

## RESEARCH REPORT

# INFECTION AND REPRODUCTION OF *MELOIDOGYNE ENTEROLOBII* AND *M. JAVANICA* ON *Mi*-TOMATOES UNDER GREENHOUSE CONDITIONS IN FLORIDA

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### ABSTRACT

Méndez, M., H. X. Bui, and J. Desaeager. 2026. Infection and reproduction of *Meloidogyne enterolobii* and *M. javanica* on *Mi*-tomatoes under greenhouse conditions in Florida. *Nematropica* 56: 20-32.

Root-knot nematodes (RKN, *Meloidogyne* spp.) are major yield-limiting pests in tomato production. *Mi*-tomato cultivars resist common RKN species, including *Meloidogyne incognita*, *M. javanica*, and *M. arenaria*, making them valuable tools in integrated nematode management. However, increasing reports of guava RKN, *M. enterolobii*, in Florida and worldwide, including tomato fields, raise concern, as the *Mi*-genes reportedly do not protect against this species. This study evaluated infection and reproduction of *M. enterolobii* and *M. javanica* from Florida on *Mi*-tomato cultivars ('Sanibel', 'Southern Ripe', 'Skyway 687', and 'Mariana') and one non-*Mi* cultivar ('HM1823') under greenhouse conditions in fall 2024 and spring 2025. Parameters assessed included gall numbers and nematode penetration at 14 days post inoculation (DPI) and gall rating, egg production, and reproduction factor and plant growth at 56 DPI. Except for 'Sanibel', all *Mi*-cultivars provided good protection against *M. javanica* with lower root gall damage and nematode reproduction. All *Mi* cultivars allowed high reproduction of *M. enterolobii* and were severely damaged by *M. enterolobii*, similar to the non-*Mi* cultivar. On the susceptible cultivar, *M. enterolobii* was also more damaging than *M. javanica* producing higher gall numbers, greater penetration rates, and more severe galling, higher egg numbers and reproduction factors, and smaller plants. These findings highlight the urgency of diversifying resistance sources and enhancing integrated management approaches to mitigate the threat of *M. enterolobii* in Florida tomato production.

*Key words:* Guava root-knot nematode, Javanese root-knot nematode, *Mi*-gene resistance, *Solanum lycopersicum*

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### RESUMEN

Méndez, M., H. X. Bui, and J. Desaeager. 2026. Infección y reproducción de *Meloidogyne enterolobii* y *M. javanica* en tomates portadores del gen *Mi* bajo condiciones de invernadero en Florida. *Nematropica* 56: 20-32.

Los nematodos agalladores (RKN, *Meloidogyne* spp.), limitan significativamente el rendimiento en la producción de tomate. Los cultivares de tomate con el gen *Mi* son resistentes a las especies más comunes de RKN, incluyendo *Meloidogyne incognita*, *M. javanica* y *M. arenaria*, lo que los convierte en herramientas valiosas para el manejo integrado de nematodos. Sin embargo, el incremento reciente de reportes del nematodo agallador del guayabo, *M. enterolobii*, en Florida y en otras regiones del mundo son

motivo de preocupación, ya que se conoce que el gen *Mi* no protege contra esta especie. En el presente estudio, se evaluó la infección y reproducción de *M. enterolobii* y *M. javanica* de Florida en cultivares de tomate con el gen *Mi* ('Sanibel', 'Southern Ripe', 'Skyway 687' y 'Mariana'), así como en un cultivar sin el gen *Mi* (HM1823), todo ello bajo condiciones de invernadero durante el otoño de 2024 y la primavera de 2025. Los parámetros evaluados incluyeron el número de agallas y el número de nematodos que penetraron la raíz a los 14 días después de la inoculación (DDI), así como el índice de agallamiento, producción de huevos, factor de reproducción y crecimiento de la planta a los 56 DDI. A excepción de 'Sanibel', todos los cultivares con el gen *Mi* proporcionaron buena protección contra *M. javanica*, con menor daño a las raíces y menor reproducción de nematodos. Todos los cultivares con el gen *Mi* permitieron una alta reproducción de *M. enterolobii* y fueron dañados severamente por esta especie; esta condición fue muy similar a la observada en el cultivar sin el gen *Mi*. En este cultivar, *M. enterolobii* también fue más dañino que *M. javanica*, produciendo un mayor número de agallas, mayores tasas de penetración de nematodos, agallamiento más severo, mayor producción de huevos, factores de reproducción más altos y plantas más pequeñas. Estos hallazgos dan cuenta de la urgencia de diversificar las fuentes de resistencia y fortalecer los enfoques de manejo integrado para mitigar la amenaza de *M. enterolobii* en la producción de tomate en Florida.

