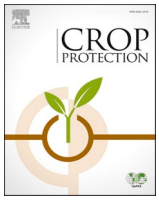
Crop Protection 190 (2025) 107082

Contents lists available at ScienceDirect

Crop Protection

journal homepage: www.elsevier.com/locate/cropro



Short communication

Comparative performance of biological formulations for the management of *Meloidogyne enterolobii* in chickpea (*Cicer arietinum*)

Dwillian Firmiano Cunha [a,*], Thávio Júnior Barbosa Pinto [a], Valdir Ribeiro Correia [b], Aldegundes Batista Miranda Júnior [c], Felipe Santos Rafael [c], Leandro Alves Santos [c], Érica Vicente dos Santos [a], Juvenil Enrique Cares [a], Leonardo Silva Boiteux [a,d], Jadir Borges Pinheiro [d]

[a] University of Brasilia (UnB), Institute of Biological Sciences, Department of Plant Pathology, Brasília, DF, 70910-900, Brazil
[b] Instituto Federal do Tocantins, Dianópolis, TO, 77.300-000, Brazil
[c] Centro Universitário ICESP, Brasília, DF, 71.961-540, Brazil
[d] Embrapa Vegetable Crops (Hortaliças), Brasília, DF, 70.359-970, Brazil

ARTICLE INFO

Keywords:
Biological control
Pulses
Guava root-knot nematode

ABSTRACT

Meloidogyne enterolobii can reduce yield and quality of chickpea. Thus far, no resistant cultivars have been reported. Hence, a study was carried out to evaluate the relative performance of biological products for the management of *M. enterolobii* on chickpea. Greenhouse experiments were conducted with ten treatments (five formulations of antagonistic fungi and bacteria applied either individually or in mixtures) and four controls (non-inoculated and inoculated chickpea and tomato plants). Each plant was inoculated with 4000 eggs and second-stage *M. enterolobii* juveniles (J2). Evaluation was done 60 days after inoculation for gall index, number of eggs per gram of roots, reproduction factor (RF), plant height, shoot, and root weight. None of the treatments fully suppressed infection. However, a subset of formulation mixtures displayed significant reduction in the levels of damage when compared to the untreated check. The treatments with best performance were [*Purpureocillium lilacinum* + *Trichoderma harzanium*] (57–74% reduction) and [*Pochonia chlamydosporia* + *P. lilacinum* + *Bacillus amyloliquefaciens* + *B. pumilus* + *B. subtilis*] (58–65% reduction), whereas [*P. chlamydosporia* + *P. lilacinum* + *T. harzanium*] and [*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis* + *T. harzanium*] displayed the lowest levels of suppression (0–42%). Higher plant height and fresh shoot weight were observed with [*P. chlamydosporia* + *P. lilacinum* + *B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*]. Hence, considering the low efficiency of the currently available management methods, the employment of these microbiological products might help to reduce the negative impacts of *M. enterolobii* in infested fields.

1. Introduction

Chickpea (*Cicer arietimum* L.) is an important crop worldwide. In Brazil, a gradual increase in the acreage farming of chickpea has been observed since this crop can serve as an alternative source income to the farmers (Avelar et al., 2018). Root-knot nematodes (RKNs) of the genus *Meloidogyne* are important constraints on chickpea production across the Indian subcontinent, the Mediterranean region, and the Americas, impacting both yield and quality (Castillo et al., 2008). *Meloidogyne incognita* (Kofoid and White, 1919); Chitwood, 1949, *M. javanica* (Treub, 1885); Chitwood, 1949, and *M. artiellia* (Franklin, 1961), as well as other RKNs are among the major soil-borne pathogens of chickpea worldwide (Kofoid and White, 1919; Castillo et al., 2008; Nascimento et al., 2016; El-Nagdi et al., 2019; Zwart et al., 2019). Recently, *M. enterolobii* Yang and Eisenback (1983) (guava race) (Carneiro et al., 2001) has been also reported as a major threat to chickpea, tomato, bell pepper and orchid pepper (Sikandar et al., 2023).

The genetic management of *M. enterolobii* is difficult under field conditions due to its wide host range, aggressiveness, and ability to parasitize host cultivars resistant to other RKNs (Carneiro et al., 2006; Gabriel et al., 2020; Sikandar et al., 2023; Pinto et al., 2023). For example, chickpea cultivars resistant to other *Meloidogyne* species

* Corresponding author.
E-mail address: cunha.dwillian@aluno.unb.br (D.F. Cunha).

https://doi.org/10.1016/j.cropro.2024.107082
Received 8 August 2024; Received in revised form 7 December 2024; Accepted 11 December 2024
Available online 13 December 2024

displayed susceptible reaction to *M. enterolobii* and no sources of resistance have been found thus far (Sharma and Fonseca, 2000; Ansari et al., 2004; Bittencourt and Silva, 2010; Nascimento et al., 2016; Bernardes Neto et al., 2019; Pinto et al., 2024).

The use of other eco-friendly management strategies is preferred since some chemical nematicides have been forbidden due to negative effects to human health and to the environment (Azlay et al., 2023). For all these reasons, microbial biocontrol is a promising alternative for managing RKNs (Sharma and Pandey, 2009). Effective agents against *M. enterolobii* include a wide array of bacteria, particularly *Bacillus* strains (Puttawong et al., 2024). *Bacillus* species produce antagonistic molecules and secondary metabolites beneficial for host plants (Ongena and Jacques, 2008; Liu et al., 2013; Liang et al., 2019; Maqsood et al., 2024). *Bacillus* species also produce Cry toxins (Li et al., 2008; Yu et al., 2015) and lytic enzymes (Padgham and Sikora, 2007; Köhl et al., 2019) that impact RKNs. Additionally, these bacteria enhance host plant resistance by increasing the production of volatile organic compounds (Ayaz et al., 2021) and defense gene expression (Tian et al., 2022).

Nematophagous fungi of the genus *Trichoderma* (Kruger and Bacchi, 1995) also suppress (RKNs (Sahebani and Hadavi, 2008; Martinez-Medina et al., 2016). These fast-growing fungi synthesize antibiotics and cell wall-degrading enzymes (Vinale et al., 2008), while *T. harzianum* Rifai, promotes plant growth, enhances the overall host resistance (Sahebani and Hadavi, 2008; Contreras-Cornejo et al., 2024). Additionally, this fungus can parasitize nematode eggs and induce nematode paralysis (Druzhinina et al., 2018; Hamrouni et al., 2021; You et al., 2022; Mardani et al., 2024).

