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REVIEW

Tackling the plant parasitic nematode *Meloidogyne enterolobii*: Challenges and strategies for control in relevant crops

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Abstract
Nematodes are vital in terrestrial ecosystems, shaping global food chains and soil nutrient cycling. Root-knot nematodes, however, such as *Meloidogyne enterolobii*, pose a great threat as plant parasites, affecting diverse plant species. This review explores essential environmental factors and tactics for handling *M. enterolobii.* The influences of climate and soil composition on the pathogen life cycle and on its global distribution will be highlighted. We also discuss molecular and imaging techniques for nematode identification, and on different control strategies, such as chemical, cultural and biological. Features such as plant genetic resistance and the chemical basis of susceptibility and resistance to these phytopathogens are covered together with important advances on marker-assisted selection, genetic modification of plants with resistance genes and suppression of specific nematode effector-coding genes. Despite the progress in this field, the control of *M. enterolobii* remains a challenge, requiring additional research efforts. From a biotechnological perspective, the development of biological inputs for this nematode control holds promise. These bioinputs offer advantages beyond their direct effects, promoting sustainability, reducing environmental impacts, reducing costs associated with intensive pesticide and fertilizer applications, and increasing productivity while maintaining food security.

Keywords Agriculture · Control · Crops · Integrated management · Resistance · Root-knot nematodes

Introduction

Nematodes comprise about 80% of subterranean life, occupying key roles in soil trophic levels through their influence on nutrient cycles, microbial populations, and carbon dynamics (van den Hoogen et al. 2019). Among them, 4,100 species are plant-parasitic nematodes (PPNs), which cause plant diseases and serious economic losses (Poveda et al. 2020). PPNs are categorized as ectoparasites, semi-endoparasites, or endoparasites. Sedentary endoparasites, such as root-knot nematodes (RKNs) and cyst nematodes (CNs), are particularly destructive and pathogenic (Sato et al. 2019; Sikandar et al. 2023b).

RKNs are recognized as one of the most destructive pests of plants, and their economic impact is significant. *M. enterolobii* nematode is a RKN, belonging to the class Chromadorea, family Meloidogynidae, that holds a leading position amongst the top 10 phytonematodes (Jones et al. 2013; Przybylska and Stęplowska 2020). The genus *Meloidogyne* comprises approximately 100 species (Diyapoglu et al. 2022). *M. enterolobii* has become one of the most threatening pathogenic nematodes in both tropical and subtropical regions of the world, with estimated potential yield loss of 20%. Additionally, the recent identification of this species in Europe is thus a major concern (Koutsovoulos et al. 2020).

In 1983, *M. enterolobii* was first identified as *M. incognita* on the Chinese pacara tree *(Enterolobium contortisiliquum)* (Yang and Eisenback 1988). In 1988, it was recognized as a new species in Puerto Rico and named *M. mayaguensis* (Rammah and Hirschmann 1988) but both cases were reviewed and now it is recognized as *M. enterolobii*. It is widely referred to as the"guava root-knot nematode"due to the significant damages caused to guava trees (*Psidium guajava* L.) in South America (Brida et al. 2018).

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In Brazil, the species *M. enterolobii* caused a 70% reduction in guava yield over seven years, resulting in an estimated direct loss of US$ 61 million (Sikandar et al. 2023b). Furthermore, it has been observed that varieties of important economic crops and rootstocks, such as tomato, banana, cherry, grape, fig, and melon, are excellent hosts for *M. enterolobii* (Liang et al. 2020; Sikandar et al. 2023b, a). It is important to note that nematodes, including *M. enterolobii,* can exhibit different genetic lineages within a species, which can affect their virulence on different potential hosts (Schwarz et al. 2020).

Meloidogyne enterolobii predominantly thrives in tropical and subtropical regions but also occurs in temperate zones across Africa, the Americas, Asia, Europe, and Oceania (Sikandar et al. 2023b). Pan et al. (2023) highlight its varying distribution: high suitability in West, Central, and Southern Africa; widespread presence in South America, particularly Brazil, Argentina, and neighboring countries; notable regions in East, South, and Southeast Asia; and in North and Central America, including the southeastern U.S. and parts of Mexico. In Oceania, key areas are in northern and eastern Australia. Europe shows limited suitability, except for parts of France, Portugal, and Italy. Climate, especially temperature, significantly influences its distribution and lifecycle (Velloso et al. 2022). It is an obligate biotrophic endoparasite that feeds and develops entirely within the tissue of the host plant until reaching the adult stage of life (Philbrick et al. 2020).Root-knot nematodes (RKNs) are already notorious for their detrimental effects on plants. *M. enterolobii,* especially, poses an even more serious global threat due to its broad host range and the ability to infest tomato genotypes bearing *Mi* resistance genes. These genes are effective against some of the 100 known *Meloidogyne* species, such as *M. incognita*, *M. arenaria, M. javanica, M. luci* and *M. ethiopica,*, but not against *M. enterolobii* (Philbrick et al. 2020; Santos et al. 2020).

Recent studies have focused on the discovery of new sources of genetic resistance against root-knot plant diseases caused by *M. enterolobii* nematodes. Overcoming the challenges posed by nematode reproduction in crops with established resistance genes is crucial. The combination of natural resistance strategies and genetic engineering holds promise for the effective management of nematode infections in agriculture (Sikandar et al. 2023b).

This work explores these challenges, as well as recent Integrated Nematode Management (INM) strategies to control *M. enterolobii* in relevant crops. We covered chemical, cultural, and biological control strategies, as well as genetic resistance, along with recommendations for future research to combat this agricultural pathogen.

Life cycle, infection mechanism and taxonomic complexity of *Meloidogyne enterolobii*

Meloidogyne spp. nematodes, stemming from a theoretical amphimictic ancestor, employ diverse reproductive strategies including sexual reproduction (amphimixis), asexual reproduction with genetic recombination (facultative meiotic parthenogenesis), and asexual reproduction without genetic recombination (apomixis) (Castagnone-Sereno 2006; Bellé et al. 2019). *M. enterolobii* reproduces exclusively through obligatory mitotic parthenogenesis (apomixis), without male participation. This suggests that genetic variability might be linked to epigenetic modifications, prompting inquiries about genome plasticity, which in turn could drive genetic diversity and adaptive evolution in these organisms (Castagnone-Sereno 2006; Bellé et al. 2019). That is probably the reason for its much greater ability to find different hosts in diverse environmental conditions.

The nematode life cycle progresses from egg to juvenile stages (J1–J4) and culminates in the adult stage, with a chromosome number of $2n = 44/46$ (Khan et al. 2022). *Meloidogyne enterolobii* reproduces similarly to destructive root-knot nematodes (*M. incognita, M. javanica,* and *M. arenaria*) (Koutsovoulos et al. 2020). Embryogenesis involves molting from J1 to J2, where the motile juveniles migrate toward host roots, attracted by exudates. J2 initiates giant cell (GC) formation, inducing hyperplasia in surrounding cells, leading to gall formation (Ibrahima et al. 2019; Przybylska and Stęplowska 2020). Sedentary J3 and J4 stages establish themselves in the vascular cylinder, developing into reproductive females under favorable conditions (20–35 °C). Females produce up to 600 eggs in ~ 30–35 days (Philbrick et al. 2020). Environmental stress can trigger male development, contributing to soil biomes (Ibrahima et al. 2019).

Figures 1 and 2 show, respectively, microscopic images of the stages of *M. enterolobii* individuals extracted from the roots of *Psidium spp.* in Casa Nova, Bahia, Brazil, and a schematic representation of a plant attacked a RKN species of the genus *Meloidogyne*, such as *M. enterolobii,* showing some plant physiological responses to its invasion.

