



Scientific Article

Competitive interaction between *Rotylenchulus reniformis* and *Meloidogyne enterolobii* in tomato and cucumber plants

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ABSTRACT

Background/Objective. The production of tomato (*Solanum lycopersicum*) and cucumber (*Cucumis sativus*) is affected by the nematodes *Rotylenchulus reniformis* and *Meloidogyne enterolobii*; however, the interaction between these two nematodes on these plant species is unknown. The aim of this study was to determine the interaction of *R. reniformis* and *M. enterolobii* in tomato and cucumber plants through artificial inoculations under greenhouse conditions.

Materials and Methods. Twenty-one-day-old seedlings were inoculated with 2000 juveniles (J2) of each nematode per plant. The experiment followed a completely randomized three-factor design with six treatments: T1= *R. reniformis*; T2= *M. enterolobii*; T3= *R. reniformis* was inoculated and 15 days later *M. enterolobii* was added; T4 = *M. enterolobii* was inoculated and 15 days later *R. reniformis* was added; T5 = both species were inoculated on the same day; T6 = uninoculated control. The reproduction factor (RF) of both nematodes, galling index for *M. enterolobii*, and root necrosis percentage for *R. reniformis* were recorded at 30 and 50 days after inoculation.

Results. In cucumber plants, *M. enterolobii* reduced its reproduction by up to 73% in the presence of *R. reniformis*, while in tomato plants, its reproduction decreased by 52%, with a reduction in the galling index of 72 and 60% in cucumber and tomato plants, respectively, compared to T1 and T2. On the other hand, *R. reniformis* reduced its reproduction by 72% in cucumber plants and 67% in tomato plants in the presence of *M. enterolobii*, and a reduction in symptom severity was observed by 78 and 77% in cucumber and tomato plants, respectively, compared to T1 and T2.



Conclusion. In treatments where one species was inoculated before the other, the species inoculated first showed a higher RF and caused greater disease severity. In simultaneous co-inoculations, both nematodes reduced their RF and caused lower symptom severity in tomato and cucumber plants.

Keywords: *Solanum lycopersicum*, *Cucumis sativus*, Reproduction factor, Severity, Gallings index

INTRODUCTION

Mexico is one of the world's leading vegetable producers, ranking ninth in tomato (*Solanum lycopersicum*) production with 4,271,914 tons in 2022, and fifth in cucumber (*Cucumis sativus*) production with 1,038,999 tons. The state of Sinaloa is the main producer of both tomato and cucumber, with 677,612 and 314,150 tons, respectively (SIAP, 2023).

Rotylenchulus reniformis and *Meloidogyne enterolobii* are highly significant species and are among the top 10 most economically impactful and scientifically important plant-parasitic nematodes worldwide (Jones *et al.*, 2013). These nematodes have been reported to severely affect vegetable crops in the state of Sinaloa (Martínez-Gallardo *et al.*, 2019; Salazar-Mesta *et al.*, 2023a, 2023b; Valdez-Morales *et al.*, 2024).

Both *Rotylenchulus* spp. and *Meloidogyne* spp. form feeding sites in the roots of plants. *Meloidogyne enterolobii* is a sedentary endoparasitic nematode, and its parasitism involves the induction of giant cells in the parenchyma (Starr *et al.*, 2002; Perry and Moens, 2013). Meanwhile, *R. reniformis* is a semi-endoparasitic nematode and induces the formation of syncytia, primarily in pericycle cells (Starr *et al.*, 2002). Although the infection sites of ectoparasitic and endoparasitic nematodes differ, interactions between species can occur, and these interactions may be antagonistic or suppressive to one of the species involved (Khan *et al.*, 1985; Robinson *et al.*, 2007; Gomes *et al.*, 2014).

Studies on interactions between plant-parasitic nematodes have shown that such relationships can be antagonistic for either nematode when feeding on the same plant (Diez *et al.*, 2003; Melakeberhan and Dey, 2003; Manzanilla-Lopez and Starr, 2009; Ferreira *et al.*, 2015; Fontana *et al.*, 2018). Moreover, the effects of nematode species interactions are related to the nature of parasitism and competition, as the competitive relationship increases with the complexity of the host-parasite interaction (Kesba *et al.*, 2005; Moens *et al.*, 2006; Robinson *et al.*, 2007; Bhat and Parveen, 2012).