Strains of *Purpureocillium lilacinum* Luangsa-ard, Houbraken, Hywel-Jones and Samson, are also effective microbial biocontrol agents against RKNs. This soil-borne fungus parasitizes nematode eggs, juveniles, and females (Aminuzzaman et al., 2013; Dahlin et al., 2019) and produces hydrolytic enzymes and secondary metabolites that degrade nematode eggshells, facilitating fungal establishment (Yang et al., 2015; Wang et al., 2016; Mukhtar et al., 2013) and lowered the overall RKN infestation (Kepenekci et al., 2018; Dahlin et al., 2019).

Chickpea cultivation has emerged as an economic option for the second crop ('safrinha') after soybean during the summer season in the Brazilian 'Cerrado' biome. Chickpea is a drought-tolerant species that thrives with minimal rainfall. However, the employment of chickpea after soybean poses risks to its sustainable production in this system due to the vulnerability of both crops to *M. enterolobii* (Pinheiro et al., 2021; Verssiani et al., 2023).

Hence, due to the challenges of controlling *M. enterolobii* under field conditions and the lack of tolerant cultivars, microbiological control methods offer promising alternatives. In the present study we evaluated the effectiveness of commercial formulations with antagonistic bacteria and fungi for managing *M. enterolobii* on chickpea under greenhouse conditions.

2. Materials and methods

The experiments were carried out under greenhouse conditions at the Nematology Laboratory at Embrapa Vegetable Crops (Hortaliças), Brasília–DF, Brazil, across two seasons, January to March/2023 (summer) and May to July/2023 (autumn). The average temperature in the first experiment was 27 °C, while in the second experiment the average temperature was 26 °C.

2.1. Plant accessions

The chickpea cultivar 'BRS Aleppo' was used in all experiments. This cultivar was reported as resistant to several *Meloidogyne* species (Santos et al., 2021), but not to *M. enterolobii* (Pinto et al., 2024). As controls were employed the tomato (*Solanum lycopersicum* L.) cultivars 'Rutgers' (susceptible) and 'Nemadoro', carrying the *Mi*-1.2 resistant gene that confers resistance to 13 *Meloidogyne* species but not *M. enterolobii* (Pinheiro et al., 2020; Gabriel et al., 2020). These tomato cultivars were included in the experiments to estimate inoculum viability and optimum growth conditions for the nematode.

2.2. Inoculum

Meloidogyne enterolobii inoculum was obtained from a pure culture multiplied by periodic subculturing on plants of the tomato cultivar 'Santa Cruz' (25–30 °C), being previously identified as M2 (RM 0.7–0.9) using esterase and SCAR PCR phenotyping (Carneiro and Almeida, 2001; Tigano et al., 2010). For the experimental trials, nematode eggs, and occasional second-stage juveniles (J2), which were extracted from infected roots following the methodology of Boneti and Ferraz (1981). This suspension was quantified under a light microscope (Nikon Eclipse 80i model) using a nematode counting slide (Peter's slides).

2.3. Experimental design

The experiments were conducted in a completely randomized design with eight treatments and six replicates (six formulations containing antagonistic fungi and bacteria plus two controls). Tomato 'Rutgers' (susceptible control) and Tomato 'Nemadoro' (*Mi*-1.2 gene-carrying control) were used to assess the viability of the inoculum of *M. enterolobii* (Table 3). Each plant per pot was considered as an experimental unit.

2.4. Obtaining the biological agents, formulations, and preparation of formulation mixtures

All microbiological agents were provided by the manufacturers (Table 1). The six biological formulations evaluated in the present study were as follows: [*B. subtilis* + *B. licheniformis,* Water-Soluble Powder (WS), 200 g/ha]; [*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*, Concentrated Suspension (SC), 250 mL/ha]; [*T. harzanium*, Wettable Powder (WP), 250 g/ha]; [*P. chlamydosporia* + *P. lilacinum*, Dispersible Granules (WG), 50 g/ha] and [*P. lilacinum,* Wettable Powder (WP), 600 g/ha]. The dosage and preparation of the biological formulation mixtures were used as recommended by the manufacturer (Table 2). Based on the mixtures, the ten treatments were organized as follows: **(*i*)** non-inoculated control, **(*ii*)** Inoculated control, **(*iii*)** plants treated with the mixture [*B. subtilis* + *B. licheniformis*], **(*iv*)** plants treated with the mixture [*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis* + *T. harzianum*], **(*v*)** plants treated with the mixture [*P. chlamydosporia* + *P. lilacinum* + *T. harzianum*], **(*vi*)** plants treated with the mixture [*P. chlamydosporia* + *P. lilacinum* + *B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*], **(*vii*)** plants treated with the mixture [*P. lilacinum* + *T. harzianum*], **(*viii*)** plants treated only with *T. harzianum*, **(*ix*)** tomato 'Rutgers', and **(*x*)** tomato 'Nemadoro' (Table 3).

Table 1
The microorganisms used in the experiments and concentrations in terms of colony forming units (CFU) per gram or liter of the product.

Microorganisms	CFU (per g or L)
Bacillus subtilis lineage FMCH002 (DSM32155)	Minimum of 1.0×10^{11} per g
B. licheniformis lineage FMCH001 (DSM32154)	Minimum of 1.0×10^{11} per g
B. amyloliquefaciens strain D-747	Minimum of 1.0×10^{10} per mL
B. pumilus isolate CNPSo 3203	4.6 x 10^{11} viable endospores/L of product
Trichoderma harzianum isolate IBLF 006	1.0×10^{10} per g of product
Paecilomyces lilacinus strain URM 7661	Minimum of 1.0×10^{7} per g
P. lilacinus isolate Uel Pae 10	7.5×10^{9} CFU per g of commercial product
Pochonia chlamydosporia strain URM 8121	Minimum of 1.0×10^{7} CFU per g

Table 2
The dosage and preparation of the mixtures of microbiological formulations used in the two experiments employing chickpea 'BRS Aleppo' plants with a population of *Meloidogyne enterolobii*.