Environmental conditions can significantly impact the life cycle of *M. enterolobii.* In a study with tomato, cucumber, and pepper, gall symptoms appeared between 25 to 33 °C at 21 days after inoculation (DAI), with egg masses present at 28 DAI in all cultivars (Salazar-Mesta et al. 2023). In South Africa, where temperatures reached 32 °C, *M. enterolobii* infected tomato, soybean, and corn, with mature females and eggs observed at 15 DAI and

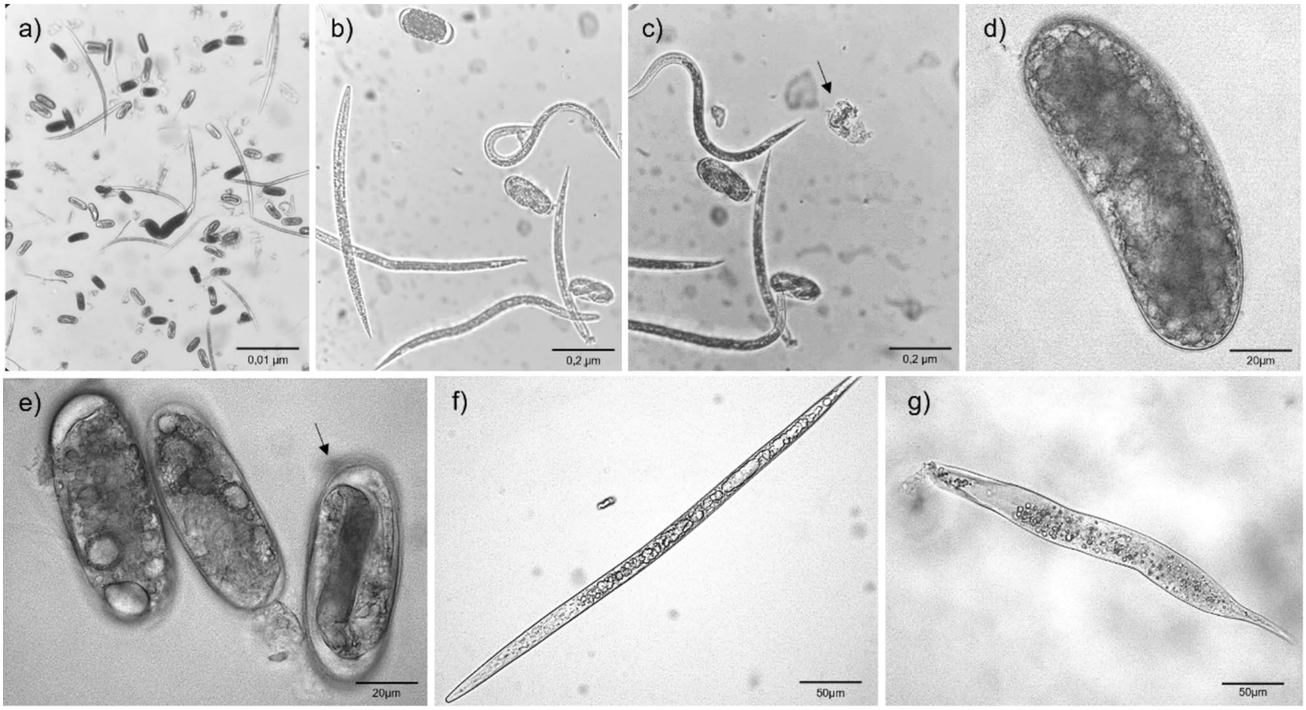

Fig. 1 Microscopic images of different life cycle stages of *M. enterolobii*, extracted from the roots of *Psidium spp*. in Casa Nova, Bahia, Brazil: **a**), **b)** and **c**) eggs and juveniles are shown, indicating different stages of the pathogen; **c)** remaining eggshells (pointed by arrow); **d**) egg; **e)** eggs with vacuolar sacs and a J1 egg about to hatch (pointed by arrow); **f)** and **g)** infective juvenile

mobile J2 of the second generation at 20 DAI. Nematode degree-days (DD) were recorded as 216 for tomato, 195 for soybean, and 232 for corn (Collett et al. 2023). Additionally, Velloso et al. (2022) found that root infection in tomato seedlings was 33% higher at 30 °C than at 25 °C, with faster development from J2 to reproductive stage. The life cycle was completed in 23 days and 506.9 DD at 30 °C, with lower temperatures delaying development.

The diversity of terrestrial nematodes is often underreported, with many species still unclassified. Nematode taxonomy is largely based on morphology, which is crucial for classification (Nisa et al. 2022). Second-stage juveniles of *M. enterolobii* are worm-like and ringed, measuring 250 to 700 µm in length and 12 to 18 µm in width. Their tail length ranges from 15 to 100 µm, with the hyaline part 5 to 30 µm long (Rammah and Hirschmann 1988; Yang and Eisenback 1988). Females are globular, pear-shaped, sedentary, and pearly white, measuring 400 to 1300 µm in length and 300 to 700 µm in width. Males are worm-like, measuring 700 to 2000 µm in length and 25 to 45 µm in width (EPPO 2016, 2024). *M. enterolobii* is highly similar with other tropical RKN like *M. incognita*, *M. arenaria*, and *M. javanica*. However, it can be distinguished from these species by its perineal pattern, male and female stylet morphology, male morphology, body length, lip region, tail, and hyaline tail part in second-stage juveniles (EPPO 2016). Yet, morphometric and morphological tools alone can incorrectly identify *M. enterolobii* as *M. incognita* (Collett et al. 2021). Traditional morphological methods that rely on the female perineal pattern, morphology of the lip region, stylet, basal swellings of males, as well as the morphometrics of second-stage juveniles, are often challenging and subjective. Therefore, identification is typically complemented by electrophoretic and molecular techniques (Ye et al. 2021).

The identification of *Meloidogyne* species is more accurately performed through PCR and DNA analyses. These techniques reveal specific genetic markers, differentiating closely related species and exploring genetic diversity and virulence potential (Schwarz et al. 2020). CoxII-16S has emerged as a valuable marker for distinguishing *Meloidogyne* species (Ye et al. 2021). Quantitative PCR (qPCR) effectively detects various nematode species and provides nematode density estimates that strongly approximates those traditional counts from soil samples (Hodson et al. 2023). Droplet Digital PCR (ddPCR) offers high sensitivity, even at low DNA concentrations, without pre-enrichment (Shao et al. 2023).

Biochemical analyses, like non-specific esterase (EST) electrophoresis, combined with molecular techniques such as internal transcribed spacer PCR–RFLP (ITS-PCR–RFLP), sequence characterized amplified region (SCAR) markers, real-time PCR, and loop-mediated isothermal amplification