In the case of plant-parasitic nematodes from the genera *Helicotylenchus*, *Pratylenchus*, and *Rotylenchulus*, it has been demonstrated that interactions occur due to competition for space and nutrients (Bhat and Parveen, 2012; Ferreira *et al.*, 2015a, 2015b; Gomes *et al.*, 2014; Fontana *et al.*, 2018). Additionally, several studies have determined the interaction between *R. reniformis* and *Meloidogyne* spp., including *M. javanica* and *M. incognita*, in various host plants such as pineapple (*Ananas comosus*), cotton (*Gossypium hirsutum*), tomato, and castor bean (*Ricinus communis*).

These studies recorded that *R. reniformis* has a competitive advantage over *Meloidogyne* species in joint inoculations, as a reduction in root galling was observed (Diez *et al.*, 2003; Faske and Hurd, 2015; Ferreira *et al.*, 2015a, 2015b). The interaction

of *M. enterolobii* with lesion nematodes, such as *Helicotylenchus dihysteroides*, has also been evaluated in guava (*Psidium guajava*) seedlings; however, symptoms caused by *M. enterolobii* were observed in both separate and combined inoculation treatments (Gomes *et al.*, 2014).

The interactions between *M. enterolobii* and *R. reniformis* in tomato and cucumber plants have not been studied, but it is suggested that *R. reniformis* may have a competitive advantage over the root-knot nematode due to its high degree of parasitism (Diez *et al.*, 2003; Robinson, 2007; Aryal *et al.*, 2011). Therefore, the objective of this study was to determine the competitive interaction between *R. reniformis* and *M. enterolobii* in tomato and cucumber plants under greenhouse conditions.

MATERIALS AND METHODS

The experiments were conducted under greenhouse conditions from December 2022 to May 2023. Tomato (*Solanum lycopersicum* cv. Imperial) and cucumber (*Cucumis sativus* cv. Zeus) seeds were germinated in 60-cell trays filled with sterile substrate (Peat Moss). Twenty-one days after germination, seedlings were directly inoculated into the germination trays with 2000 juveniles (J2) of each nematode (*R. reniformis* and *M. enterolobii*). The experimental unit was one plant in a cell. Treatments were as follows: T1 = *R. reniformis*; T2 = *M. enterolobii*; T3 = *R. reniformis* was inoculated, followed by *M. enterolobii* 15 days later; T4 = *M. enterolobii* was inoculated, followed by *R. reniformis* 15 days later; T5 = both species were inoculated on the same day; T6 = uninoculated control. The populations of *R. reniformis* and *M. enterolobii* used in this experiment were previously characterized and identified through a combination of morphological and molecular analyses by Valdez-Morales *et al.* (2024) and Salazar Mesta *et al.* (2023a), respectively.

Evaluations were conducted at 30 and 50 days after inoculation (DAI). The variables measured were the reproduction factor (RF) of each nematode, the galling index for *M. enterolobii*, and root necrosis percentage for *R. reniformis*. To evaluate the galling index, roots were extracted, washed with tap water, and the number of galls per root was counted for each treatment.

For the reproduction factor assessment, the final population of each nematode species was determined using the formula $RF = Pf/Pi$, where Pi represents the initial nematode population at the time of inoculation, and Pf is the final nematode count at root extraction (Ferris *et al.*, 1993). Roots were stained with 1% acid fuchsin (Byrd *et al.*, 1983), females and egg masses of each species were observed and counted using a stereoscopic microscope. In addition, juvenile and male nematodes were extracted from the substrate of each root using the Baermann funnel and Cobb's sieving methods (Christie and Perry, 1951).

