilacinus* and the nematode-trapping fungus *Monacrosporium lysipagum* were assayed for their ability to reduce the populations of three economically important phytoparasitic nematodes (*M. javanica*, *H. avenae* and *R. similis*), resulting in nematode populations substantially controlled by both individual and combined applications of the fungi (Khan et al. 2006).

Several formulations consisting of two or more bacterial components have been proposed for the control of RKNs (Migunova and Sasanelli 2021). The inoculants Equity (47 strains of bacilli), BioYield (*B. subtilis* strain GB03 and *B. amyloliquefaciens* strain GB99) induce significant reductions of *M. incognita* eggs, juveniles, and galling in tomato (Burkett-Cadena et al. 2008); whereas bioinoculant Micronema (*Serratia* spp., *Pseudomonas* spp., *Azotobacter* spp., *B. circulans* and *B. thuringiensis*) caused a significant reduction of stage-2 juveniles, galls and egg masses (97%, 80%, and 88%, respectively) (Youssef et al. 2017).

Biological control strategies for RKNs differ in their efficacy level. A comparison between advantages, disadvantages and compatibility of control strategies is provided in Table 1; while synergistic effects among control agents is presented in Table 2.

Current control strategies of *Meloidogyne* RKN in Mexico

Being *M. incognita* a cosmopolitan nematode occurring in various agricultural areas and with the ability to infest more than 2000 plant species including grasses, vegetables, fruit trees and forestry, in Mexico it can also cause damage to commercially important crops such as tomatoes, coffee, eggplant, bananas, beans, papaya, chili, gardenias, cucumbers, and guavas, severely affecting yields and productivity. Infestation with *M. incognita* is widespread in warm climates, and although the exact distribution of species and races of this pathogen in Mexico is not established, it is known to be the most representative species, accounting for more than 60% prevalence in surveyed states (Cid del Prado Vera et al. 2001); *M. incognita* is also found in combination with other species occurring in some locations as they occupy the same ecological niche. Although *M. incognita* is an RKN with a wide distribution and prevalence under different environmental conditions, it is more common in tomato crops in warm climates, whereas *M. javanica* is more common in temperate regions (Cid del Prado Vera et al. 2001). Field conditions vary widely in different agricultural regions in Mexico, hindering population management with phytosanitary measures.

The Official Mexican Norm (NOM—EM -034-FITO-2000; http://www.dof.gob.mx/nota_detalle_popup.php?codigo=2062881), establishes that the processes of production,

Table 1 Advantages, disadvantages, and compatibility of nematode biocontrol strategies used in Mexico

Control strategy	Advantages	Disadvantages	Compatibility	Examples	References
Biological control	Promotes plant growth Environmentally friendly and safe to human health Reduces the incidence or severity of various other diseases in different host plants Appropriate in soils with low populations of nematodes, well below the thresholds of the crop in question Demand for effective and high-quality natural enemies has increased in the last 20 years	Low residual activity in the field Limited shelf life The level of control is lower than chemical product When used along with chemical products, compatibility must be tested	Compatible with traditional practices of pest control Compatibility with chemical products must be tested before use	Bacteria Nematophagous fungi Predatory nematodes	Stirling (2000), Tamez-Guerra et al. (2005), Jennings (2009), Rodríguez-del-Bosque et al. (2015), Peiris et al. (2020)
Traditional practices of control	Relatively cheaper than other control methods Environmentally friendly and safe to human health The use of trap crops such as *Tagetes sp.* have beneficial purposes, besides nematicidal activity	The level of control is lower than using chemical products	Compatible with biological control agents Compatible with chemical control products	Weed control Fertilization with compost high in organic matter Planting trap crops as marigolds (*Tagetes* spp.) or rattlepods (*Crotalaria* spp.) before sowing, in rotation, or after cultivation Aeration of the soil before sowing Solarization	Serrato-Cruz et al. (2008)
Chemical control	Can reach efficiencies between 80 and 90% Long shelf life Easy to apply	Represent a risk to human health High contamination of the environment, soil, and water	Compatible with traditional practices of control Compatibility with biological control agents must be tested before use	Ethoprophos Abamectin (avermectin) Cadusafos Fluensulfone	Jennings (2009), Peiris et al. (2020) COFEPRIS