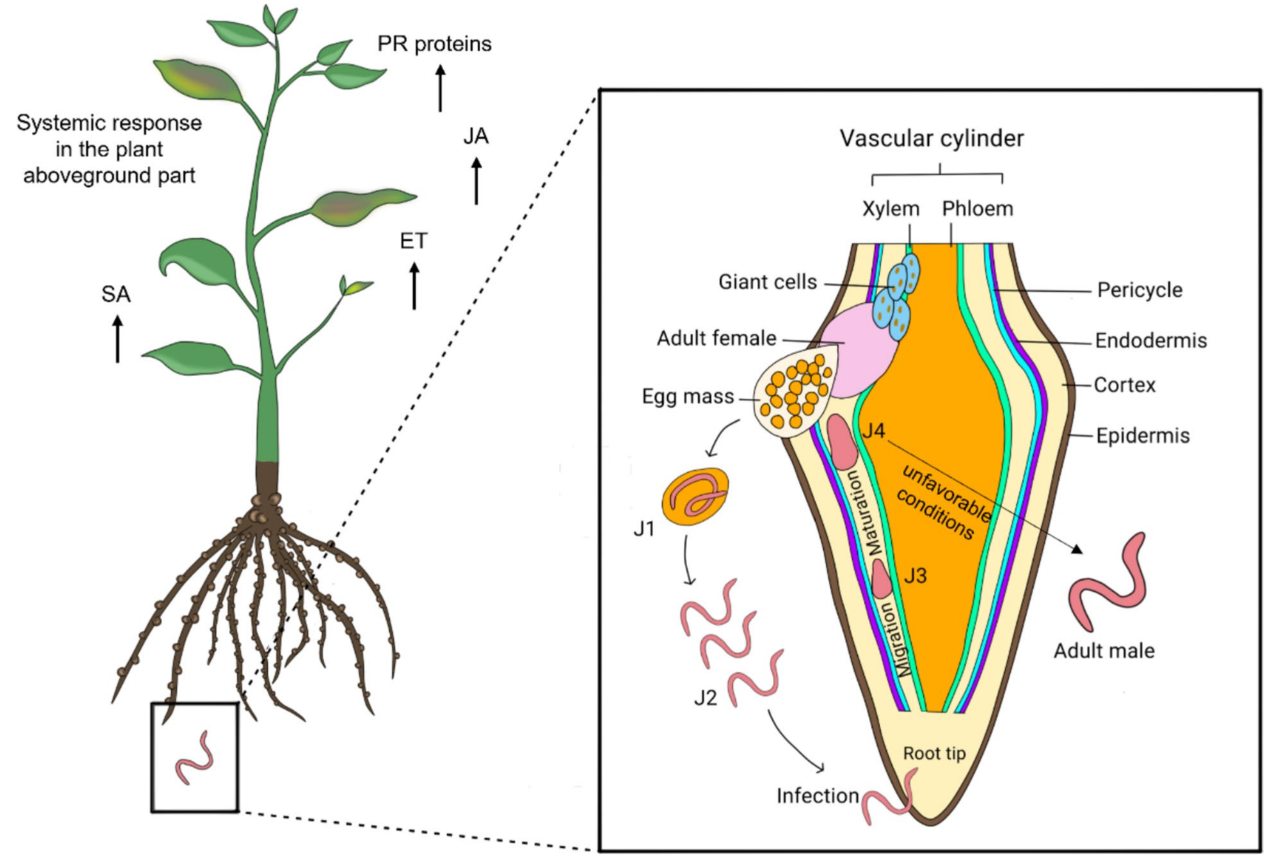

Fig. 2 Schematic representation of a plant with roots infected by *M. enterolobii,* showing how the pathogen establishes itself and completes its developmental cycle. SA – Salicylic acid; ET – ethylene; JA – Jasmonic acid; PR proteins – Pathogenesis-related proteins

(LAMP), help to identify economically relevant *Meloidogyne* species (Rusinque et al. 2023). The LAMP assay, targeting the 5S rDNA-IGS2 region, is increasingly popular for point-of-service detection due to its speed and simplicity. RPA (Recombinase Polymerase Amplification), another isothermal technique, amplifies minimal DNA samples in minutes, targeting rDNA IGS and SCAR markers (Shao et al. 2023).

Field applications require integrating detection processes with practical solutions. For example, NemaNet, a machine learning tool, simplifies soybean nematode identification using a convolutional neural network trained on an extensive image dataset (Abade et al. 2022).In a comparative analysis of published works (Table 1S – supplementary materials), 174 species of host plants for the nematode *M. enterolobii* were listed and grouped into 57 families. The majority of those belong to the Solanaceae, Lamiaceae, Myrtaceae and Euphorbiaceae families (Bellé et al. 2019; Rashidifard et al. 2019; Santos et al. 2019; Khan et al. 2022; Rusinque et al. 2023; Sikandar et al. 2023b). The graphical representation of these data is presented in Fig. 3.

It is important, however, to keep in mind that *M. enterolobii* continues to conquer new environments and hosts. The first report of this nematode on several crops around the world, in the last 5 years, has been recorded (Table 1). This clearly demonstrates the importance of publishing such data, especially through open access.

Plant defense mechanisms against disease

Plants trigger robust defense mechanisms following infection by RKN, such as *M. enterolobii*. These defenses include physical barriers (cell wall and cuticle) and chemical defenses (defense proteins and secondary metabolites). Phenolic and carotenoid accumulations, reinforcement of cell walls with lignin and suberin, and the production of metabolites inhibiting egg hatching and nematode development are key components (Sato et al. 2019).

Although chemotaxis is considered the most critical feature for RKN to locate hosts, the mechanisms that attract them to root exudates are not fully understood. It has been reported that chemotactic responses are specific to species within the genus *Meloidogyne*. A work by Silva et al (2020) showed that J2 of *M. enterolobii* migrate faster than *M. incognita* and are able of penetrating tomato roots as early

Table 1 First report of *M. enterolobii* attack in different crops since 2018

Location	Family	Botanical name	Reference
Africa*	Euphorbiaceae	*Manihot esculenta*	(Oyetunde et al. 2021)
	Poaceae	*Zea mays*	(Pretorius 2018)
	Fabacea	*Arachis hypogaea*	(Rashidifard et al. 2018)
Brazil	Convolvulaceae	*Ipomoea batatas*	(Silva et al. 2021)
	Malvaceae	*Gossypium hirsutum*	(Galbieri et al. 2020)
	Musaceae	*Musa* spp.	(Luquini et al. 2019)
	Moraceae	*Morus celtidifolia*	(Soares et al. 2018)
China	Plantaginaceae	*Antirrhinum majus*	(Lu et al. 2023)
	Rubiaceae	*Ixora chinensis*	(Fan et al. 2022)
	Lamiaceae	*Mesona chinensis*	(Wu et al. 2022a)
	Fabaceae	*Ormosia hosiei*	(Wu et al. 2022b)
	Euphorbiaceae	*Acalypha australis*	(Jia et al. 2022)
	Convolvulaceae	*Ipomoea batatas*	(Jia et al. 2021)
	Theaceae	*Camellia oleifera*	(Zhu et al. 2020)
	Cannabaceae	*Cannabis sativa*	(Ren et al. 2020)
	Rubiaceae	*Gardenia jasminoides*	(Sun et al. 2019)
	Moraceae	*Morus* spp.	(Sun et al. 2019)
	Zingiberaceae	*Zingiber officinale*	(Zhuo et al. 2018)
	Solanaceae	*Solanum negro*	(Chen et al. 2023a)
	Euphorbiaceae	*Euphorbia pulcherrima*	(Liang and Chen 2021)
	Amaranthaceae	*Celosia argentea*	(Ho et al. 2022)
Egypt	Myrtaceae	*Psidium guajava*	(Ibrahim et al. 2023)
India	Myrtaceae	*Psidium guajava*	(Bhati and Parashar 2020)
Mexico	Rubiaceae	*Coffea arabica*	(Torres-López et al. 2022)
	Amaranthaceae	*Beta vulgaris*	(Salinas-Castro et al. 2022)
	Apiaceae	*Daucus carota*	(Salinas-Castro et al. 2022)
	Solanaceae	*Solanum melongena*	(Salazar-Mesta et al. 2022)
	Cucurbitaceae	*Cucumis sativus*	(Gómez-González et al. 2020)
Nigeria	Musaceae	*Musa* spp.	(Olajide et al. 2022)
United States	Ulmaceae	*Ulmus parvifolia*	(Moore et al. 2020)
	Convolvulaceae	*Ipomoea batatas*	(Gu et al. 2021b; Hajihassani et al. 2023)
	Lamiaceae	*Ocimum basilicum*	(Gu et al. 2021a)

*There is no specific location information

as 3 days after infection. Both species penetrated marigold roots just at 9 DAI, indicating a delay in J2 migration of *M. incognita*. In this sense, further studies must be performed to elucidate how nematodes, through their sensory organs, are able to distinguish attractive and repellent substances of root exudates from the same host (Dutta et al. 2021).