Statistical analysis. The experiment followed a completely randomized three-factor design with six treatments and three replicates. The response variables were the reproduction factor of both nematodes and disease severity, which included the galling index of *M. enterolobii*, and the percentage of root necrosis caused by *R. reniformis*. Root necrosis was evaluated on a visual scale of 1 to 100% based on root damage (Speijer and De Waele, 1997; Nega and Fetena, 2015). The galling index (GI) was evaluated using the

Taylor and Sasser (1978) scale, where: 0 = 0 galls, 1 = 1–2 galls, 2 = 3–10 galls, 3 = 11–30 galls, 4 = 31–100 galls, and 5 = >100 galls. The data obtained were transformed to log (x + 1) to standardize variance. The transformed means were compared using Fisher's LSD test (P < 0.05) with SAS software version 9.3 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Reproduction and pathogenicity of *R. reniformis* and *M. enterolobii*. The initial inoculum levels of both nematodes increased during the trial, and the species displayed variable reproduction factors depending on the host. However, *M. enterolobii* exhibited a higher reproduction factor (RF) (41.9 and 20.9 in cucumber and tomato, respectively) compared to *R. reniformis* (7 and 1.8 in cucumber and tomato, respectively) on both hosts (Figures 1 A, C and 2 A, C).

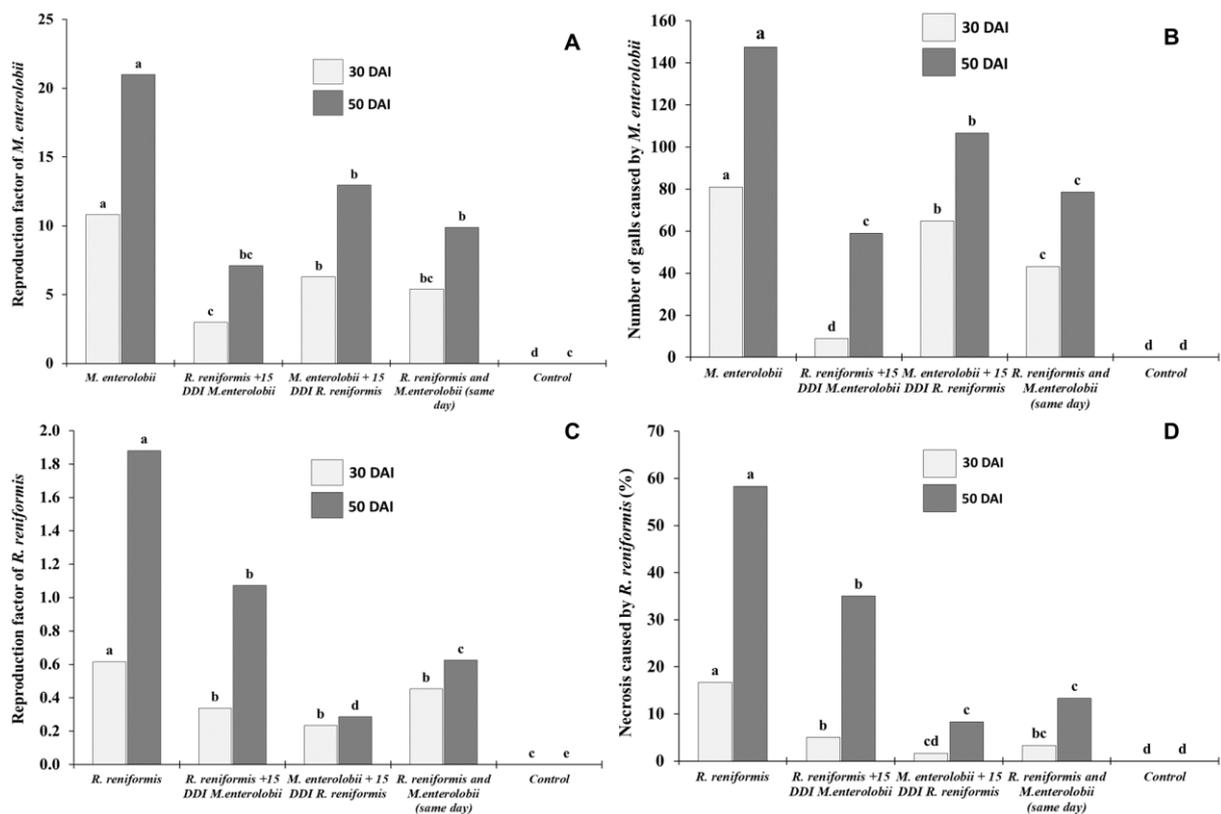


Figure 1. Reproduction and severity of *R. reniformis* and *M. enterolobii* in cucumber plants at 30 and 50 days after inoculation (DAI). A) Reproduction factor of *M. enterolobii*. B) Number of galls caused by *M. enterolobii*. C) Reproduction factor of *R. reniformis*. D) Percentage of root necrosis caused by *R. reniformis*. The comparison of means was conducted between bars of the same color; means that do not share a letter are significantly different.