Mixtures of microbiological formulations	Preparation
[*Bacillus subtilis* + *B. licheniformis*]	0.10 g diluted in 200 mL Milli-Q water
[*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*] + [*Trichoderma harzianum*]	3 mL [*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*] + 1 mL [*T. harzianum*], diluted in 200 mL Milli-Q water
[*Paecilomyces lilacinum* + *Pochonia chlamydosporia*] + [*T. harzianum*]	2 mL [*Paecilomyces lilacinum* + *P. chlamydosporia*] + 1 mL [*T. harzianum*], diluted in 200 mL Milli-Q water
[*P. lilacinus* + *P. chlamydosporia*] + [*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*]	2 mL [*P. lilacinus* + *P. chlamydosporia*] + 3 mL [*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*], diluted in 200 mL Milli-Q water
P. lilacinus + *T. harzianum*	2 mL [*P. lilacinus*] + 1 mL [*T. harzianum*], diluted in 200 mL Milli-Q water
T. harzianum	1 mL [*T. harzianum*] diluted in 200 mL Milli-Q water

Table 3
Biological formulations applied to the root systems of chickpea 'BRS Aleppo' plants, which were simultaneously inoculated with a population of *Meloidogyne enterolobii*.

Treatments	Dosage per hectare
Non-inoculated control	–
Inoculated control	–
Trichoderma harzianum	250 g
[*Bacillus subtilis* + *B. licheniformis*]	200 g
[*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*] + [*T. harzianum*]	250 mL; 250 g
[*Pochonia chlamydosporia* + *Purpureocillium lilacinum*] + [*T. harzianum*]	50g; 250 g
[*P. chlamydosporia* + *P. lilacinum*] +[*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*]	50g; 250 mL
[*P. lilacinum*] + [*T. harzianum*]	600 g; 250 g
Tomato 'Rutgers'[a] (susceptible control) inoculated	–
Tomato 'Nemadoro'[b] (*Mi*-1.2 gene-carrying control) inoculated	–

[a,b] Tomato plants used as standards for viability and quality of *M. enterolobii* inoculum.

2.5. Efficacy of the biological formulations against M. enterolobii

Chickpea plants (25-day-old seedlings) were grown in 2000 cm^3 plastic pots with a diameter of 12 cm, filled with sterilized sand and soil (75% sand, 5% silt, and 20% clay) and commercial substrate (Bioplant®) were inoculated with 4000 eggs and occasional J2 of *M. enterolobii* by placing 10 mL of the suspension into two holes around the stem base. Simultaneously, plants were treated with the formulations on the soil surface as a soil drench and repeated 30 days later, following the manufacturer's recommendations to achieve satisfactory control levels. Plants were kept under greenhouse conditions and evaluated after 60 days.

2.6. Sample processing and statistical analyses

Sixty (60) days after inoculation the chickpea plants were carefully removed from the soil, and their root systems were washed with running tap water, dried with a paper towel, and stained with floxin B (15 mg/L water) (Daykin and Hussey, 1985) to facilitate the visualization and quantification of the external egg masses. The following parameters were then determined: Gall Index (**GI**) and Egg Mass Index (**EMI**) (Taylor and Sasser, 1978), the number of eggs and J2 per gram of root (NGR) was calculated as the final population divided by the fresh root weight (g). The reproduction factor (RF) was then determined as the ratio of the final population to the initial population (Oostenbrink, 1966). Infected roots were processed in a blender with sodium hypochlorite, following the techniques of Hussey and Barker (1973), modified by Boneti and Ferraz (1981). After counting the nematodes (eggs + J2s already hatched) under a light microscope (Nikon Eclipse 80i model), the total number of nematodes extracted from the root system was divided by the fresh root weight, which was recorded prior to nematode extraction. This calculation provided the number of nematodes per gram of fresh root. Based on these values, the RF for each treatment was calculated.

The data were subjected to Scott-Knott analysis ($p < 0.05$) using the Agricolae package (Mendiburu, 2015) in the R 1.2-3 statistical program. For the statistical analyses, including the normality test, analysis of variance (ANOVA), and the Scott-Knott test ($p < 0.05$), the data were transformed using the $\sqrt{x} + 0.5$ transformation. The results were back-transformed to present the original values.

3. Results

The results showed high RF values for tomato 'Rutgers' (susceptible control) (RF = 25 and 39, respectively for experiments 1 and 2), indicating adequate inoculum viability and suitable growth conditions for the nematode (Table 4). In addition, the nematode reproduced well on

Table 4
Reaction to *Meloidogyne enterolobii* of chickpea 'BRS Aleppo' in two experiments after treatment with distinct formulations containing antagonistic fungi and bacteria under greenhouse conditions 60 days after inoculation.

Treatments	GI[a]		NGR [b]		RF[c]	
	Exp. 1[f]	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Inoculated control	5.0	3.5	9579 a	1826 b	16.64 a	6.88 a
Bacillus subtilis + *B. licheniformis*	4.0	4.3	4549 b	1529 c	7.53 b	3.75 b
B. amyloliquefaciens + *B. pumilus* + *B. subtilis* + *Trichoderma harzianum*	4.7	3.7	9946 a	2449 b	11.19 a	6.04 a
Pochonia chlamydosporia + *Purpureocillium lilacinum* + *T. harzianum*	3.7	3.6	15692 a	13886 a	9.61 a	7.55 a
P. chlamydosporia + *P. lilacinum* + *B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*	4.0	2.5	3055 b	732 c	5.68 b	2.88 b
P. lilacinum + *T. harzianum*	2.8	3.2	2491 b	1056 c	4.21 b	2.95 b
T. harzianum	3.7	3.3	11016 a	3499 b	12.03 a	5.42 a
Average	4.0	3.4	8047	3568	9.55	5.06
Tomato 'Rutgers' [d]	4.8	4.0	19524	9715	39.77	25.41
Tomato 'Nemadoro' [d]	4.3	3.7	11485	6161	23.85	16.94
CV (%) [e]	9.2	12.9	34.1	31.7	29.4	34.6

The data were transformed as $\sqrt{x}+0.5$ for statistical analysis. Original data set are shown. Means ($n = 6$) followed by different letters within a column are significantly different according to Scott-Knott's test ($P < 0.05$). The F value was 6.26 for **Experiment 1**, with a P value less than 0.001; in **Experiment 2**, the F value was 2.21, and the P value was 0.046.

[a] GI (gall index): scale 1 to 5 according to Taylor and Sasser (1978).

[b] NGR: Nematodes per Gram of Root = final population/fresh weight of root (g).

[c] RF: nematode reproduction factor = final population/4000 eggs of *M. enterolobii*.

[d] Tomato 'Rutgers' is a standard susceptible control; tomato 'Nemadoro' is a *Mi*-1.2 gene-carrying control cultivar.

[e] CV = coefficient of variation.