Innate immunity or basal resistance is the first system activated by the interaction between pathogen-associated molecular patterns (PAMPs) and damage-associated molecular patterns (DAMPs), leading to a pattern-triggered immunity (PTI). Effector-triggered susceptibility (ETS) occurs when PTI is neutralized, but plants can still exhibit disease resistance through effector-triggered immunity (ETI) activated by resistance genes (*Avr*-R). In non-host (resistant) plants, ETI is accelerated, and PTI is enhanced (Shao et al. 2021). The Hypersensitive Response (HR) is a critical innate mechanism against pathogens, characterized by rapid and specific tissue collapse surrounding the infection. This response involves the release of toxic compounds affecting the pathogen, inducing programmed cell death, and triggering the production of Pathogenesis-Related (PR) proteins. HR results in necrotic lesions crucial for the Systemic Acquired Resistance (SAR), limiting the movement of plant-parasitic nematodes (PPN) and disrupting their life cycle (Przybylska and Stęplowska 2020).

Plants have developed defense mechanisms against invasion by RKN, and if these are violated, more complex defense systems kick in. PPNs also serve as vectors for microorganisms, both beneficial and pathogenic, as they associate with the nematode cuticle and are transported to plant roots during feeding on root tissues (Li et al. 2023a). Example of a such beneficial interaction was reported by

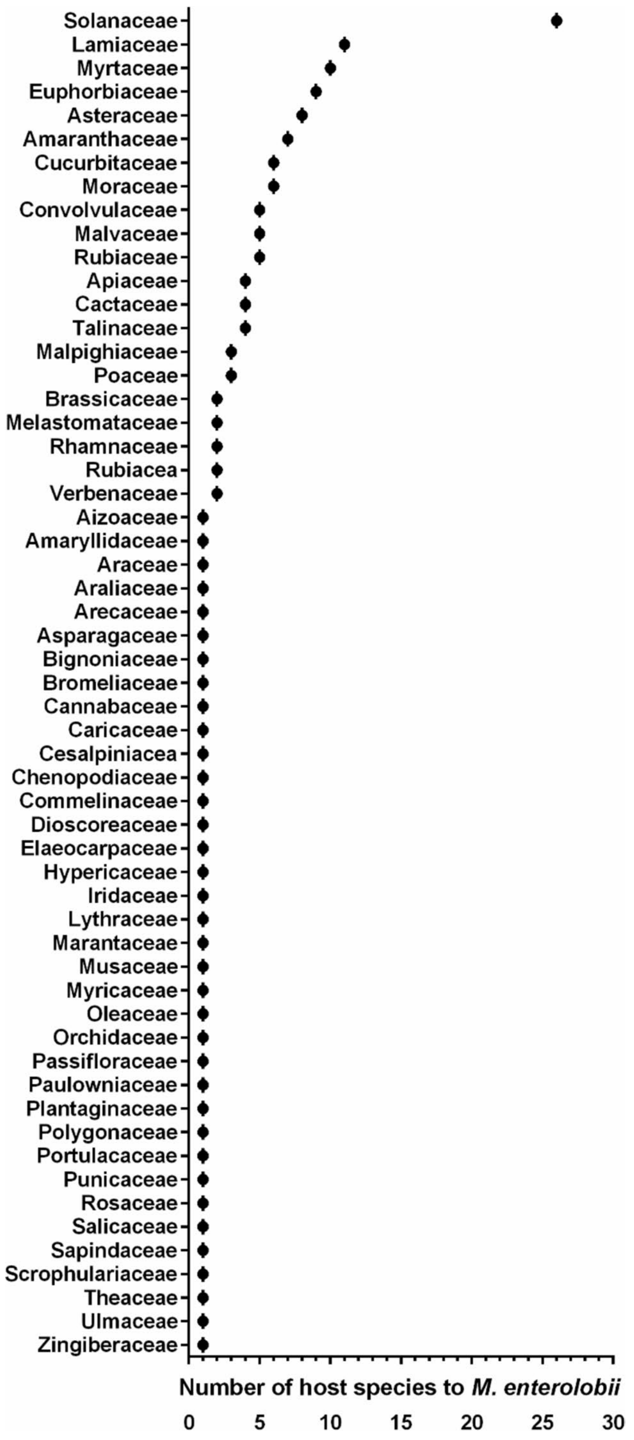

Fig. 3 Graphical representation of 174 host plant species for *M. enterolobii*, grouped into 57 families

Li et al (2023b) who showed significant enrichments of bacteria belonging to Rhizobiales, Betaproteobacteriales, and Rhodobacterales in the endophytic microbiota of *Meloidogyne*-parasitized tomato root samples. At the other end of the spectrum, co-infection of *M. enterolobii* with *Fusarium* spp. leads to a complex gall disease, impacting crop yields. In this synergistic interaction, the fungus colonizes inner root tissues after penetrating through lesions previously performed by the nematode. Symptoms include curling of apical leaves, stunted growth, leaf discoloration, and fruit changes, posing challenges to control (Shi et al. 2019; Dutta et al. 2021).

Plant pathogen nematodes (PPN), including *M. enterolobii*, rely on pheromones for development and communication (Manohar et al. 2020).). These molecules influence their behavior and responses, such as the release of effector proteins that alter plant structure and functions, facilitating parasitism. Nematode secreted compounds possessing immunosuppressive properties play a pivotal role in parasitism, particularly in the modification and degradation of the plant cell wall (Khan et al. 2023a). They are collectively referred to as"secretomes"or"para sitomes"and have been associated with a diverse set of molecular functions, such as polysaccharide binding and cellulosic activity, all linked to plant cell wall modification and degradation. Pheromones from PPN serve as a"signature,"initiating immune responses in the host plant and allowing nematodes to manipulate plant cellular machinery (Koutsovoulos et al. 2020; Manohar et al. 2020). Figure 4 shows the plant defense mechanisms triggered in response to nematodes, which follow different paths in host and non-host plants.

Ascarosides are one example of such pheromone molecules linked to the weakening of host immune responses. The Ascr #18 specifically serves as a pathogen-associated molecular pattern (PAMP) known to activate early immune responses. It is recognized by the plant as a nematode-associated molecular pattern (NAMP), leading to the activation of pathways involving MAPKs, defense signaling, gene expression, and the generation of reactive oxygen species (ROS) (Klessig et al. 2019).

A recent study identified the effector MeMSP1 as a key player in plant responses to both abiotic and biotic stresses, specifically targeting glutathione-S-transferase class Phi family proteins (GSTFs). *Arabidopsis* mutant lines lacking AtGSTF9 exhibited increased susceptibility to RKN infection. Subsequent analyses revealed that MeMSP1 significantly influenced *A. thaliana* metabolic pathways, leading to the accumulation of amino acids, nucleic acids, and organic acids, and disrupting flavonoid production (Chen et al. 2023b).

In plants, two groups of essential compounds are distinguished: primary metabolites, crucial for growth and involved in major metabolic pathways; and secondary metabolites (specialized metabolites), related to plant interactions with the environment. The Fig. 1S (supplementary materials) illustrates the interconnectedness of primary and secondary metabolism pathways.