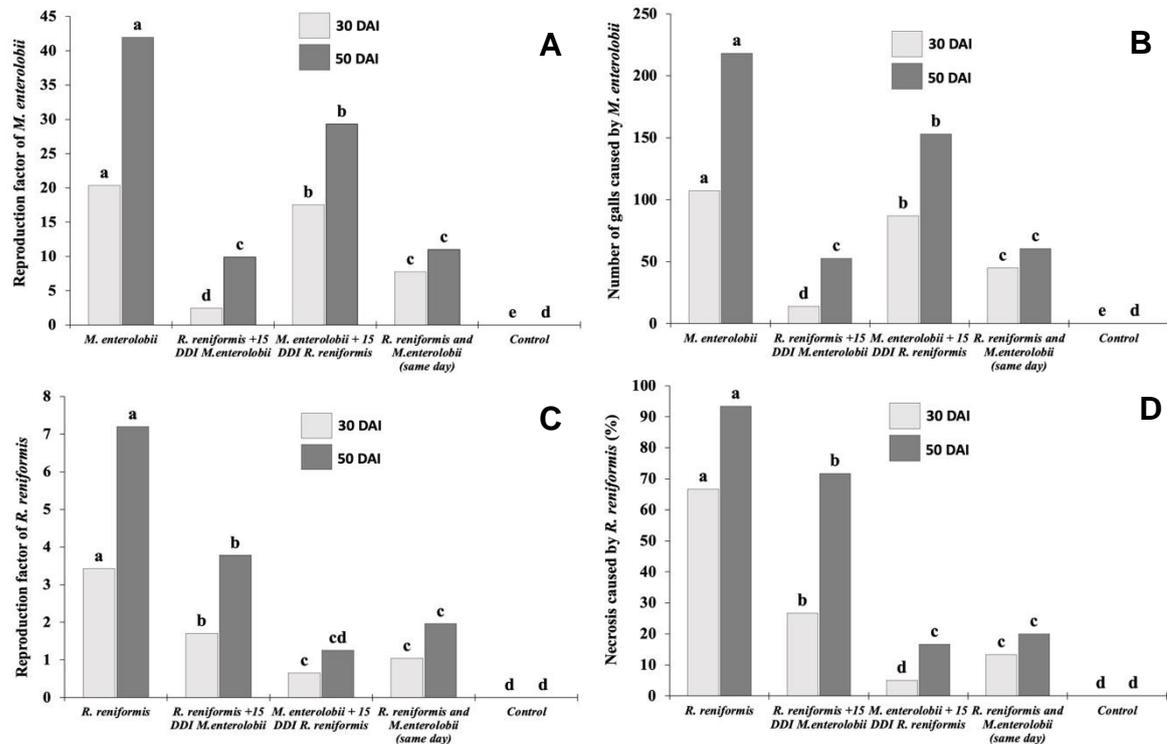


Figure 2. Reproduction and severity of *R. reniformis* and *M. enterolobii* in tomato plants at 30 and 50 days after inoculation (DAI). A) Reproduction factor of *M. enterolobii*. B) Number of galls caused by *M. enterolobii*. C) Reproduction factor of *R. reniformis*. D) Percentage of root necrosis caused by *R. reniformis*. The comparison of means was conducted between bars of the same color; means that do not share a letter are significantly different.

In cucumber plants, mature females and egg masses of both nematodes were observed in all inoculated treatments at 30 days after inoculation (DAI) (Figure 3A, C, E). In contrast, in tomato plants, mature females and egg masses of *M. enterolobii* were seen at 30 DAI, but *R. reniformis* only showed mature females without egg masses. The highest reproduction of both nematodes occurred at 50 DAI (mature females and egg masses) in both plant species (Figures 3B, D, F).



Figure 3. Micrographs of *Rotylenchulus reniformis* and *Meloidogyne enterolobii* parasitizing cucumber and tomato roots at 50 days after inoculation (DAI). A) Female of *M. enterolobii* in cucumber root. B) Female of *M. enterolobii* causing galls in tomato root. C) Female of *R. reniformis* affecting cucumber roots. D) Female of *R. reniformis* in tomato root. E) Cucumber root with a gall caused by *M. enterolobii* and three mature females of *R. reniformis* around it. F) Tomato root with a gall from *M. enterolobii* and necrosis caused by *R. reniformis*. Scale Bars: A= 300 µm; B, E, F= 500; C, D= 100 µm.