Table 2 Comparison of biological nematocide agents

Biological control agent	Advantages	Disadvantages	Compatibility and synergy	Examples	References
Bacteria	Can enhance plant growth Obtained from natural environments and widely spread in the rhizosphere Can induce systemic resistance in plants Diverse mechanisms to control nematodes: antibiotics, toxins and volatile organic compounds production, endospore parasitism	Low residual activity in the field, compared to chemical products Limited shelf life The level of control is lower than using chemical products	Compatible with nematophagous fungi Compatible with other nematocidal bacteria Compatibility with chemical products must be tested before use E. g: *Serratia* spp., *Pseudomonas* spp., *Azotobacter* spp., *B. circulans,* and *B. thuringiensis* in a commercial bioinoculant had a significant reduction of stage-2 juveniles, galls, and egg masses against *M. incognita* (97%, 80%, and 88%, respectively)	*Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Clostridium*, *Desulfovibrio*, *Pasteuria*, *Serratia*, *Burkholderia*, *Azospirillum*, *Bacillus*, *Chromobacterium*, *Pseudomonas*, *Corynebacterium*	Jatala (1986), Gupta et al. (2015), Migunova and Sasanelli (2021) Kavitha et al. (2012), de Souza et al. (2015), Engelbrecht et al. (2018), Kahn et al. (2021)
Nematophagous fungi	Most of these fungi are facultative saprotrophs, meaning that in the absence of nematodes, they persist in fields by decomposing organic matter Diverse mechanisms to control nematodes: predation (trapping), endoparasitism, toxin production Some of them can control phytopathogens and insects	On their own, levels of control are lower than using chemical products Limited shelf life	Compatible with other nematophagous fungi Compatible with nematocidal bacterias Compatibility with chemical products must be tested before use E. g: mixtures of *F. oxysporum* and *P. lilacinus* caused a 68.5% reduction in nematode density E. g: *F. oxysporum* and *B. firmus* were effective in controlling *R. similis* on banana (86.2%) compared to the control	*Trichoderma, Dactylella, Arthrobotrys*, *Nematoctonus*, *Aspergillus*, *Penicillium, Pochonia*, *Paecilomyces*, *Metarhizium, Verticillium, Drechslerella, Drechmeria, Pleurotus*	Jatala (1986), Lopez-Llorca et al. (2007), Jennings (2009), Mendoza and Sikora (2009), Peiris et al. (2020), Sikandar et al. (2020)
Predatory nematodes	Juveniles possess great tolerance to unfavorable environmental conditions Some predators switch to feeding on bacteria and fungi, which enhances their survival when prey nematodes are scarce	Biology, behavior, feeding preferences, prey relationships, and other ecological parameters are limited for their use Predator persistence might be lower The level of control is lower than using chemical products	Not compatible with other nematicides methods Compatibility with chemical products must be tested before use	Orders Mononchida, Diplogasterida, Rhabditida, Aphelenchida; superfamilies Dorylaimoidea, Nygolaimoidea, Actinolaimoidea; and families Ironidae, Oncholaimidae, Monohysteridae, and Thalassogeneridae	Khan et al. (1995), Siddiqi et al. (2004), Bilgrami et al. (2005), Bilgrami (2008), Roy and Borah (2020)

Table 2 (continued)

Biological control agent	Advantages	Disadvantages	Compatibility and synergy	Examples	References
Microbial consortia	Combines different mechanisms of control by diverse organisms	Low residual activity in the field, compared to chemical products Limited shelf life The level of control is lower than using chemical products	Compatible with traditional practices of pest control Compatibility with chemical products must be tested before use E.g: Bioinoculants Equity (47 strains of bacilli) and BioYield (*B. subtilis* strain GB03 and *B. amyloliquefaciens* strain GB99) induced significant reductions of *M. incognita* eggs, juveniles, and galling in tomatoes	Nemaxxion Biol Nematon Plus Micronema Equity BioYield	Burkett-Cadena et al. (2008), Youssef et al. (2017), Peiris et al. (2020), Migunova and Sasanelli (2021)

harvesting, selection, storage and transportation of fresh fruits and vegetables must be regulated by the Manual of Good Agricultural Practices, considering that the phytosanitary status of these products may be affected or contaminated by biological, chemical and physical elements that may pose a risk to public health if the necessary measures are not implemented. These measures regulate the management of crops from pre-sowing, cleaning of fields and cultivated areas, pest control, farmer hygiene, among others, to the handling, packaging, and transport of final products for national consumption or international export. Before sowing, aeration of the soil and natural disinfection must be promoted. For this purpose, solarization (covering the soil with plastic and exposing it to the sun to reach high temperatures that are lethal to microorganisms) or disinfection with steam is suggested. Similarly, it is recommended to use seeds or propagation materials that are pest-free or resistant to pests, or that have been treated with methods and products effective against plant pests that verify the suitability of the planting material. Irrigation must be conducted with water that is free of microorganisms and avoiding the use of water from ponds or canals, also the washing and decontamination of farm equipment after each use, to name a few measures.