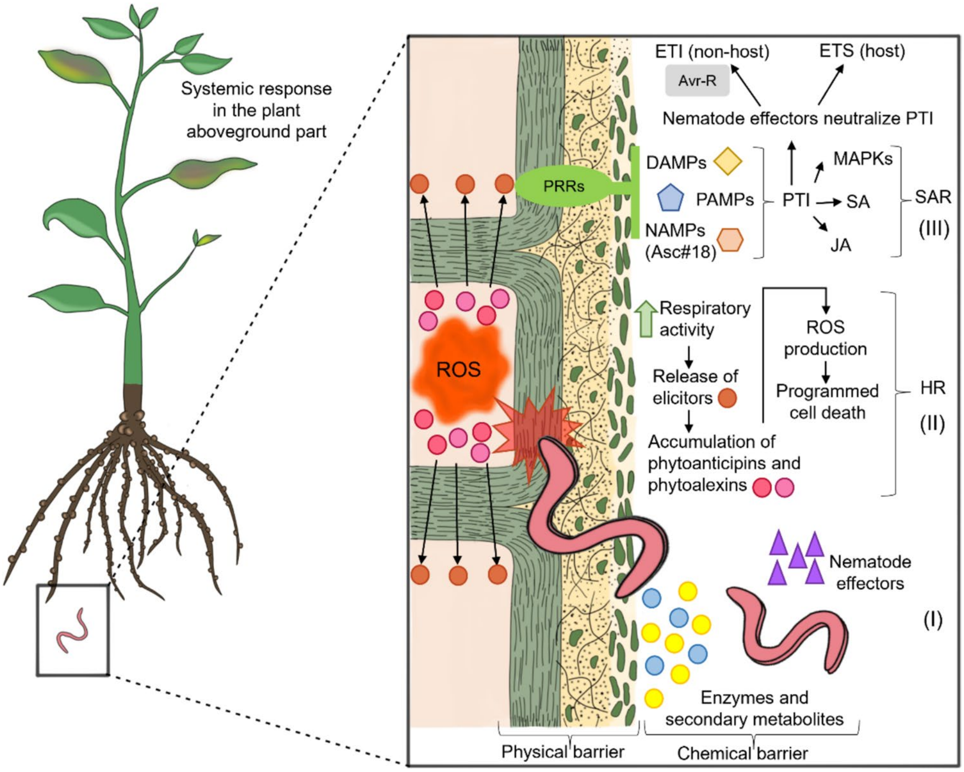

Fig. 4 Schematic representation of an infected plant and its defense mechanisms against *Meloidogyne* spp., including *M. enterolobii*: (I) Physical and chemical barriers; (II) Hypersensitive Response (HR)—Programmed cell death; and (III) Systemic Acquired Resistance (SAR)

Plant metabolites stored in or exuded from roots to the rhizosphere significantly impact nematode behavior, development, and reproduction. About 5 to 20% of photosynthesis products are released into the rhizosphere via root exudates, emphasizing the potential for enhancing microbial control of plant-parasitic nematodes through a comprehensive understanding of chemical interactions among plants, rhizosphere microbiomes, and nematodes (Sikder and Vestergård 2020).

Anti-nematode phytochemicals (ANPs) fall into three categories: root-released metabolites with nematode-repelling action; with nematicidal activity regardless of nematode presence; and anti-nematode compounds produced in response to nematode penetration (Desmedt et al. 2020). Chemical signaling and transduction play vital roles in plant-microorganism interactions, initiating metabolic responses involving key secondary metabolites such as alkaloids, peroxidase, polyphenol oxidase, phenylalanine ammonia-lyase, phenolic compounds, and terpenes in defense against biotic stresses (Jha and Mohamed 2022).

Integrated Nematode Management (INM) of *M. enterolobii* in plant species of interest to global agribusiness

Climate changes, including global warming, higher CO2 levels, and extreme environmental conditions, profoundly affect nematodes. They can boost or undermine their reproduction, extend or shorten transmission periods, alter gender ratios, and shift their abundance and diversity in hot and humid climates, akin to other parasites and pathogens (Dutta and Phani 2023). Pioneering work on the effect of these climate changes on the geographic distribution of *M. enterolobii* predicted that, by 2090, the nematode could reach higher latitudes, which, in the case of the country of origin of the authors, would make northern China a more suitable habitat for these pests, and globally highly suitable regions for the nematode would be concentrated in Africa, South America, Asia, and North America between latitudes 30°S to 30°N (Pan et al. 2023). Zhou et al. (2022) recommended that research be conducted spanning multiple trophic levels, including plants, soil microorganisms, and the nematodes themselves, in order to effectively understand the impact of global changes on soil nematodes. The complexity of the nematode distribution is related to global temperature but organic carbon availability shall also be considered (van den Hoogen et al. 2019).

In addition, soil management practices also impact nematodes. Soil compaction can limit root growth in surface layers, where plant-parasitic nematodes thrive. This underscores the vital connection between soil physical properties (texture) and chemical attributes (pH, organic matter, nutrients), and phytonematode populations (Leiva et al. 2020). The addition of nitrogen, along with tillage reduction, had a synergistically negative impact, reducing soil nematode abundance and diversity (Wang et al. 2021). It has also been demonstrated that in highly inorganic soil, plant phosphorus acquisition depends heavily on phytate-mineralizing bacteria (Ranoarisoa et al. 2020). Soil properties and biology impact nematode survival and predation, revealing a strong interconnectedness of ecosystems.

The INM aims to control diseases in a sustainable and environmentally friendly manner, reducing the negative impacts of nematodes on agricultural crops, preventing disease outbreaks, and increasing agricultural production. Managing *M. enterolobii* poses challenges due to its multiple hosts and rapid reproductive cycles, but its suppression can be achieved through two or more control techniques, such as physical control, cultural practices, biological control, and genetic resistance (Philbrick et al. 2020; Timper and Davis 2022; Sikandar et al. 2023b).

Cultural control

Cultural control, a cost-effective nematode management method, is vital for *Meloidogyne* species, notably *M. enterolobii*. It involves tactics like crop rotation and cover crops. Rigorous studies on cultural measures and equipment sterilization are crucial for successful management, emphasizing preventive actions to curb nematode spread (Khan et al. 2023b). In a study focusing on mitigating nematode infestations in tomato plantations, researchers tested irrigation water treatment with ozone to render the eggs of *M. enterolobii* inviable. It was found that a low residual concentration of ozone for a short period reduces egg viability. Exposure to 0.2 mgO3 L^{-1} for 15 min resulted in almost 90% egg inactivation, while 0.55 mgO3 L^{-1} for 10 min inactivated over 95% of the nematode population (Fernández et al. 2019).

Crop rotation, a valuable technique for annual crops, offers multiple approaches, including the use of non-host plants, different hosts, reservoir plants (weeds), and antagonist plants. These methods contribute to suppressing *M. enterolobii* populations through various mechanisms. A study on the impact of crop rotation on *M. enterolobii* found that combinations of sorghum/corn and alfalfa/corn significantly reduced the quantities of nematode eggs and juveniles compared to a monoculture of corn. Sorghum/corn rotations reduced the population density of *M. enterolobii* by 81% in the first experiment and 60% in subsequent experiments, followed by alfalfa/corn rotations, with reductions of 54% and 43%, respectively. (Rashidifard et al. 2021).

Antagonistic plants play a crucial role in nematode management by producing anti-helminthic compounds during growth. Key species like *Tagetes* spp., *Azadirachta indica*, *Brassica* spp., and *Crotalaria* spp. release nematotoxic compounds, acting as traps or triggering unfavorable responses for PPNs. For instance, *Crotalaria juncea* boosts nematode antagonistic microorganisms and releases the nematotoxic substance monocrotaline, while neem (*A. indica*) produces nematotoxic compounds like azadirachtins (Chetia et al. 2019; Abd-Elgawad 2021).

Cover crops have the ability to incorporate organic matter, which is fundamental for soil fertility. Effective selection of cover crops requires attributes such as easy establishment, rapid growth, effective soil coverage, resistance to pests and diseases, suitability for intercropping, and a robust root system capable of producing ample dry matter for no-till farming techniques (Djian-Caporalino et al. 2019; Zhang et al. 2022). In a conducted study, it was observed that sunn hemp (*C. juncea*) and sudangrass (*Sorghum sudanensis)* were considered poor hosts or non-hosts for *M. enterolobii*. Therefore, these crops can be recommended as cover crops in most cases, except when root lesion nematodes are present in the field. On the other hand, cowpea (*Vigna unguiculata)* and sunflower (*Helianthus annuus*) were identified as good hosts for this RKN, consequently, they are not suitable options for cultivation in fields where RKN are present (Bui and Desaeger 2021).