Both *R. reniformis* and *M. enterolobii* showed significant differences between treatments across both plant species. Notably, both nematodes had higher RF when inoculated separately (T1 and T2) with values of 49.1 and 20.9, respectively, in cucumber plants, and 7 and 1.8, respectively, in tomato plants, compared to the combined

inoculation treatments (T3, T4, and T5). In treatments where one species was inoculated first and the other 15 DAI (T3 and T4), the species inoculated first exhibited a higher number of eggs, females, juveniles, and consequently a higher RF (Table 1), and caused greater symptom severity compared to the species inoculated later (Figures 1 and 2).

Table 1. Number of females, eggs, and juveniles of *R. reniformis* and *M. enterolobii* by treatment in cucumber and tomato plants at 50 days after inoculation.

Species	Treatments	Cucumber			Tomato		
		Females	Eggs	Juveniles	Females	Eggs	Juveniles
<i>Rotylenchulus reniformis</i>	T1 ^z	170	13,340	1,056	45	3,613	154
	T2	0	0	0	0	0	0
	T3	81	6,520	1,039	24	1,933	213
	T4	30	2,466	40	6	453	121
	T5	43	3,493	430	12	960	290
	T6	0	0	0	0	0	0
<i>Meloidogyne enterolobii</i>	T1	0	0	0	0	0	0
	T2	419	83,866	66	209	41,966	0
	T3	99	19,833	13	71	14,233	0
	T4	291	58,333	266	129	25,900	0
	T5	110	22,033	0	99	19,800	0
	T6	0	0	0	0	0	0

^zT1 = *R. reniformis*; T2 = *M. enterolobii*; T3 = *R. reniformis* was inoculated, followed by *M. enterolobii* 15 days later; T4 = *M. enterolobii* was inoculated, followed by *R. reniformis* 15 days later; T5 = both species were inoculated on the same day; T6 = uninoculated control.

Rotylenchulus reniformis displayed higher RF in individual inoculations for both cucumber and tomato plants; however, its RF decreased when co-inoculated with *M. enterolobii* in the same root. Specifically, *R. reniformis* showed an RF reduction of up to 83% in cucumber and 88% in tomato compared to the treatment where only *R. reniformis* was inoculated. Moreover, when *R. reniformis* was inoculated first and *M. enterolobii* 15 DAI, the reproduction of *R. reniformis* decreased by 58 and 44% in cucumber and tomato plants, respectively, in the presence of *M. enterolobii* (Figures 2A, C).

Meloidogyne enterolobii also exhibited a higher RF in individual inoculations, but its RF decreased by 76 and 66% in cucumber and tomato plants, respectively, when co-inoculated with *R. reniformis* (Figures 1A, C).

Symptom severity caused by *R. reniformis* and *M. enterolobii*. All plants inoculated with *R. reniformis* showed root necrosis symptoms, and all treatments inoculated with *M. enterolobii* exhibited gall symptoms. Both nematodes caused symptoms in roots at 30 DAI, with greater severity observed at 50 DAI (Figures 4 and 5). In both crops, all *R. reniformis* and *M. enterolobii* treatments showed significant differences ($P < 0.05$) compared to the uninoculated control.



Figure 4. Tomato roots at 50 days after inoculation (DAI). A) Control without inoculation. B) Root with galls caused by *M. enterolobii*. C) Root with stunting and necrosis caused by *R. reniformis*. D) Root with galls, necrosis, and stunting symptoms, inoculated with *R. reniformis* and *M. enterolobii* simultaneously.