The origin of infections may have multiple causes or arise from different sources, e.g., infected seeds, contaminated vegetative material, contaminated growing soil or substrate, use of contaminated equipment or tools, among others. Damage at the seedling stage is more evident at the time of transplanting at the definitive growing site (FAO, http://www.fao.org/3/v9978e/v9978e05.htm).

To prevent propagation, Mexico follows recommendations from the Food and Agriculture Organization of the United Nations (FAO) to avoid transporting infected seedlings into the field, which consist of inspecting the roots and removing seedlings showing symptoms of nematode infestation at the time of transplanting. Weeds are also recommended to be controlled regularly as many are infested with nematodes and often host RKNs. Fertilization with compost high in organic matter is recommended. To reduce nematode populations, it is advisable to plant trap crops such as marigold (*Tagetes* spp.) or rattlepods (*Crotalaria* spp.) before sowing, in rotation or after cultivation.

Genus *Tagetes* distributes across the American continent and includes more than 50 species, mainly found in Mexico (Kurpis et al. 2019). Mexican culture employs *Tagetes* for various purposes: antioxidant, medicine, food pigment, flavouring, perfume, resin, ornamental and insecticide; in agriculture it is used as a nematicide, larvicide, attractant or insect repellent, and as fertilizer (Serrato-Cruz et al. 2008). The most used species of *Tagetes* in pest control are. *T. erecta, T. patula, T. minuta* and *T. filifolia*, due to biocidal activity extracted from roots, stems, leaves, inflorescences, or the whole plant. To control nematodes, *Tagetes* is applied in the form of organic manure to the plants or in the form of aqueous extracts and powders, and it is used in crop rotation. Pyrethrins and thiophenes (such as α-terthienyl) found in marigold roots are responsible for its nematocidal and nematostatic activity (Serrato-Cruz et al. 2008; Hamaguchi et al. 2019).

Rattlepod plants (*Crotalaria* spp.) for their part are not nematode hosts and are used as a preceding crop or cover crop to suppress nematode populations by disrupting their life cycle (especially at the reproductive stage) (Osei et al. 2010). They can also provide a niche for natural nematode enemies (Wang et al. 2002), or release lethal or toxic metabolites for nematodes.

Currently, the use of chemical products and crop resistant varieties are the most popular strategies to control RKNs in Mexico. However, the risks of chemical nematicides to the environment and human health have led to the discontinuation of several products in some crops (Peiris et al. 2020). Globally, the demand for effective and high-quality natural enemies that can replace chemical pesticides to control phytopathogenic nematodes has increased in the last 20 years (Rodríguez-del-Bosque et al. 2015), but in Mexico, biological control of nematodes is hardly used in farms. As mentioned before, nematode control with microorganisms represents a green solution that in some cases also promotes plant growth, significantly reducing the incidence or severity of various other diseases in different host plants. However, farmers expect products formulated based on bioactive (mainly microbial) agents to have similar properties to chemical pesticides, i.e., high efficacy, long shelf life (2 years on average), ease of application, and preferably without toxicity during application, among others (Perlatti et al. 2013). Therefore, bioactive agents must solve two important problems inherent to their nature: (1) loss of viability/efficacy during transport, storage or after application; and (2) loss of stability within the storage range (− 5 to 30 °C), for both marketers and farmers.

Some disadvantages of bioactive agents (microorganisms or natural extracts) are their low residual activity in the field, mainly due to inactivation by solar radiation, removal by rain, and limited shelf life (Tamez-Guerra et al. 2005), obstacles that in many cases discourage commercialization and use. This is the case of *Purpureocillium* and *Trichoderma* species-based products, which are the best-studied and the most used fungal genera for controlling nematodes that can even show improvement in growth and plant performance, but this unique control method cannot eradicate nematodes. Fungi partially control *M. incognita* and improve plant growth and yield (Peiris et al. 2020); however, on their own, population reduction is only up to 45% compared to untreated conditions, with varying levels of performance. This level of control is lower than chemical products, which can reach efficiencies between 80 and 90% (Jennings 2009). Thus, chemical nematicides remain the first choice for nematode control especially when population thresholds are high. Biological control, on the other hand, is appropriate in soils with low populations, well below the thresholds of nematode population able to affect a crop, which in most cases is quite low [even as low as one RKN/200 g soil for sweet potato (Stirling 2000; Peiris et al. 2020)]. It is a fact that inferior products affect consumer confidence and positive perception towards organic products in general. Many of these commercial products have been labelled "weak products" due to their variable efficacy and questionable quality control (Jenkins and Grzywacz 2003; Montesinos-Matías et al. 2020).