In a U.S. evaluation of summer cover crops against *M. enterolobii*, sunflower (*Helianthus annuus* L.) and cowpea (*V. unguiculata* L.) elicited high nematode reproduction, while buckwheat (*Fagopyrum esculentum* M.) and sunn hemp (*C. juncea* L.) led to lower nematode reproduction. Sesame (*Sesamum indicum* L.) caused low reproduction. Millet and sorghum varieties, including pearl millet and sorghum-sudangrass, did not host nematodes and had greater biomass compared to tomatoes (Khanal and Harshman 2022).

Despite the effectiveness of cultural control techniques, their adoption by producers may be hindered due to the requirement for fallow periods or frequent crop rotation, especially when dealing with perennial crops of economic importance.

Chemical control

The utilization of chemical nematicides for the control of *Meloidogyne* species entails notable risks. Nematicides can be broadly classified into two categories: fumigants, characterized as volatile gases or easily evaporated liquids, and non-fumigants, typically formulated as liquids or granules mixed with water or directly applied to the soil. Both types present substantial hazards as they can be absorbed by plants and accumulated in the environment, and they have already been detected at various levels in the food chain. Additionally, these nematicides disrupt soil ecosystems, adversely affecting beneficial microorganisms and potentially causing severe environmental consequences (Sikandar et al. 2023b, a).

However, there is a growing movement towards the gradual phase-out of methyl bromide and other toxic fumigants from the soil and nematicides due to their toxicity to humans and other non-target organisms (Oka 2020). The practice of soil fumigation faces increasing social and regulatory pressure, but it remains the primary management tool for nematodes in the production of many high-value crops. In the long term, improving soil health and developing more resilient soils may be one of the greatest benefits of phasing out soil fumigants and adopting more selective and safer nematicides (Sikora et al. 2023).According to what was proposed by Desaeger et al (2020) the ideal characteristics of a nematicide vary between the perspectives of the producer and the regulator. For the producer, it's important that it controls a wide range of nematodes, has good mobility and residual activity in the soil, in addition to being low in toxicity to plants and requiring low dosages. For the regulator, selectivity is essential, protecting non-target organisms, avoiding leaching and residues in crops, without impacting the quality of the final product and with low human toxicity. Next-generation nematicides include fluazaindolizin, fluensulfone, fluopyram, spirotetramat, and cyclaniliprole. However, iprodione has been banned in Europe due to concerns about cancer and risks to aquatic life. The release of thiozafenone for seed treatment has been postponed due to reports of skin irritation. There is an urgency for more selective nematicides (Burns et al. 2023).

Common soil fumigants employed for controlling *Meloidogyne* spp. include 1,3-dichloropropene (e.g., Telone II), metam sodium (e.g., Vapam, Sectagon-42), and metam potassium (e.g., K-Pam). In the United States, non-fumigant nematicides such as fluensulfone (e.g., Nimitz), fluopyram (e.g., Velum Prime and Velum Total), oxamyl (e.g., Vydate), etoprope (e.g., Mocap), and terbufos (e.g., Counter) find application. In certain regions, like the European Union, metam sodium and dazomet (e.g., Basamid) have been shown effective against *M. enterolobii* (Philbrick et al. 2020). However, metam-sodium has been withdrawn by industry from the approval process under Regulation (EU) No 528/2012. The effect of that withdrawal is that metam-sodium is banned from all use in the subcategory 'other pesticide including biocides', by the Commission Delegated Regulation (EU) 2023/1656 of 16 June 2023 (EUR-Lex 2023).

The Phytosanitary Pesticides System of Brazil (Ministério da Agricultura Pecuária e Abastecimento do Brazil 2023) lists 34 formulated products with synthetic nematicidal activity for national agriculture. Among these, 24 are applicable to crops affected by the following species from the *Meloidogyne* genus: *M. javanica*, *M. incognita*, *M. exigua*, *M. hapla*, *M. paranaensis*, and *M. enterolobii*. In the toxicological and environmental classification of this pesticides, a lower index indicates greater danger, while a higher index

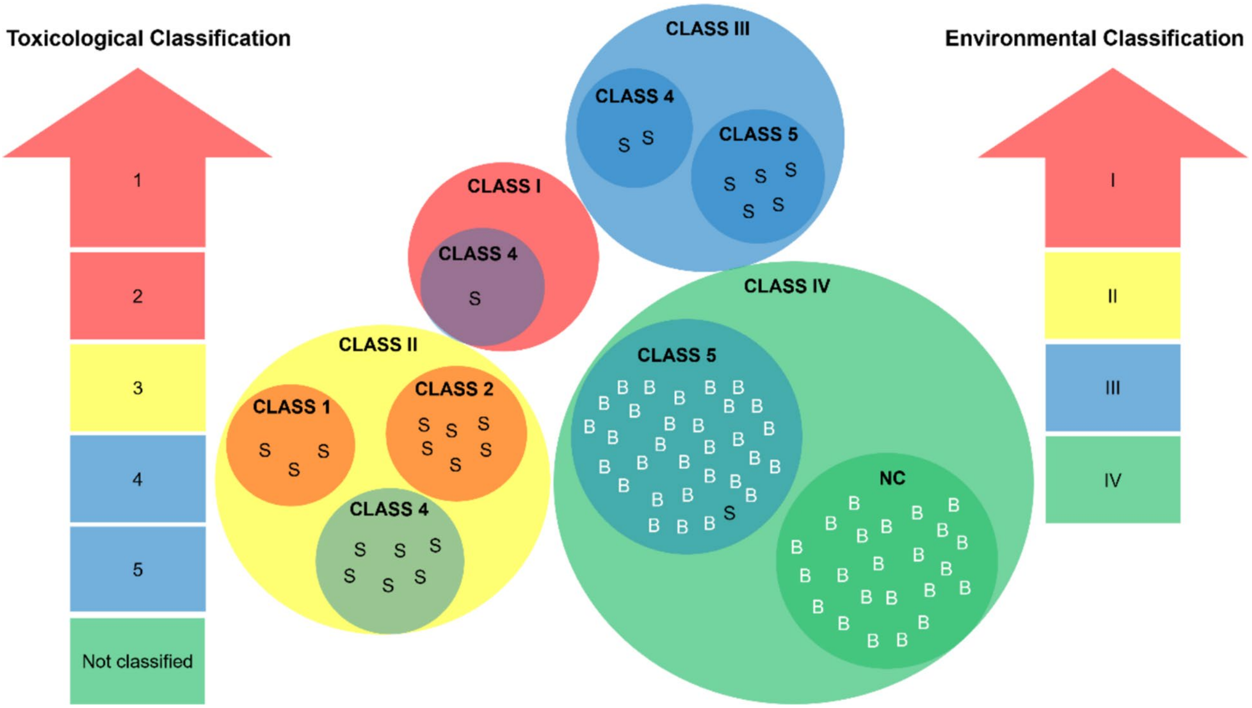

Fig. 5 Schematic representation of the comparison among toxicological (between 1 and 5, below 5 are those not classified) and environmental (between I and IV) classifications of synthetic (S) and biological (B) nematicides registered and commercially released in Brazil for control of *Meloidogyne* spp

indicates lesser danger. Figure 5 presents a comparison of the toxicological (between 1 and 5, below 5 are unclassified) and environmental (between I and IV) classifications of 24 synthetic (S) (Tab. 2S – supplementary materials) and 56 biological (B) (Tab. 3S – supplementary materials) nematicides registered and commercially released in Brazil for control of *Meloidogyne* spp.