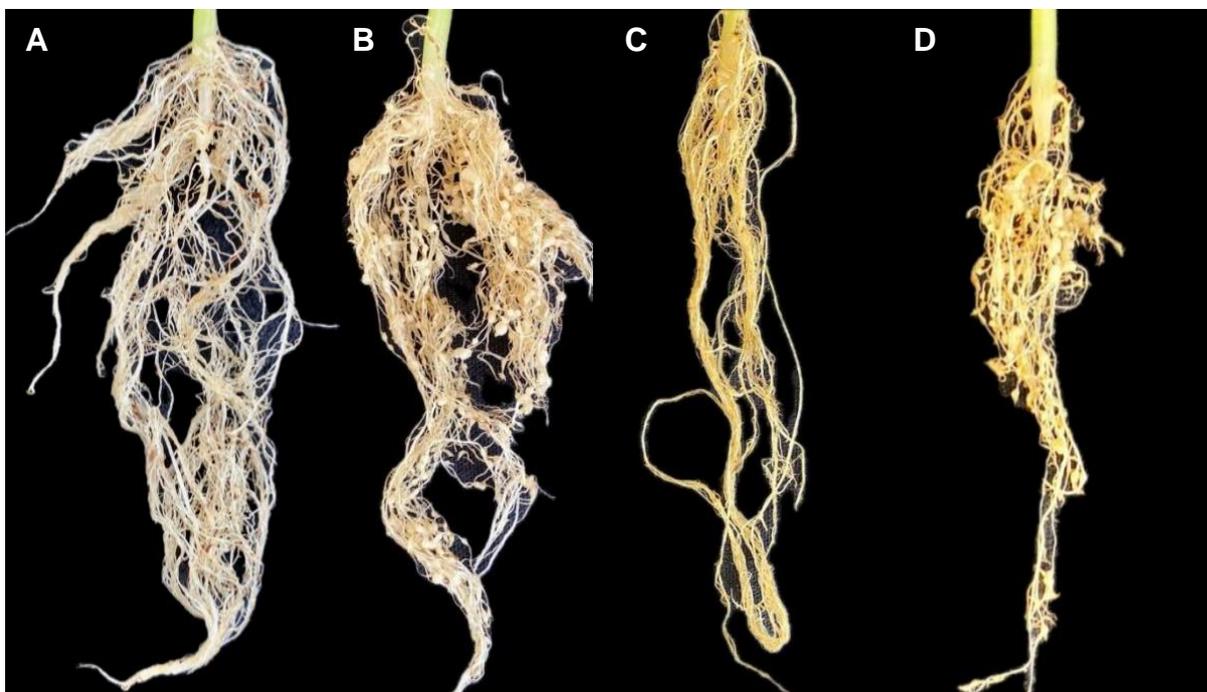


Figure 5. Cucumber roots at 50 days after inoculation (DAI). A) Control without inoculation. B) Root with galls caused by *M. enterolobii*. C) Root with symptoms of stunting and necrosis caused by *R. reniformis*. D) Root with galls, necrosis, and stunting symptoms, inoculated with *R. reniformis* and *M. enterolobii* simultaneously.

At 50 DAI, *R. reniformis* caused 93.3 and 58.3% necrosis in tomato and cucumber roots, respectively. However, when co-inoculated with *M. enterolobii*, the necrosis percentage decreased by 82% in cucumber roots and 85% in tomato roots. In other words, the presence of *M. enterolobii* in the same root reduced the severity of symptoms caused by *R. reniformis* in both cucumber and tomato plants (Figures 1D and 2D).

Meloidogyne enterolobii exhibited a similar pattern to *R. reniformis* in those individual inoculations resulted in more severe symptoms. However, when co-inoculated with *R. reniformis*, the galling index (GI) decreased, with T3 (where *R. reniformis* was inoculated first and *M. enterolobii* 15 DAI) showing the lowest symptom severity, with GI reductions of 76 and 60% in cucumber and tomato plants, respectively (Figures 1B and 2B). Overall, the presence of *R. reniformis* in the same root reduced the severity of symptoms caused by *M. enterolobii* in both cucumber and tomato plants (Figures 4 and 5).

It is worth mentioning that the highest severity in both cucumber and tomato roots was observed in those where both nematodes were co-inoculated, as these roots showed a combination of symptoms such as necrosis, galls, stunting, etc., caused by both nematode species (Figures 4D and 5D).