*Palabras-clave:* nematodo agallador del guayabo, nematodo del nudo de la raíz, resistencia *Mi*, *Solanum lycopersicum*

## INTRODUCTION

Tomatoes (*Solanum lycopersicum* L.) are among the most important cultivated and economically important vegetable crops worldwide. In 2024, tomato production in Florida was valued at approximately \$330 million (USDA National Agricultural Statistics Service, 2024). However, tomato productivity is frequently threatened by root-knot nematodes (RKN; *Meloidogyne* spp.), particularly in warm climates and sandy soil conditions, such as Florida (Regmi & Desaegeer, 2020a). Due to the intensive and continuous nature of tomato production in the state, often involving plasticulture systems and limited crop rotation, RKN pressure remains consistently high, making effective and sustainable management strategies essential.

Various strategies have been developed for the integrated management of RKN with the use of the *Mi*-gene tomato cultivars being one of the most effective and environmentally sustainable approaches (Seid et al., 2015). These cultivars resist several common RKN species, including *Meloidogyne incognita*, *M. javanica*, and *M. arenaria*. To date, multiple *Mi*-genes conferring different levels of resistance to RKNs have been identified (*Mi-1*, *Mi-2*, *Mi-3*, *Mi-4*, *Mi-5*, *Mi-6*, *Mi-7*, *Mi-8*, *Mi-9*, and *Mi-HT*) with five of them (*Mi-1*, *Mi-3*, *Mi-5*, *Mi-9*, and *Mi-HT*) having been genetically mapped (El-Sappah et al., 2019;

Philbrick et al., 2020). It is difficult to determine the extent of adoption of *Mi*-gene tomato cultivars in commercial tomato production in Florida, as big growers often use their own proprietary cultivars and the information is not publicly available. However, they are used in several states where RKN are a major damaging nematode, including Georgia, Louisiana, North Carolina, South Carolina, and California (California Department of Food and Agriculture (CDFA), 2024). Among these states, *M. enterolobii* has not been detected in California yet (CDFA, 2024). In contrast, recent nematode surveys in Florida have detected *M. enterolobii* in tomato fields (Riva et al., 2024). *Meloidogyne enterolobii* is particularly concerning due to its wide host range, high reproductive capacity, and its ability to overcome known resistance genes in tomato, pepper, and sweetpotato (Brito et al., 2020; Kiewnick et al., 2009). These characteristics raise serious concerns about the durability of *Mi*-gene resistance in commercial tomato cultivars.

Although *M. enterolobii* has been reported in tomato fields, comparative studies evaluating its virulence relative to *M. javanica* (commonly found in Florida tomato production) on *Mi*-gene tomato cultivars remain limited. This study aims to compare the infection and reproduction of two RKN species from Florida, *M. enterolobii* and *M. javanica* on *Mi*-tomato cultivars 'Sanibel', 'Southern Ripe', 'Skyway 687', and 'Mariana',

with cultivar ‘HM1823’ as a susceptible check, under greenhouse conditions. We hypothesize that *M. enterolobii* is more infective and reproductive than *M. javanica* and capable of overcoming *Mi*-gene resistance. The results will help assess the durability of *Mi*-gene resistance and inform future strategies for integrated nematode management in tomato production.

## MATERIALS AND METHODS

Two separate greenhouse experiments were carried out at the Gulf Coast Research and Education Center (UF/GCREC) in Wimauma, Florida, in the fall of 2024 (November to January) and the spring of 2025 (February to May).

### *Root-knot nematode inoculum and soil type*

*Meloidogyne enterolobii* was isolated from water spinach (*Ipomoea aquatica*), a leafy vegetable commonly grown on an Asian vegetable farm in Wimauma, Florida. *Meloidogyne javanica* was obtained from a tomato field at the University of Florida Gulf Coast Research and Education Center (UF/GCREC) farm (27.757662° N, 82.223466° W). Nematode species were molecularly identified using the protocol described in Riva et al. (2024). Nematode eggs were extracted from infected roots using the sodium hypochlorite (NaOCl) method (Hussey & Barker, 1973). In brief, the galled tomato roots were cut into 1-cm pieces and placed in a Mason jar. A 10% Clorox (active ingredient 6.25% sodium hypochlorite) solution was added to cover the chopped roots, and the jar was shaken for 3 min. The root suspension was then poured through a stack of 250 µm, 75 µm, and 25 µm sieves arranged from top to bottom, respectively, to collect RKN eggs at 25 µm sieves and used as the inoculum source for the experiments.