Specifically designated for *M. enterolobii* control, there are only two chemical nematicides among the 24 previously mentioned as applicable to the genus *Meloidogyne*: Nimitz EC® (fluensulfone) for guava crops and Verango Prime® (benzamid) for various crops. Both are categorized as Class III, posing environmental hazards. These chemicals, while versatile and effective against different *Meloidogyne* species, are recognized for their environmental risks (Ministério da Agricultura Pecuária e Abastecimento do Brazil 2023). A comparative study on nematicide efficacy (fluopyram, fluensulfone, fluazaindolizine, and oxamyl) demonstrated similar reductions in root infectivity for both *M. enterolobii* and *M. incognita*. Fluopyram effectively inhibited hatching in both species, while fluensulfone strongly inhibited root penetration. Nematicide application at label-recommended doses reduced gall formation on roots and decreased egg production in both species (Watson 2022). Alam et al (2023) analysed the effects of non-fumigant nematicides on *M. enterolobii* and showed that fluensulfone caused decreases of 71% in eggs and 86% in J2 juveniles, fluopyram did not significantly affected nematode reproduction and oxamyl suppressed J2 by 80%, but had a lesser impact on eggs (50%). Fluensulfone showed the greatest reduction in disease severity (64%), followed by oxamyl (54%) and fluopyram (48%). Except for fluensulfone, none of the non-fumigant nematicides significantly affected root or shoot biomass. Thus, the application of nematicides remains a more common short-term management strategy against RKN and although substitute chemical products have been developed, they have not been entirely successful in achieving hjgh levels of efficiency, especially towards *M. enterolobii* (Forghani and Hajihassani 2020).

These studies underscore the complex interactions between phytonematicides, plant growth, and *M. enterolobii* control. Non-fumigant nematicide development, driven by concerns about fumigant properties, has progressed, but environmental and human health risks must be considered in their use.

Biological control

By 2030, UN's Sustainable Development Goal 2 aims to promote sustainable agriculture, boost productivity, enhance climate resilience, and ensure food security for the expanding global population (ONU 2015).

Biocontrol, or biological control, involves using organisms to reduce specific pest populations, thereby diminishing their harmful impact. In the management of nematodes, biocontrol offers a sustainable approach, reducing reliance on synthetic chemicals and minimizing risks to human health and the ecosystem (Francisco et al. 2021). Such interest in harnessing microorganisms has grown due to their crucial role in INM, but the effectiveness of this strategy depends on factors like adaptability, nematode density, microorganism selection, rhizosphere performance, cooperation with microbiota, nutrient competition, and host plant protection from pathogens (Tariq et al. 2020). Integrating agriculture and livestock farming enhances soil properties, such as organic matter, cation exchange capacity, microbial activity, and structural integrity (Dias-Arieira et al. 2021). Organic soil amendments enhance soil quality by bolstering water retention, microbial diversity and biomass, aiding pest management. However, careful application is crucial to prevent excessive salt and phosphorus levels, detrimental to plant growth and water quality. Organic waste composting further benefits soil and plant vitality (Kanagaraj and Sundaravadivelu 2021; Tefu et al. 2022).

In biological control for managing plant pathogens, antagonism (antibiosis) and the induction of resistance are recognized strategies. In nematode biocontrol, fungi and bacteria, particularly *Bacillus* spp. and *Trichoderma* spp., play key roles as antagonistic agents. The Brazilian Phytosanitary Pesticides System database lists 64 biological products formulated for nematicidal activity, with 41 using *Bacillus* spp. as active ingredients (Ministério da Agricultura Pecuária e Abastecimento do Brazil 2023). This bacteria exhibits nematicidal potential through the synthesis of proteases, chitinases, antibiotics, crystalline proteins, and secondary metabolites, enhancing systemic plant resistance (Tapia-Vázquez et al. 2022).

The combined effects of phytonematicides Biocult and Nemafric-BL on cowpea growth and *M. enterolobii* population reduction was evaluated. Biocult enhanced plant growth and decreased nematode populations, while the combination showed no significant effects on nematode population densities. These findings suggest separate use for these phytonematicides in cowpea production (Pofu and Mashela 2022a). In'Congo'watermelon plants, natural phytonematicides (Nemarioc-AL and Nemafric-BL) and Velum (fluopyram) enhanced plant growth, yield, and fruit quality. All three products significantly reduced nematode eggs and juveniles in both roots and surrounding soil, indicating their effectiveness (Pofu and Mashela 2022b).

Fungal biological agents can reduce RKN populations, leading to decreased damage compared to untreated conditions (Peiris et al. 2020). *Trichoderma* spp. employ mycoparasitism, antibiosis, and resource competition to target *Meloidogyne* spp. eggs and juveniles. Some strains produce enzymes that degrade cell walls and release secondary metabolites inhibiting egg hatching and killing juveniles (Mukhopadhyay and Kumar 2020; Gouveia et al. 2022). Additionally, *Trichoderma* species act as plant growth-promoting microorganisms, enhancing photosynthetic efficiency, nutrient solubilization, and producing compounds beneficial to plant growth (Pofu and Mashela 2022b). For these arbuscular mycorrhizal fungi (AMF), which act as obligate symbionts of plant roots, the plant provides photosynthetic carbon, while they help roots absorb higher nutrients and promote root growth and structure. Additionally, they typically compete for nutrition and space with PPNs and induce systemic resistance in plants (Abd-Elgawad 2021).

Although a systematic analysis, carried out with 23 genera comprising 40 fungal species, indicated only *Trichoderma* as effective against *M. enterolobii* (Peiris et al. 2020), *Pochonia chlamydosporia* (var. *catenulata* and *chlamydosporia*) and *Purpureocillium lilacinum* strains negatively affected *M. enterolobii* populations in tomato and banana plants, but the intensity of the effects was dependent on the level of infestation (Silva et al. 2017). Also, when *Purpureocillium lilacinum* https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/purpureocilligical-sciences/purpureocillium-lilacinum strain PL251 was combined with *Bacillus amyloliquefaciens* https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/bacillus-amylo/20/20 https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/bacillus-amyloliquefaciens strains D747 (Ba) and these were simultaneously inoculated on cucumber roots there was an 84% reduction in the number of *M. enterolobii* eggs (Paula et al. 2024). So, rather than isolated fungi species, for some cases the association among fungi species and strains may be the proper way to apply this biological control. Another study demonstrated that two formulations (specific suspension and wettable powder) of *Metarhizium carneum*, a nematophagous fungus, decreased *M. enterolobii* population density by 78% and 66%, respectively, compared to the control. Additionally, the liquid formulation of *M. carneum* and *P. lilacinum* treatments inhibited nematode population density by 72% and 43%, respectively (López-Lima et al. 2023).

While the strategy is significant for crop protection and ecological equilibrium, introducing potent microorganisms requires caution to prevent disruptions in the delicate soil ecosystem.

Plant growth-promoting rhizobacteria enhance plant growth directly or indirectly by inhibiting pathogens, including nematodes. Predominant Gram-negative and Gram-positive bacteria contribute to plant well-being (Xiang et al. 2018). Also, research on the endophytic fungus *P. chlamydosporia* reveals positive effects on tomato growth beyond nematode control, influencing phytohormones, root phenolic compounds, and flavonoids (Gouveia et al. 2022). *Aspergillus tubingensis* GX3 fermentation produces nematicidal enzymes or substances harming *M. enterolobii* nematode eggs and juveniles (Sikandar et al. 2023a).

Certain plants produce natural compounds effective against nematodes, including volatile organic compounds (VOCs) like terpenoids, phenylpropanoids, benzenoids, fatty acid derivatives, and amino acid derivatives. Biofumigation with *Xanthosoma sagittifolium* controls *M. enterolobii* by reducing eggs and galls and this can be due the secondary compounds present in its composition, such as aliphatic ketones shown by GC–MS, but tests are yet necessary to prove this (Gomes et al. 2020).

Genetic resistance

A crucial strategy for enhancing the development of new disease-resistant cultivars involves selecting parent plants with high resistance to gall disease. Verssiani et al. (2023) found that *M. enterolobii* derived from cotton exhibited greater aggressiveness toward soybean cultivars compared to guava-derived races. Only the soybean'BRS 7180 IPRO', genetically developed for resistance against *M. incognita* and *M. javanica*, demonstrated moderate resistance among all 16 tested cultivars, stressing the complexity of the challenge in breeding genotypes resistant to *M. enterolobii*.