[f] Experiments (Exp) 1 and 2.

tomato 'Nemadoro' (RF = 16 and 23), which is resistant to other *Meloidogyne* species due to the presence of the *Mi*-1.2 gene (Gabriel et al., 2020). These results indicated the aggressiveness of this RKN species to standard plant hosts. The variations observed across biological replicates of the two experiments may be due to differences in temperatures (summer and autumn assays).

The comparative performance of the microbiological formulations on controlling *M. enterolobii* infection in chickpea is summarized in Table 4. None of the treatments effectively controlled this *M. enterolobii* population. However, two formulations displayed superior performance, being able to significantly reduce the RKN population in comparison with the inoculated controls. These two formulations were [*P. lilacinum* + *T. harzianum*] (RF = 2.95 and 4.21, respectively), a reduction of nematode ca. 57–75% and [*P. chlamydosporia* + *P. lilacinum* + *B. amyloliquefaciens* + *B. pumilus* + *B. subtillis*] (RF = 2.88–5.68, reduction of 58–65%) (Table 4). Further, if considering the susceptible tomato control 'Rutgers', reduction in nematode population ranged from 88.4 to 89.4% and 85.7–88.7%, respectively for these two treatments. The treatment [*B. subtillis* + *B. licheniformis*] (RF = 3.75–7.5, reduction of 45–55%) was classified as intermediate, while the treatments [*P. chlamydosporia* + *P. lilacinum* + *T. harzianum*] (RF = 7.5–9.6, reduction of 0–42%), *T. harzianum* (RF = 5.4–12, reduction of 21–27%), and [*B. amyloliquefaciens* + *B. pumilus* + *B. subtilis* + *T. harzianum*] (RF = 6–11, reduction of 12–33%) displayed the lowest levels of reduction of the RKN population. Overall, most of the treatments did not result in improved plant growth parameters, except the treatment [*P. chlomydosporia* + *P. lilacinum* + *B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*], which showed higher plant height and shoot weight as compared to the inoculated control (Table 5) (Supplementary Figs. 1 and 2).

Table 5
Plant height (cm), fresh aboveground weight, and root weight (g) of chickpea 'BRS Aleppo' plants treated with formulations containing antagonistic fungi and bacteria under greenhouse conditions 60 days after inoculation with *Meloidogyne enterolobii*.

Treatments	Plant height (cm)		Fresh weight aboveground (g)		Fresh root weight (g)	
	Exp. 1[3]	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Non-inoculated control	70.50[a] a	58.83 a	34.33 a	30.50 a	27.4 a	28.67 a
Inoculated control	45.33 c	54.50 b	16.33 b	21.83 c	8.75 b	14.92 b
Bacillus subtilis + *B. licheniformis*	42.33 c	43.67 c	13.25 c	12.33 d	7.17 b	9.08 d
B. amyloliquefaciens + *B. pumilus* + *B. subtilis* + *Trichoderma harzianum*	38.50 d	51.50 b	12.75 c	15.58 d	6.58 b	10.58 c
Pochonia chlomydosporia + *Purpureocillium lilacinus* + *T. harzianum*	34.67 d	40.17 d	8.25 d	7.67 e	2.58 c	3.75 e
P. chlomydosporia + *P. lilacinus* + *B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*	50.67 b	59.50 a	16.50 b	25.75 b	8.50 b	15.92 b
P. lilacinum + *T. harzianum*	38.33 d	46.33 c	9.75 d	13.58 d	5.75 b	11.17 c
T. harzianum	36.00 d	40.83 d	9.67 d	8.92 e	4.25 c	6.08 e
Average	44.54	49.42	15.10	17.02	8.88	12.52
CV (%) [b]	11.2	6.4	18.9	18.4	20.1	19.2

[a] Means (n = 6) followed by different letters within a column are significantly different according to Scott-Knott's test ($P < 0.05$).
[b] CV = coefficient of variation. [3]Experiments 1 and 2.

4. Discussion

Although none of the treatments completely prevented nematode reproduction, the formulation mixtures containing [*P. lilacinum* + *T. harzianum*] and [*P. chlamydosporia* + *P. lilacinum* + *B. amyloliquefaciens* + *B. pumilus* + *B. subtilis*] significantly decreased the population of *M. enterolobii* by 57%–75% in the experiments. These results are in agreement with the pioneering findings of Silva et al. (2017), which highlighted the challenges of controlling *M. enterolobii* in soils with high infestation levels.

The results indicated that all treatments reduced the FR in Experiment 1 in comparison with the to Experiment 2. However, the performance patterns across treatments were similar, consistently reducing *M. enterolobii* populations. A possible explanation for this difference across bioassays is the more favorable climatic conditions for nematode development, egg hatching, and soil movement in summer, when soil temperatures are higher (Leitão et al., 2021) and diffusion of root exudates is greater (Neumann and Römheld, 2000). Although the chickpea cultivar 'BRS Allepo' is susceptible to *M. enterolobii*, it exhibits resistance to other *Meloidogyne* species (Santos et al., 2021). In this context, employing cultivars with broad-spectrum resistance to different RKNs, in conjunction with effective biological formulations against *M. enterolobii*, could contribute to reducing population levels to economic thresholds.

The combination of *P. lilacinum* and *T. harzianum* in our study resulted in a 75% reduction in the reproduction of *M. enterolobii*, demonstrating greater efficiency in managing this nematode compared to the use of *T. harzianum* alone. The synergy between these fungi reduced the infectivity and reproduction of the nematode, likely due to the production of hydrolytic enzymes, volatile organic compounds, secondary metabolites, and egg parasitism (Khan et al., 2006; Khan et al., 2021; Sahebani and Hadavi, 2008; Rajendran et al., 2024). Although we did not directly assess these parameters, the strong antagonistic capacity of both fungi is well-documented (Pocurull et al., 2020; Yan et al., 2021; Paula et al., 2024; Rajendran et al., 2024).