DISCUSSION

In this study, both *M. enterolobii* and *R. reniformis* reproduced and caused symptoms in cucumber and tomato plants. However, both nematodes exhibited higher reproduction factors (RF) and caused more severe symptoms in cucumber, making it the more susceptible host. This observation aligns with findings by Salazar-Mesta *et al.* (2023b), who determined that cucumber is more susceptible to *M. enterolobii* compared to tomato and pepper (*Capsicum annuum*). This increased susceptibility may be due to the larger size and branching of cucumber roots compared to tomato roots, leading to greater root exudation, which nematodes detect through their sensory systems. Additionally, cucumber root exudates are primarily composed of sugars and compounds preferred by nematodes, such as stigmaterol, while tomato roots mainly release phenolics, sterols, terpenoids, glycosides, and other substances that are less favorable to nematodes (Mateos and Leal, 2003; Lagunes and Zavaleta, 2016).

Both *R. reniformis* and *M. enterolobii* exhibited their highest RFs at 50 days after inoculation (DAI), which was expected since both nematodes typically complete their reproductive cycle (egg mass formation) between 18 and 30 days after inoculation in host plants such as tomato, eggplant (*Solanum melongena*), and cucumber (Salazar-Mesta *et al.*, 2023a, 2023b; Valdez-Morales *et al.*, 2024). The results indicated that reducing the RF of both nematodes also decreased symptom severity. It has been observed that RF is closely related to the severity of root symptoms. Previous studies have reported that an increase in *M. enterolobii* RF elevates galling in tomato and pepper plants (Salazar-Antón *et al.*, 2014; Salazar-Mesta *et al.*, 2023b; Salazar-Mesta *et al.*, 2024). Similarly, an increase in *R. reniformis* RF has been associated with higher necrosis percentages in cowpea (*Vigna unguiculata*), cotton, and tomato plants (Aryal, 2011; Karthika *et al.*, 2020).

In tomato plants, *M. enterolobii* reproduction was reduced in the presence of *R. reniformis*, regardless of the order of inoculation. Treatments T3, T4, and T5 were statistically similar (Figure 5). This may be due to the high reproductive rate of *M.*

enterolobii compared to *R. reniformis*. Under favorable conditions, the life cycle of most *Meloidogyne* species, including *M. enterolobii*, is completed in 25–30 days, with each female producing 500–1000 eggs per mass (Da Silva *et al.*, 2019; Philbrick *et al.*, 2020). In contrast, *R. reniformis* completes its life cycle in 18–25 days, with each female producing 30–200 eggs under favorable conditions (Robinson, 2002).

The life cycle duration of plant-parasitic nematodes largely depends on soil temperature (Bridge and Starr, 2007). The optimal temperature for *M. enterolobii* development ranges between 20 and 30 °C (Greco and Di Vito, 2009; Tomaz *et al.*, 2021), while for *R. reniformis*, it fluctuates between 23 and 30 °C (Starr *et al.*, 2002). Our experiments were conducted under temperatures close to the optimal ranges for both nematodes, with the first experiment held at 18 to 30 °C and the second at 20 to 35 °C.

In cucumber plants, *R. reniformis* exhibited a similar behavior to *M. enterolobii* in terms of RF and symptom severity in treatments where both nematodes were inoculated simultaneously. This indicates that nematode reproduction depends significantly on host susceptibility. According to other authors, *R. reniformis* has a broad host range, with cucumber and eggplant being among its preferred hosts (Starr *et al.*, 1991; Robinson *et al.*, 1997; Vhadera *et al.*, 2001; Valdez-Morales *et al.*, 2024). It has been reported that *R. reniformis* population densities are dependent on host susceptibility (Davis *et al.*, 2003; Stetina *et al.*, 2007; Moore and Lawrence, 2013).

In the combined inoculations, the nematode species inoculated first—whether *M. enterolobii* or *R. reniformis*—showed a higher RF in both tomato and cucumber plants. This result could be due to the clustering of infective units of the first species in the root, leading to competition for space with the second species. This reduced penetration influenced the competition between both nematodes. A high initial population may deteriorate infection sites and lead to an accumulation of metabolic waste, affecting nematode development. Therefore, RF decreases when nematode populations are excessive due to limited food and space (Salazar-Antón *et al.*, 2013). These findings align with other studies that have evaluated the interaction of *R. reniformis* with various *Meloidogyne* species in cotton, pineapple, and castor plants (Diez *et al.*, 2003; Aryal *et al.*, 2011). However, these studies propose space and nutrient competition as the mechanism for the antagonistic interaction between the nematodes. Recent studies, however, have concluded that prior infection of the host with *Rotylenchulus* or *Meloidogyne* can induce greater defense against the other species through the induction of systemic resistance (Aryal *et al.*, 2011; Aryal *et al.*, 2012; Osman *et al.*, 2012). This resistance, mediated by the salicylic acid pathway (Van Loon *et al.*, 2006), enhances the plant natural defense systems against subsequent infections and provides broad-spectrum resistance to various pathogens, including plant-parasitic nematodes (Osman *et al.*, 2012).