To address this problem, several government agencies are working together to establish programs to control the quality of commercialised products, with the main objective of ensuring that raw materials meet manufacturer's specifications, that production batches and their quality are consistent, and that finished products meet the criteria established for their use. In implementing quality control plans, formulators must follow guidelines without viewing them as a constraint or burden on production processes, but rather as a mechanism to benefit interested parties, i.e., the biological control industry and its customers (Montesinos-Matías et al. 2020).

Mexican regulation guidelines for nematicides

The world market demands that agricultural products are safe for humans (Codex Alimentarius Commission). Therefore, international parameters for maximum levels (ML) of pesticides have been established, and an increasing number of importing countries require certifications of good agricultural practices (GAP) leading to the promotion of the study of biological control alternatives based on microorganisms associated with plants. In Mexico, the Federal Commission for Protection against Sanitary Risks (COFEPRIS in Spanish) is the official body responsible for monitoring the biosafety of agricultural inputs used in the national territory, which can be classified as low-risk due to their pesticide activity and have specificity and safety towards the environment in which they are released. Approval of pesticides for use in agriculture also requires opinions from the Ministry of Health, the Ministry of Agriculture and Rural Development (SADER), and the Ministry of Environment and Natural Resources (SEMARNAT). For its part, the National Service of Agri-Food Health, Safety and Quality (SENASICA) supervises, according to its assignments:

1. That the pesticides for agricultural use to be registered to comply with the characteristics of the application pattern (crop, pest, dose, number, and application intervals), by evaluating their efficacy, and that they can obtain their Biological Effectiveness Opinion.

2. The provision of technical opinions on the biological efficacy of pesticides for agricultural use and on the phytosanitary aspects of the maximum levels (ML) of pesticide residues in the cases specified in the Regulations on Registration, Importation and Export Authorizations (http://www.dof.gob.mx/nota_detalle.php?codigo=5332473&fecha=13/02/2014).
3. That the process of manufacture, formulation, assembly, importation, commercialization, and aerial application of pesticides for agricultural use conforms to phytosanitary and good use specifications, which must be followed in accordance with the technicians' Opinion of Biological Effectiveness (dose, pests, cultivation, expiration).

The following link shows the current list of pesticides approved in Mexico by COFEPRIS: http://siipris03.cofepris.gob.mx/Resoluciones/Consultas/ConWebRegPlaguicida.asp. Supplementary Table 1 lists approved nematicide products currently registered with COFEPRIS. At the time of writing of this paper (October 2021), 43 products with nematocidal activity were registered, 11 of which are synthetic chemical formulations, 13 are products formulated from plant extracts, 17 are bionematicides derived from bacteria and fungi, and two are mixtures of plant extracts and microbial consortia. The proportion of products made from natural compounds including living organisms or extracts, therefore is higher than the proportion of chemical-synthetic products recognised by the national regulatory body (Fig. 3).

Although the most used method of controlling nematodes in Mexico is still chemical-based, and they have not yet being adopted as a complementary solution by Mexican farmers, bionematicides have gained ground in the national market (Supplementary Table 1; Fig. 3); these offer a wider range of products that could help meet the needs of farmers of different crops and whose properties can be adapted to the agricultural conditions of soils in different regions of the country. The availability of several biological formulations indicates a promising future for the use of natural nematode enemies in Mexican major crops, with the hope that they will achieve comparable results to chemical agents when combined with other physical and natural methods for nematode control. To accomplish this goal Mexican government programs (from SENASICA-and the National Reference Centre for Biological Control -CNRCB in Spanish) have been developed to encourage producers and farmers to adopt practices of biocontrol use, based on a recently implemented national development plan that includes integral policies linking environmental sustainability with costs and benefits to society (Williams et al. 2013). Additionally, the Mexican National Society of Biological Control promotes collaboration and training among researchers, farmers, producers, and companies.