The experimental soil was classified as Myakka fine sand (Khatri et al., 2020), consisting of 96% sand, 3% silt, and 1% clay, with a pH of 7.6 and an organic matter content of 0.8%. Prior to use, the soil was pasteurized at 70°C for 12 hr using an

SST-15 120V Soil Sterilizer (Pro-Grow Supply Corp., Brooksville, WI, USA) to reduce pathogen and nematode contamination.

### *Tomato cultivars tested*

In 2024, three *Mi*-tomato cultivars showing intermediate resistance were tested: ‘Sanibel’<sup>1</sup> (Amazon marketplace), ‘Southern Ripe’<sup>2</sup> (GrowHoss) and ‘Skyway 687’<sup>3</sup> (Rupp Seeds), while cultivar ‘Mariana’<sup>4</sup> (Sakata Vegetables) was included in the 2025 experiment (Regmi & Desaeger, 2020b). The susceptible tomato ‘HM1823’<sup>5</sup> (Seedway), which does not carry the *Mi*-gene, was used as positive control in both experiments. All seed source URLs are provided in footnotes [1–5].

### *Experimental set-up*

Two-liter pots were filled with pasteurized soil and inoculated with 5,000 eggs of either *M. enterolobii* or *M. javanica*. The inoculum was added into three 5-cm-deep holes spaced approximately 2 cm from the center of each pot. Greenhouse temperature (°C) and relative humidity (%) were measured daily at 02:00, 06:00, 10:00, 14:00, 18:00, and 22:00 during the Fall 2024 and Spring 2025 experiments. Average greenhouse temperature and humidity were 22.61 ± 0.28°C and 78.30 ± 0.40 %, respectively, in Fall 2024; in Spring 2025, these parameters were 22.20 ± 0.50°C and 74.76 ± 0.76 %, respectively. Three-week-old tomato seedlings, grown in steamed transplant flats filled with potting mix containing perlite, were transplanted into the center of each pot one day post-inoculation (DPI). Pots were irrigated for 1 min daily using an automatic timer and given a weekly application of 20-20-20 NPK fertilizer at 50 ml per pot (20 g NPK fertilizer in 3.8 L of water). The experiment followed a randomized complete block design (RCBD) with 10 replicates per treatment.

For each treatment, 10 pots were prepared: five pots per treatment were sampled for evaluating the early infection at 14 days post inoculation (DPI)

<sup>1</sup><https://www.amazon.com/Sanibel-Hybrid-Tomato-Seeds-Package/dp/B09CZYGMYY>,

<sup>2</sup><https://growhoss.com/products/southern-ripe-tomato?variant=47689304801590>,

<sup>3</sup><https://www.ruppseeds.com/vegetables/products/tomatoes/fresh-market/skyway-687>,

<sup>4</sup><https://sakatavegetables.com/vegetable/mariana/>

<sup>5</sup><https://www.seedway.com/product/hm-1823-tomato-pelleted/>

and five pots for evaluating the root damage and nematode reproduction at 56 DPI. From the pots designated for early infection analysis, roots were collected and stained with acid fuchsin to aid in visualization and quantification of the total number of galls and nematode juveniles that had penetrated (Tylka, 2022). At 56 DPI, roots were examined for the presence of galls and rated for severity of root galling (Galling Index; GI) using the 0–10 damage scale where 0 indicates no visible root galling, while 10 indicates 100% galled and no visible fibrous roots (Bridge and Page, 1980). In addition, nematode eggs were extracted from entire root system using the method described earlier, and number of eggs per root system, eggs per gram of root, and the reproduction factor ( $R_f = (\text{Population}_{\text{final}})/(\text{Population}_{\text{initial}})$ , where  $\text{Population}_{\text{final}} = \text{eggs extracted from root} + \text{J2 extracted from the soil}$ ) were recorded (Bui and Desaegeer, 2022). Nematode J2 were extracted from 200 cc soil using modified Baermann funnel method by using a salad spinner bowl and basket, in which a 200 cm<sup>3</sup> soil sample from each pot was incubated for 2 days and then passed through a 25- $\mu\text{m}$  sieve, transferred into water-filled vials, and stored at 5°C for counting (Bui et al., 2025; Forge & Kimpinski, 2007; Hooper & Evans, 1993; Saikai et al., 2021). In addition, plant growth parameters were also measured at 56 days post-inoculation (DPI). Plant height was recorded from the soil surface to the tip of the main stem using a meter ruler. Shoot fresh weight and root fresh weight were measured immediately after harvest using a digital balance, while shoot dry weight was obtained by sun-drying the shoots in the greenhouse for two weeks.