Similarly, the mixture of *P. chlamydosporia, P. lilacinum*, *B. amyloliquefaciens*, *B. pumilus*, and *B. subtilis* reduced nematode reproduction by 66% and increased the height and biomass of the plant canopy, indicating synergy and enhancing the effect of the biological formulation. In some cases, the combination of different organisms can mutually benefit both parties, as the activity of mycorrhizae can be enhanced by mycorrhizal auxiliary bacteria (MAB), which are themselves influenced by mycorrhizal fungi (Ahmadzadeh, 2013). Previous studies indicated high compatibility between *P. chlamydosporia* and *Bacillus subtilis*, as well as moderate compatibility with *P. lilacinus in vitro* (Muthulakshmi et al., 2017), confirmed by Jacobs and Crump (2003). In the study by Sohrabi et al. (2020), the combined application of *Glomus mosseae*, *B. subtilis*, and *T. harzianum* reduced J2 populations of *M. javanica* in the soil by 36%. Recently, it was observed that the strains *B. amyloliquefaciens* D747 and *P. lilacinum* PL251, when applied separately, were ineffective in reducing *M. enterolobii* in cucumber. However, when combined, they exhibited a synergistic effect, resulting in a significant 84% reduction in the number of eggs in the roots (Paula et al., 2024). One possible explanation for this efficacy is the ability of these biological agents to produce chitinases that degrade the eggshells, disrupting development and metabolism of the nematodes (Sahebani and Hadavi, 2008; Migunova and Sasanelli, 2021).

The results obtained herein are encouraging, particularly considering the challenges in finding effective methods for managing *M. enterolobii* in the field. This strategy could represent an effective option for the integrated management of this nematode in chickpea cultivation. However, the isolated use of biological control agents tends to be less effective than using microbial consortia (Pires et al., 2022). In our study, the mixtures of microorganisms yielded superior results, likely due to synergistic effects among them. This synergy supports the hypothesis that combining antagonists may be a more effective strategy

for nematode management, integrating different mechanisms of action and nematicidal substances (Stirling and West, 1991; Ferraz et al., 2010; Baron et al., 2020).

Despite the promising potential of these microorganisms for managing plant-parasitic nematodes, their efficacy under field conditions, their long-lasting effects, and environmental adaptation will pose challenges when implementing biological control in the field (Pires et al., 2022). In summary, considering the challenges in finding and deploying efficient control methods for *M. enterolobii*, our results are promising and could be implemented alongside other management strategies as integrated control methods in chickpea production.

CRediT authorship contribution statement

Dwillian Firmiano Cunha: Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Thávio Júnior Barbosa Pinto:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Valdir Ribeiro Correia:** Writing – review & editing, Methodology, Data curation. **Aldegundes Batista Miranda Júnior:** Investigation, Formal analysis. **Felipe Santos Rafael:** Investigation, Formal analysis. **Leandro Alves Santos:** Investigation, Formal analysis. **Érica Vicente dos Santos:** Investigation, Formal analysis. **Juvenil Enrique Cares:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Leonardo Silva Boiteux:** Writing – review & editing, Methodology, Data curation. **Jadir Borges Pinheiro:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

All authors are grateful for the financial support provided by grants from Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Apoio à Pesquisa do Distrito Federal (FAP-DF). This study was also financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001. Dwillian Firmiano Cunha is grateful to the Dean of the Graduate Program of the University of Brasilia (UnB) for financial support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2024.107082.

Data availability

Data will be made available on request.

References

Ahmadzadeh, M., 2013. Biological control of plant diseases (plant probiotic bacteria). Tehran University Press and Publishing, Tehran.

Aminuzzaman, F.M., Xie, H.Y., Duan, W.J., Sun, B.D., Liu, X.Z., 2013. Isolation of nematophagous fungi from eggs and females of *Meloidogyne* spp. and evaluation of their biological control potential. Biocontrol Sci. Technol. 23, 170–182. https://doi.org/10.1080/09583157.2012.745484.

Ansari, M.A., Patel, B.A., Mhase, N.L., Patel, D.J., Douaik, A., harma, S.B., 2004. Tolerance of chickpea (*Cicer arietinum* L.) lines to root-knot nematode. Meloidogyne javanica (Treub) Chitwood. Genet. Resources Crop Evol. 51, 449–453. https://doi.org/10.1023/B:GRES.0000023460.26690.23.

Avelar, R.I.S., Costa, C.A., Silva, F.R., Oliveira, N.L.C., Nascimento, W.M., 2018. Yield of chickpeas sown at different times. Rev. Caatinga 31, 900–906. https://doi.org/10.1590/1983-21252018v31n412rc.

Ayaz, M., Ali, Q., Farzand, A., Khan, A.R., Ling, H., Gao, X., 2021. Nematicidal volatiles from *Bacillus atrophaeus* GBSC56 promote growth and stimulate induced systemic resistance in tomato against *Meloidogyne incognita*. Int. J. Mol. Sci. 22, 5049. https://doi.org/10.3390/ijms22095049.

Azlay, L., El Boukhari, M.E.M., Mayad, E.H., Barakate, M., 2023. Biological management of root-knot nematodes (*Meloidogyne* spp.): a review. Organic Agriculture 13, 99–117. https://doi.org/10.1007/s13165-022-00417-y.

Baron, N.C., de Souza Pollo, A., Rigobelo, E.C., 2020. *Purpureocillium lilacinum* and *Metarhizium marquandii* as plant growth-promoting fungi. PeerJ 8, e9005. https://doi.org/10.7717/peerj.9005.

Bernardes Neto, J.F., Pinheiro, J.B., Silva, G.O., Biscaia, D., Macedo, A.G., Silva, P.P., Nascimento, W.M., 2019. Reação de genótipos de grão-de-bico aos nematoides-das galhas *Meloidogyne incognita* raça 1 e *Meloidogyne enterolobii*. Rev. Agrária. 2, 63–70. https://doi.org/10.32406/v2n42019/63-70/agrariacad.

Bittencourt, N.V., Silva, G.S., 2010. Reação de genótipos de fava a *Meloidogyne incognita* e *M. enterolobii*. Nematol. Bras. 34, 184–186.

Boneti, J.I.S., Ferraz, S., 1981. Modificações no método de Hussey & Barker para extração de ovos de *Meloidogyne exigua* em raízes de cafeeiro. Fitopatol. Bras. 6, 533.

Carneiro, R.M.D.G., Almeida, M.R.A., 2001. Técnica de eletroforese usada no estudo de enzimas dos nematoides de galhas para identificação de espécie. Nematol. Bras. 25, 35–44.

Carneiro, R.M.D.G., Moreira, W.A., Almeida, M.R.A., Gomes, A.C.M.M., 2001. Primeiro Registro de *Meloidogyne mayaguensis* em Goiabeira no Brasil. Nematol. Brasiliana 25, 223–228.

Carneiro, R.M.D.G., Almeida, R.M.A., Braga, R.S., Almeida, C.A., Gioria, R., 2006. Primeiro registro de *Meloidogyne mayaguensis* parasitando plantas de tomate e pimentão resistentes à Meloidoginose no Estado de São Paulo. Nematol. Bras. 30, 81–86.