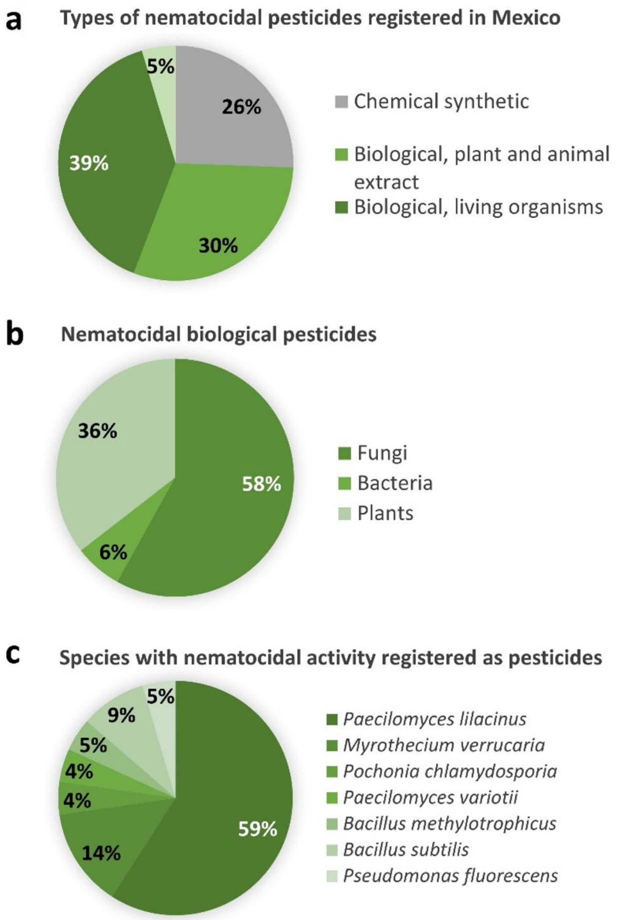

Fig. 3 Nematocidal products approved by COFEPRIS. **a** Percentage of product types of different formulations and method of production of commercially available products in the Mexican market. **b** Type of organisms used in formulations of commercial bionematicides. **c** Species of organisms present in approved products with nematocidal activity presented as a percentage

Despite numerous studies using a variety of fungal and bacterial species with nematocidal activity, products approved by COFEPRIS are limited to the bacterial species *B. subtilis* and *B. methylotrophicus* GF267 and the fungi *Trichoderma* spp., *P. lilacinus* and *Myrothecium verrucaria*. However, other formulations in the market exist without COFEPRIS certification, not because the bioactive ingredients are ineffective, but because production processes do not yet meet quality control guidelines or because the requirements demanded by government regulators are still to be met, or because certification process (which takes several years) is still in process. In these cases, the user must monitor the biological safety of the product and its efficacy based on the concentration of the active ingredient and its viability, as well as other quality control parameters such as correct storage, expiration date, toxicological level, persistence in the environment, waste management (Montesinos-Matías et al. 2020). Bioassays performed under rigorous conditions are expected to select the most virulent strains among isolated candidates. A desirable attribute of these strains is that they remain genetically stable even after scaling processes to maintain infectivity or production of active ingredients with high yields. Strains of genetically improved microorganisms with this characteristic can be obtained as alternative biocontrol agents (Robledo-Monterrubio et al. 2009; Lovett and St. Leger 2018); however, due to current regulation policies in Mexico the use of strains obtained by recombinant DNA techniques is not currently allowed.

Conclusion

The limitations and disadvantages of conventional control provide an important opportunity for the integrated management and biological control of *Meloidogyne* RKN to deliver effective and sustainable alternatives. Products based on PGPB such as *Bacillus*, *Pseudomonas,* and *Serratia* are promising strategies since they not only suppress phytoparasitic nematodes but also stimulate plant growth and control other plant pathogenic microorganisms. Similarly, control through nematophagous fungi offers multiple beneficial traits, as many of these fungi can also control diverse diseases, insect pests and have the potential to stimulate induced resistance on the plant. Predatory nematodes also offer an ecologically safe alternative to chemical nematicides, but maybe not as an attractive option as previously mentioned, as other beneficial traits besides predation of phytoparasitic nematodes are not widely researched. To improve efficiency beyond current levels of biological control strategies it is desirable to develop a tailored microbial control method that considers environmental factors, crop type (as susceptibility varies among crops), soil parameters (moisture, pH, temperature), and whether trials are conducted in greenhouses or in the field. Future studies should consider all these factors to produce merchandise that maintains viability and improves the predatory efficiency of nematophagous (approximately 45% so far), so that biological control becomes a truly viable alternative to achieve a real impact in the control of *Meloidogyne*. For this purpose, collaborative academic, scientific and industrial work is needed to formulate new products or to establish practical and real-world parameters for the use of new and existing products under specific growing conditions, in quality control programs, and in accordance with regulatory guidelines to provide a broader range of bionematicidal products with better yields that will eventually replace or reduce the use of synthetic chemical pesticides for nematode control.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest relevant to the content of this article.

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