Ninety-one sweet potato (*Ipomoea batatas*) genotypes were evaluated for potential resistance to *M. enterolobii*. Only 19 displayed resistance (Schwarz et al. 2021). While nematodes could invade and thrive in resistant sweet potato cultivars, their egg production capacity was reduced compared to susceptible ones.'CIP BRS Nuti'and'Canadense'displayed resistance to *M. enterolobii* in greenhouse conditions, with reproduction factors of 0.14 and 0.04, respectively, after 90 days of nematode inoculation (Mello et al. 2022).

In 2010, Embrapa Semiárido in Brazil achieved a genetic improvement milestone by developing the BRS Guaraçá hybrid (Fig. 6) through crossbreeding of guava (*Psidium guajava*, Gua 116 PE) with araçá (*P. guineense*, ARA 138RR) (Souza et al. 2018). This cultivar, registered (#35,849) and protected (#20,180,185) by the Ministry of Agriculture, Livestock in Brazil (Flori and Deon 2022), demonstrates resistance to *M. enterolobii* and compatibility with guava trees (Simões et al. 2023). Seedling production is influenced by factors such as branch health, growth regulators, substrate selection, misting regimen, and cutting method. Tailoring the seedling production process is crucial for optimizing yield, especially in cultivars resulting from interspecific crosses like BRS Guaraçá (Castro and Ribeiro 2020; Santos 2020). Assessments of compatibility, productivity, and morphological variation revealed signs of incompatibility, but guava accessions grafted onto BRS

Fig. 6 Photographic records of *Psidium guajava* (Paluma) and BRS Guaraçá in the city of Petrolina, Pernambuco—Brazil: **a)** whole individual of Paluma attacked by *M. enterolobii*; **b)** emphasis on leaf chlorosis; **c and d)** presence of galls on the roots; **e)** the original BRS Guaraçá with 10 years of planting after crossing between *P. guajava* (susceptible to the nematode, mother) and *P. guineense* (resistant to the nematode, father), in the Embrapa Semiárido Bebedouro Field; **f)** aboveground part of an araçá tree using BRS-Guaraçá seedlings as rootstock; **g)** highlight of gall-free roots from a rootstock

Guaraçá produced healthy plants in the second harvest cycle (Lourenço et al. 2022).

The path to plant breeding is not always smooth, and often involves extensive crosses and field trials before selecting resistant genotypes, a process that can span decades before making resistant seedlings available for production. Also, limited molecular-level resistance information may render the whole operation vulnerable to various factors.

Innovative approaches for enhancing plant resistance against *M. enterolobii*

Enhancing plant identification based on desired traits is pivotal for farmers. Utilizing advanced selection methods and data analysis helps experts to pinpoint promising plants, expediting the development of high-quality varieties. While our understanding of molecular plant resistance to *M. enterolobii* remains incomplete, it guides improvement strategies.

In this direction, some metabolites can either promote or reduce infection by PPN. Deepening our understanding of chemical interactions between plant roots and PPN lays the groundwork for pesticide-free strategies in crop cultivation (Sikder and Vestergård 2020). Metabolic analysis of healthy, infected, diseased, and resistant plants, can unveil disruptions in signaling or output pathways crucial in plant-microorganism interactions. Gathering and associating data on the fields of metabolomics, proteomics, transcriptomics and genomics is essential for a more solid knowledge on plant diseases, pathogen nutrient acquisition, as well as plant immunity activation and adaptation to disease pressure (Castro-Moretti et al. 2020).

The diverse functions of these substances can illuminate patterns of plant defense development, considering them as components of metabolic networks shaped by the environment (Marciniak et al. 2019). In a recent study, both polar (tannins and hydrolyzable lignans) and nonpolar (terpenes) substances were regulated in *Psidium* spp. after an *M. enterolobii* infection. Terpenes, acting as inhibitors, enhance guava resistance by repelling or reducing oxidative stress during infection (Costa et al. 2023). Alkaloids, basic nitrogenous organic compounds, originating from amino acids like phenylalanine, lysine, and tryptophan, are of growing interest in the Solanaceae family. Steroid glycoalkaloids (GAs) found in various plants, including potatoes, black nightshade, and tomatoes, are some examples (Marciniak et al. 2019). Such identification of anti-nematode phytochemicals (ANPs) offers targets for crop improvement through genetic engineering. The ANPs can also serve as biomarkers for nematode resistance, aiding high-throughput metabolomics screening of breeding lines. Recent advancements in gene cloning for resistance, especially with genetically modified plants containing cloned resistance genes, correlate with ANPs (Desmedt et al. 2020).

The importance of identifying and integrating disease resistance (R) genes is also crucial for controlling nematode infections. Despite the variable genetics of nematode resistance, recent advancements in gene cloning have emerged (Jiang et al. 2023). Resistance mediated by *NtRk1* (Neurotrophic Receptor Tyrosine Kinase 1 gene) in tobacco plants against *M. incognita* involves early-stage expression changes. Overexpressing *NtRk1* elevates resistance, while RNAi of *NtRk1* in a resistant variety makes it susceptible. The *Mi-1* gene provides nematode resistance in tomatoes, but *Mi-9*, isolated from wild tomatoes, offers consistent resistance even at high temperatures, opposed to *Mi*−1. More relevant, the *Ma* and *RMja* genes from *Prunus cerasifera* were seen able to control both "the peach RKN," *M. floridensis* (Handoo et al. 2004), and *M. enterolobii* (Claverie et al. 2011; Duval et al. 2019).

CRISPR/Cas9 technology has proven effective in precisely altering crop genomes, perfecting breeding programs (Abd-Elgawad 2022). Genome editing using CRISPR/Cas9 alters specific DNA sequences, allowing large-scale efficient gene editing. Targeted changes in rice metallothionein-like protein 04 via CRISPR/Cas9 conferred resistance to rice RKN. Marker-Assisted Selection (MAS) has transformed plant breeding, employing markers to pinpoint desirable traits and streamline the breeding process. SNP (Single Nucleotide Polymorphisms) genotyping and genomic sequence analysis have led to the development of markers linked to nematode resistance loci in potatoes (Bali et al. 2022). Nematode resistance in cotton cultivars is inherited from specific varieties, with QTLs (Quantitative Trait Locus) on chromosomes 11 and 14 playing key roles. Effector genes from nematode esophageal glands are also promising targets for nematode control through Host-Induced RNAi (HD-RNAi), as also the essential collagen gene *Me-col-1*, which is vital for egg formation in root-knot nematodes (Pei et al. 2022).

Conclusions

In summary, the root-knot nematode *Meloidogyne enterolobii* represents a serious threat to crops on a global scale. Understanding the molecular interactions between this nematode and plants is essential for developing molecular control strategies and effective management. Omics approaches, which focus on the genes and proteins involved in *M. enterolobii* activities and plant resistance responses, play a crucial role in this advancement. Continued progresses in computational biology and bioinformatics analysis support these techniques, allowing for precise identification of elements related to *M. enterolobii* parasitism and plant responses.

Genome editing technologies offer a powerful tool for genetically improving plants by mapping relationships between genes and phenotypic traits. However, it is crucial to apply these methods with care to avoid unintended consequences, such as increased nematode virulence and impacts on crop productivity. Challenges arise, including the transfer of resistance to various diseases and the specificity of virulent nematodes to established techniques. Ultimately, *M. enterolobii* control should be addressed through integrated pest and crop management, ensuring food security and crop health. This becomes crucial in a challenging scenario with increasing agricultural demands.

From a biotechnological perspective, the development of biological inputs for *M. enterolobii* control is promising. Compared to conventional non-biological products, bioinputs offer advantages that extend beyond their direct effects. In the long term, this transition tends to favor the agriculture of the future, promoting sustainability and environmental preservation by reducing environmental impacts.

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Declarations

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