Castillo, P., Navas-Cortés, J.A., Landa, B.B., Jiménez-Díaz, R.M., Vovlas, N., 2008. Plant-parasitic nematodes attacking chickpea and their *in planta* interactions with rhizobia and phytopathogenic fungi. Plant Dis. 92, 840–853.

Chitwood, B.G., 1949. A revision of the genus *Meloidogyne* Goeldi, 1887. Proc. Helm. Soc. Wash. 16, 90–104.

Contreras-Cornejo, H.A., Schmoll, M., Esquivel-Ayala, B.A., González-Esquivel, C.E., Rocha-Ramírez, V., Larsen, J., 2024. Abiotic plant stress mitigation by *Trichoderma* species. Soil Eco. Letters. 6, 240240. https://doi.org/10.1007/s42832-024-0240-8.

Dahlin, P., Eder, R., Consoli, E., Krauss, J., Kiewnick, S., 2019. Integrated control of *Meloidogyne incognita* in tomatoes using flopyram and *Purpureocillium lilacinum* satrin 251. Crop Protect. 124, 104874. https://doi.org/10.1016/j.cropro.2019.104874.

Daykin, M.E., Hussey, R.S., 1985. Chapter on staining and histopathological techniques in Nematology. Advance Treatise on Meloidogine 2, 39–46.

Druzhinina, I.S., Chenthamara, K., Zhang, J., Atanasova, L., Yang, D., Miao, Y., Kubicek, C.P., 2018. Massive lateral transfer of genes encoding plant cell wall-degrading enzymes to the mycoparasitic fungus *Trichoderma* from its plant-associated hosts. PLoS Genet. 14, e1007322. https://doi.org/10.1371/journal.pgen.1007322.

El-Nagdi, W., Youssef, M., El-Khair, H., Abd-Elgawad, M.M.M., 2019. Effect of certain organic amendments and *Trichoderma* species on the root-knot nematode, *Meloidogyne incognita*, infecting pea (*Pisum sativum* L.) plants. Egyp. J. Biol. Pest Cont. 29, 1–9. https://doi.org/10.1186/s41938-019-0182-0.

Ferraz, S., Freitas, L.G., Lopes, E.A., Dias-Arieira, C.R., 2010. Manejo sustentável de fitonematóides, 1. Editora UFV, Viçosa, p. 304.

Franklin, M.T., 1961. A British Root-knot Nematode, *Meloidogyne artiellia* n. sp. Journal of Helminthology 35, 85–92.

Gabriel, M., Kulczynski, S.M., Muniz, M.F., Boiteux, L.S., Carneiro, R.M., 2020. Reaction of a heterozygous tomato hybrid bearing the *Mi*-1.2 gene to 15 *Meloidogyne* species. Plant Pathol. 69, 944–952. https://doi.org/10.1111/ppa.13179.

Hamrouni, R., Dupuy, N., Molinet, J., Roussos, S., 2021. *Trichoderma* species: novel metabolites active for industry and biocontrol of mycotoxigenic fungi. In: Mycotoxins in Food and Beverages, first ed. Boca Raton-FL, United States, pp. 1–25.

Hussey, R.S., Barker, K.R., 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. Plant Dis. Rep. 57, 102–1028.

Jacobs, H., Crump, D.H., 2003. Interactions between nematophagous fungi and consequences for their potential as biological agents for the control of potato cyst nematodes. Mycol. Res. 107, 47–56.

Khan, A., Mfarrej, M.F.B., Tariq, M., Asif, M., Nadeem, H., Siddiqui, M.A., Hashem, M., Alamri, S., Ahmad, F., 2021. Supplementing *Pochonia chlamydosporia* with botanicals for management of *Meloidogyne incognita* infesting chickpea. Acta Agric. Scand. Sect. B Soil Plant Sci 72, 164–175. https://doi.org/10.1080/09064710.2021.2003853.

Kepenekci, I., Hazir, S., Oksal, E., Lewis, E.E., 2018. Application methods of *Steinernema feltiae, Xenorhabdus bovienii* and *Purpureocillium lilacinum* to control root-knot nematodes in greenhouse tomato systems. Crop Protect. 108, 31–38. https://doi.org/10.1016/j.cropro.2018.02.009.

Khan, A., Williams, K.L., Nevalainen, H.K., 2006. Control of plant-parasitic nematodes by *Paecilomyces lilacinus* and *Monacrosporium lysipagum* in pot trials. Biocontrol 51, 643–658. https://doi.org/10.1007/s10526-005-4241-y.

Kofoid, C.A., White, A.W., 1919. A new nematode infection of man. Journal of the American Medical Association 72, 567–569.

Köhl, J., Kolnaar, R., Ravensberg, W.J., 2019. Mode of action of microbial biological control agents against plant diseases: relevance beyond efficacy. Front. Plant Sci. 10, 845. https://doi.org/10.3389/fpls.2019.00845.

Kruger, T.L., Bacchi, L.M.A., 1995. Fungos. In: Filho, A.B., Kimati, H., Amorim, L., Rezende, J.A.M., Camargo, L.E.A. (Eds.), Manual de Fitopatologia, pp. 46–95. São Paulo, Agronômica Ceres.

Leitão, D.A., Pedrosa, E.M., Dickson, D.W., Oliveira, A.K.S., Rolim, M.M., 2021. Temperature: a driving factor for migration toward different hosts. J. Nematol. 53, 1–10. https://doi.org/10.21307/jofnem-2021-074.

Li, X.Q., Tan, A., Voegtline, M., Bekele, S., Chen, C.S., Aroian, R.V., 2008. Expression of Cry5B protein from *Bacillus thuringiensis* in plant roots confers resistance to root-knot nematode. Biol. Control 47, 97–102. https://doi.org/10.1016/j.biocontrol.2008.06.007.

Liang, L.M., Zou, C.G., Xu, J., Zhang, K.Q., 2019. Signal pathways involved in microbe–nematode interactions provide new insights into the biocontrol of plant-parasitic nematodes. Philosophical Trans. Royal Soc. B. 374, 20180317. https://doi.org/10.1098/rstb.2018.0317.

Liu, Z., Budiharjo, A., Wang, P., Shi, H., Fang, J., Borriss, R., Zhang, K., Huang, X., 2013. The highly modified microcin peptide plantazolicin is associated with nematicidal activity of *Bacillus amyloliquefaciens* FZB42. Appl. Microbiol. Biotechnol. 97, 10081–10090. https://doi.org/10.1007/s00253-013-5247-5.