#### Statistical analysis

Data for cultivars ‘Sanibel’, ‘Southern Ripe’, ‘Skyway 687’, and ‘HM1823’ from two trials were pooled and analyzed using a mixed model fitted with PROC GLIMMIX (SAS Institute, Cary, NC) to evaluate the effects of tomato cultivars and RKN species. Because the cultivar ‘Mariana’ was evaluated only in the 2025 trial, its data were used solely for comparing the two RKN species, rather than for across-trial or among-cultivar comparisons. Variety and RKN species were treated as fixed effects, while block and trial nested within block were treated as random effects. Residuals were examined for normality and

homogeneity of variances using the PROC UNIVARIATE. When data were non-parametric, data were fitted to a Negative binomial/Poisson with a log link, and the means were back-transformed for presentation. Means were separated using Tukey-Kramer test ( $P \leq 0.05$ ). We standardized reporting to two decimals for exact  $p$  values (e.g., 0.01, 0.05) and to  $P < 0.001$  for very small values.

## RESULTS

### *Early infection (at 14 DPI) of Meloidogyne enterolobii and M. javanica on tested cultivars*

For the susceptible cultivar ‘HM1823’, early RKN infection showed that *Meloidogyne enterolobii* caused significantly more root galls than *M. javanica* ( $P = 0.05$ ). This corresponded with a higher number of *M. enterolobii* juveniles in the roots than *M. javanica* juveniles, though the difference was only marginally significant ( $P = 0.08$ ). For cultivar ‘Sanibel’, *M. enterolobii* caused a slightly higher number of root galls and a higher number of juveniles inside roots than *M. javanica*, although these differences were not statistically significant ( $P = 0.08$  and  $P = 0.48$ , respectively). For cultivar ‘Southern Ripe’, *M. enterolobii* caused more root galls and a higher number of juveniles inside roots than *M. javanica* ( $P < 0.001$  for both; Table 1). For cultivar ‘Skyway 687’, *M. enterolobii* caused substantially greater galling and a higher number of juveniles inside roots than *M. javanica* ( $P < 0.001$  for both). For cultivar ‘Mariana’, *M. enterolobii* caused substantially more root galls and a higher number of juveniles inside roots than *M. javanica* ( $P < 0.001$  for both) (Table 1).

Tested cultivars infected with *M. enterolobii* showed insignificant differences in number of galls ( $P = 0.26$ ), whereas the number of nematodes inside roots varied significantly ( $P < 0.001$ ). The susceptible cultivar ‘HM1823’ and cultivar ‘Southern Ripe’ showed the significantly highest number of nematodes inside roots. The number of galls and nematodes inside roots also showed significant differences among tested cultivars infected with *M. javanica* ( $P < 0.001$  for both), where *Mi*-tomato cultivars ‘Mariana’ (numerically), ‘Skyway 687’ and ‘Southern Ripe’ showed the lowest number of galls (< 5 galls) and the number of nematodes inside roots

Table 1. Average number of galls and nematode inside roots of each tomato cultivar at 14 days post inoculation with 5000 eggs of *Meloidogyne enterolobii* (*Me*) or *M. javanica* (*Mj*). Values represent mean  $\pm$  standard error of means.

Tomato cultivar	Number of galls		Number of nematodes inside roots		<i>p</i> value
	<i>Me</i>	<i>Mj</i>	<i>Me</i>	<i>Mj</i> <sup>z</sup>	
HM1823 (n = 10)	140.7 $\pm$ 30.9 aA	98.2 $\pm$ 18.7 aB	327.4 $\pm$ 151.5 aA	117.5 $\pm$ 34.4 aA	0.08
Mariana (n = 5)	176.2 $\pm$ 17.0 A	1.4 $\pm$ 0.6 B	182.1 $\pm$ 74.7 A	0.3 $\pm$ 0.1 B	<0.001
Sanibel (n = 10)	121.5 $\pm$ 23.8 aA	83.1 $\pm$ 16.7 aA	173.8 $\pm$ 45.0 bA	109.4 $\pm$ 32.2 bA	0.48
Skyway 687 (n = 10)	105.5 $\pm$ 20.4 aA	4.8 $\pm$ 1.4 bB	161.8 $\pm$ 37.5 bA	0.6 $\pm$ 0.3 cB	<0.001
Southern Ripe (n = 10)	140.7 $\pm$ 38.1 aA	1.8 $\pm$ 0.8 bB	364.7 $\pm$ 146.6 aA	0.2 $\pm$ 0.2 cB	<0.001
<i>p</i> value	0.26	<0.001	<0.001	<0.001	