This study demonstrated that in co-inoculations, *R. reniformis* was more affected in terms of RF and symptom severity compared to *M. enterolobii* in tomato and cucumber plants. This contrasts with results from other authors, who determined that *R. reniformis* has a competitive advantage over *Meloidogyne* species (Diez *et al.*, 2003; Faske and Hurd, 2015; Ferreira *et al.*, 2015). The effects of nematode species interactions are related to the nature of parasitism and competition, as the competitive relationship intensifies with increased host-parasite complexity (Kesba *et al.*, 2005; Robinson *et al.*, 2007).

The parasitism of *M. enterolobii* involves the induction of giant cells in the parenchyma (Starr *et al.*, 2002; Perry *et al.*, 2009; Perry and Moens, 2013). Through its stylet, this nematode introduces effector molecules (pectolytic and cellulolytic enzymes) into the host, reprogramming gene expression to modify host cell metabolism, physiology, and structure, forming specialized feeding sites. The plant responds by activating defense mechanisms, such as increased activity of key enzymes in the phenylpropanoid pathway, which synthesizes secondary metabolites with antimicrobial properties and lignin monomers that play a structural and defensive role in plants (Lagunes-Fortiz and Zavaleta-Mejía, 2016).

On the other hand, *R. reniformis* is a semi-endoparasite, and its parasitism induces syncytium formation, primarily in pericycle cells (Starr *et al.*, 2002). Females insert their stylets into the host's endodermal cells and release a mix of effectors, including CLE and CEP peptide mimics (Eves-Van den Akker *et al.*, 2016; Wubben *et al.*, 2015), causing cell wall lysis in the initial cell and adjacent pericycle cells, allowing multiple cytoplasm to merge into a single syncytium (Wubben *et al.*, 2015). Effector cells are regulated by parasitism genes, such as glutathione peroxidase, pectin lyase, polygalacturonase, β -1,4-endoglucanase, β -1,4-endoxylanase, and chorismate mutase (Wubben *et al.*, 2010).

In addition to the parasitism nature of each nematode, biochemical and molecular aspects may influence their competitive interaction. Both species modify host plant metabolism and gene expression. Some studies have shown that root-knot nematodes alter host gene expression related to cell cycle control, cell wall modification, and hormone regulation to induce giant cell formation in the roots (Cabrera *et al.*, 2015; Wiczorek, 2015). Both nematodes (reniform and root-knot) suppress defense-related signaling pathways throughout the lifespan of their feeding structures (Jaouannet *et al.*, 2013; Quentin *et al.*, 2013). Previously, several genes involved in nematode parasitism and gall formation have been reported (Mathesius, 2003). For example, nodulin N-26, which encodes an aquaglyceroporin, is induced during both root-knot nematode gall formation and reniform nematode parasitism (Favery *et al.*, 2002). Similarly, the leucine-rich repeat (LRR) receptor kinase SYMRK/NORK, part of a receptor complex involved in root-knot nematode perception, has been reported to influence reniform nematode parasitism (Endre *et al.*, 2002; Stracke *et al.*, 2002; Weerasinghe *et al.*, 2005; Redding *et al.*, 2018).

Further physiological, biochemical, and molecular studies are recommended to understand in detail the key aspects of the competitive interaction between *M. enterolobii* and *R. reniformis* in tomato and cucumber plants.

CONCLUSIONS

In individual inoculations, *Meloidogyne enterolobii* and *Rotylenchulus reniformis* exhibited the highest reproduction factor (RF) and disease severity in tomato and cucumber plants. In treatments where one species was inoculated before the other, the species inoculated first showed a higher RF and caused greater disease severity. In simultaneous co-inoculations, both nematodes reduced their RF and caused lower symptom severity in tomato and cucumber plants. However, in tomato plants, the reproduction of *R. reniformis* was more affected compared to that of *M. enterolobii*.

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