Maqsood, A., Aslam, M.N., Khaliq, H., Shakeel, M.T., Wu, H., Fahad, S., 2024. Endophytic *Bacillus* spp. mediated plant growth promotion of tomato seedlings and suppression of *Meloidogyne incognita* and *Fusarium oxysporum* disease complex. J. Plant Growth Regul. 1–16. https://doi.org/10.1007/s00344-024-11279-x.

Mardani, S., Nasr-Esfahani, M., Olia, M., Molahosseini, H., Khankahdani, H.H., 2024. Efficacy of nematicides, Tricuran-P (*Trichoderma harzianum* T-22) and chicken manure on cucumber root-knot nematode populations, plant growth and soil enzyme activities. J. Plant Dis. Prot. 1–12. https://doi.org/10.1007/s41348-024-00957-3.

Martinez-Medina, A., Pozo, M.J., Cammue, B.P., Vos, C.M., 2016. Belowground defence strategies in plants: the plant–*Trichoderma* dialogue. Belowground defence strategies in plants 301–327. https://doi.org/10.1007/978-3-319-42319-7_13.

Mendiburu, F., 2015. Agricolae: Statistical Procedures for Agricultural Research. R Package Version 1.2-3 [Online]. http://CRAN.R-project.org/package=agricolae.

Migunova, V.D., Sasanelli, N., 2021. Bacteria as biocontrol tool against phytoparasitic nematodes. Plants 10, 389.

Mukhtar, T., Arshad Hussain, M., Zameer kayani, M., 2013. Biocontrol potential of *Pasteuria penetrans, Pochonia chlamydosporia, Paecilomyces lilacinus* and *Trichoderma harzianum* against *Meloidogyne incognita* in okra. Phytopathol. Mediterr. 66–76.

Muthulakshmi, M., Anita, B., Subramanian, S., 2017. Studies on compatibility of egg parasitic fungi with other biocontrol agents and carbofuran under in vitro. Journal of Entomology and Zoology Studies 5, 844–846.

Nascimento, W.M., Silva, P., Artiaga, O.P., Suinaga, F.A., 2016. Grão-de-bico. In: Nascimento, W.M. (Ed.), Hortaliças Leguminosas. Embrapa Hortaliças, Brasília, pp. 89–118.

Neumann, G., Römheld, V., 2000. The release of root exudates as affected by the plant's physiological status. The Rhizosphere: Biochemistry and organic substances at the soil-plant interface 41–93.

Ongena, M., Jacques, P., 2008. *Bacillus* lipopeptides: versatile weapons for plant disease biocontrol. Trends Microbiol. 16, 115–125. https://doi.org/10.1016/j.tim.2007.12.009.

Oostenbrink, M., 1966. Major characteristic of the relation between nematodes and plants. Mededlingen voor Landlb Hoogeschool Wageningen 66, 3–46.

Padgham, J.L., Sikora, R.A., 2007. Biological control potential and modes of action of *Bacillus megaterium* against *Meloidogyne graminicola* on rice. Crop Protect. 26, 971–977. https://doi.org/10.1016/j.cropro.2006.09.004.

Paula, L.L., Campos, V.P., Terra, W.C., Brum, D., Jacobs, D.C., Bui, H.X., Desaeger, J., 2024. The combination of *Bacillus amyloliquefaciens* and *Purpureocillium lilacinum* in the control of *Meloidogyne enterolobii*. Biol. Control 189, 105438. https://doi.org/10.1016/j.biocontrol.2023.105438.

Pinheiro, J.B., Silva, G.O., Macedo, A.G., Biscaia, D., Melo, R.A.C., 2020. Evaluation of Sources of Resistance to *Meloidogyne Enterolobii* in *Solanum Stramonifolium* and *S. Scuticum* as Potential Rootstocks for Cultivated Solanaceae, 50. Nematropica, pp. 144–150.

Pinheiro, J.B., Silva, G.O., Macedo, A.G., Jesus, J.G., Raulino, L., Magalhães, C.C., Biscaia, D., Melo, R.A.C., Silva, P.P., Nascimento, W.M., 2021. Population dynamics of the nematodes *Heterodera glycines* and *Pratylenchus brachyurus* in a succession crop of soybean and chickpea. Agron. Colomb. 39, 337–342. https://doi.org/10.15446/agron.colomb.v39n3.96469.

Pinto, T.J.B., Silva, G.O., Vendrame, L.P.C., Pinheiro, J.B., Santos, L.A., Cunha, D.F., Melo, R.A.C., Cares, J.E., 2023. Sources of root-knot nematode (*Meloidogyne enterolobii*) resistance in sweetpotato genotypes. Hortic. Bras. 41, e2588. https://doi.org/10.1590/s0102-0536-2023-e2588.

Pinto, T.J.B., Cunha, D.F., Silva, G.O., Pinheiro, J.B., Correia, V.R., Fragassi, C.F., Cares, J.E., 2024. Reaction of Brazilian genotypes of pulses (pea, chickpea and lentil) to the root-knot nematode *Meloidogyne enterolobii*. Nematology 26, 299–307. https://doi.org/10.1163/15685411-bja10309, 10.1163/15685411-bja10309.

Pires, D., Vicente, C.S.L., Menéndez, E., Faria, J.M.S., Rusinque, L., Camacho, M.J., Inácio, M.L., 2022. The fight against plant-parasitic nematodes: current status of bacterial and fungal biocontrol agents. Pathogens 11, 1178. https://doi.org/10.3390/pathogens11101178.

Pocurull, M., Fullana, A.M., Ferro, M., Valero, P., Escudero, N., Saus, E., Gabaldón, T., Sorribas, F.J., 2020. Commercial formulates of *Trichoderma* induce systemic plant resistance to *Meloidogyne incognita* in tomato and the effect is additive to that of the *Mi*-1.2 resistance gene. Front. Microbiol. 10, 3042. https://doi.org/10.3389/fmicb.2019.03042.

Puttawong, K., Beesa, N., Kasem, S., Jindapunnapat, K., Chinnasri, B., Sasnarukkit, A., 2024. Potential of *Bacillus* spp. against root-knot nematode, *Meloidogyne enterolobii* parasitizing chili (*Capsicum annuum* L.). Crop Protect., 106780 https://doi.org/10.1016/j.cropro.2024.106780.

Rajendran, J., Dubey, J., Kumar, V., Sujayanand, G.K., 2024. Nematode egg parasitic fungus, *Purpureocillium lilacinum*: efficacy of indigenous strains for the management of *Meloidogyne incognita* in chickpea. Egyptian J. Biol. Pest Control. 34, 4. https://doi.org/10.1186/s41938-024-00769-5.

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

Santos, L.P., Pereira, W.J., Silva, D.Z., Gonçalves, D.J., Alves, G.C.S., Pinheiro, J.B., Silva, G.O., Melo, R.A.C., Nascimento, W.M., Silva, P.P., 2021. Chickpea genotype resistance to *Meloidogyne javanica* and *Pratylenchus brachyurus* in field conditions. Pesqui. Agropecu. Bras. 56, 02529. https://doi.org/10.1590/S1678-3921.pab2021.v56.02529.

Sharma, P., Pandey, R., 2009. Biological control of root-knot nematode; *Meloidogyne incognita* in the medicinal plant; *Withania somnifera* and the effect of biocontrol agents on plant growth. Afr. J. Agric. Res. 4, 564–567.

Sharma, R.D., Fonseca, C.E.L., 2000. Efeito de *Meloidogyne javanica* no crescimento da ervilha. Pesqui. Agropecu. Bras. 35, 115–122. https://doi.org/10.1590/S0100-204X2000000100014.

Sikandar, A., Jia, L., Wu, H., Yang, S., 2023. *Meloidogyne enterolobii* risk to agriculture, its present status and future prospective for management. Front. Plant Sci. 13, 1093657. https://doi.org/10.3389/fpls.2022.1093657.

Silva, S.D., Carneiro, R.M., Faria, M., Souza, D.A., Monnerat, R.G., Lopes, R.B., 2017. Evaluation of *Pochonia chlamydosporia* and *Purpureocillium lilacinum* for suppression of *Meloidogyne enterolobii* on tomato and banana. J. Nematol. 49, 77–85. https://doi.org/10.21307/jofnem-2017-047.

Sohrabi, F., Sheikholeslami, M., Heydari, R., Rezaee, S., Sharifi, R., 2020. Investigating the effect of *Glomus mosseae, Bacillus subtilis* and *Trichoderma harzianum* on plant growth and controlling *Meloidogyne javanica* in tomato. Indian Phytopathol. 73, 293–300.

Stirling, G.R., West, L.M., 1991. Fungal parasites of root-knot nematode eggs from tropical and subtropical regions of Australia. Australas. Plant Pathol. 20, 149–154.

Taylor, A.L., Sasser, J.N., 1978. Biology, identification and control of root-knot nematodes (*Meloidogyne* species). North Carolina State University Graphics, p. 111.

Tian, X.L., Zhao, X.M., Zhao, S.Y., Zhao, J.L., Mao, Z.C., 2022. The biocontrol functions of *Bacillus velezensis* strain Bv-25 against *Meloidogyne incognita*. Front. Microbiol. 13, 843041. https://doi.org/10.3389/fmicb.2022.843041.

Tigano, M., De Siqueira, K., Castagnone-Sereno, P., Mulet, K., Queiroz, P., Dos Santos, M., Teixeira, C., Almeida, M., Silva, J., Carneiro, R.D.G.C., 2010. Genetic diversity of the root-knot nematode *Meloidogyne enterolobii* and development of a SCAR marker for this guava-damaging species. Plant Pathol. 59, 1054–1061. https://doi.org/10.1111/j.1365-3059.2010.02350.x.

Treub, M., 1885. *Onderzoekingen over sereh-ziek suikerriet gedaan in's Lands Plantentuin te Buitenzorg* 2. Landsdrukkerij.

Verssiani, J.B.S., Souza, C.F.B., Santos, P.S., Arias, C.A.A., Cares, J.E., Carneiro, R.M.D.G., 2023. Reaction of soybean cultivars to two races of *Meloidogyne enterolobii* and their aggressiveness under plastic house conditions. Nematology 25, 929–940. https://doi.org/10.1163/15685411-bja10266.

Vinale, F., Sivasithamparam, K., Ghisalberti, E.L., Marra, R., Woo, S.L., Lorito, M., 2008. *Trichoderma*–plant–pathogen interactions. Soil Biol. Biochem. 40, 1–10. https://doi.org/10.1016/j.soilbio.2007.07.002.

Wang, G., Liu, Z., Lin, R., Li, E., Mao, Z., Ling, J., Yang, Y., Yin, W., Xie, B., 2016. Biosynthesis of antibiotic leucinostatins in bio-control fungus *Purpureocillium lilacinum* and their inhibition on *Phytophthora* revealed by genome mining. PLoS Pathog. 12, e1005685. https://doi.org/10.1371/journal.ppat.1005685.

Yan, Y., Mao, Q., Wang, Y., Zhao, J., Fu, Y., Yang, Z., Peng, X., Zhang, M., Bai, B., Liu, A., Chen, S., Ahammed, G., 2021. *Trichoderma harzianum* induces resistance to root-knot nematodes by increasing secondary metabolite synthesis and defense-related enzyme activity in *Solanum lycopersicum* L. Biol. Control 158, 104609. https://doi.org/10.1016/j.biocontrol.2021.104609.

Yang, F., Abdelnabby, H., Xiao, Y., 2015. The role of a phospholipase (PLD) in virulence of *Purpureocillium lilacinum* (*Paecilomyces lilacinum*). Microb. Pathog. 85, 11–20. https://doi.org/10.1016/j.micpath.2015.05.008.

Yang, B., Eisenback, J.D., 1983. *Meloidogyne enterolobii* n. sp. (meloidogynidae), a root-knot nematode parasitizing pacara earpod tree in China. J. Nematol. 15, 381–391.

You, J., Li, G., Li, C., Zhu, L., Yang, H., Song, R., Gu, W., 2022. Biological control and plant growth promotion by volatile organic compounds of *Trichoderma* koningiopsis T-51. J. Fungi 8, 131. https://doi.org/10.3390/jof8020131.

Yu, Z., Xiong, J., Zhou, Q., Luo, H., Hu, S., Xia, L., Yu, Z., 2015. The diverse nematicidal properties and biocontrol efficacy of *Bacillus thuringiensis* Cry6A against the root-knot nematode *Meloidogyne hapla*. J. Invertebr. Pathol. 125, 73–80. https://doi.org/10.1016/j.jip.2014.12.011.

Zwart, R.S., Thudi, M., Channale, S., Manchikatla, P.K., Varshney, R.K., Thompson, J.P., 2019. Resistance to plant-parasitic nematodes in chickpea: current status and future perspectives. Front. Plant Sci. 10, 966. https://doi.org/10.3389/fpls.2019.00966.