<sup>z</sup> or Data were fitted to a Poisson or Negative binomial respectively with a log link, and the means were back-transformed for presentation. Within row, treatment means with different uppercase letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

Within column, treatment means with different lowercase letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

Table 2. Average plant height and root fresh weight (g) of each tomato cultivar at 56 days post inoculation with 5000 eggs of *Meloidogyne enterolobii* (Me) or *M. javanica* (Mj). Values represent mean ± standard error of means.

Tomato cultivar	Plant height (cm)		Root fresh weight (g)		p value
	Me	Mj	Me	Mj	
HM1823 (n = 10)	71.89 ± 2.79 bB	85.10 ± 2.55 abA	17.49 ± 1.51 aA	15.32 ± 1.81 aA	0.26
Mariana (n = 5)	57.46 ± 1.62 A	52.94 ± 2.07 A	15.20 ± 2.10 A	5.94 ± 0.35 B	0.001
Samibel (n = 10)	63.14 ± 5.91 bA	62.40 ± 4.03 cA	18.86 ± 1.47 aA	13.56 ± 0.82 aB	0.001
Skyway 687 (n = 10)	87.28 ± 2.12 aA	93.75 ± 3.85 aA	16.27 ± 2.02 aA	11.28 ± 1.85 aB	0.007
Southern Ripe (n = 10)	72.51 ± 6.60 bA	69.65 ± 6.14 bcA	16.46 ± 1.13 aA	9.99 ± 1.51 aB	0.001
p value	0.001	<0.001	0.57	0.06	

Within row, treatment means with different uppercase letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

Within column, treatment means with different letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

(< 1 nematode). However, these differences were not observed in *Mi*-tomato cultivar ‘Sanibel’ (Table 1).

*Effect of Meloidogyne enterolobii and M. javanica on plant growth parameters at 56 DPI*

Except for the susceptible cultivar ‘HM1823’, plant height was significantly lower in plants infected with *M. enterolobii* than those infected with *M. javanica* ( $P = 0.01$ ; Table 2). For cultivar ‘Mariana’, shoot fresh weight was significantly higher in plants infected with *M. enterolobii* than in those infected with *M. javanica* ( $P = 0.005$ ; Table 3). No significant differences in plant height or shoot fresh weight were observed for the other cultivars (Tables 2 and 3). For the susceptible cultivar ‘HM1823’, shoot dry weight and root fresh weight did not differ significantly between *M. enterolobii* and *M. javanica* infections ( $P = 0.14$ , and  $P = 0.26$ , Table 2&3). In cultivar ‘Sanibel’, shoot dry weight showed no significant difference between the two RKN species ( $P = 0.84$ ), whereas root fresh weight was significantly higher in *M. enterolobii*-infected roots ( $P = 0.001$ , Tables 2 and 3). For cultivar ‘Southern Ripe’, shoot dry weight showed no significant difference between *M. enterolobii* and *M. javanica* infections ( $P = 0.43$ , Table 3), but root fresh weight was significantly higher under *M. enterolobii* infection ( $P = 0.001$ , Table 2). For cultivar ‘Skyway 687’, shoot dry weight did not differ significantly between *M. enterolobii* and *M. javanica* infections ( $P = 0.83$ , Table 3), but root fresh weight was significantly higher in plants infected with *M. enterolobii* ( $P = 0.007$ , Table 2). For cultivar ‘Mariana’, no significant differences were found in shoot dry weight between *M. enterolobii* and *M. javanica* infections ( $P = 0.12$ , Table 3), while root fresh weight was significantly higher under *M. enterolobii* infection ( $P = 0.001$ , Table 2).

Plant heights of these tested cultivars were significantly different when infected with either *M. enterolobii* or *M. javanica* ( $P = 0.001$  and  $P < 0.001$ , respectively, Table 2). Particularly, cultivar ‘Skyway 687’ was significantly higher than other cultivars under *M. enterolobii* or *M. javanica* infection. Among tested cultivars ‘HM1823’, ‘Sanibel’, ‘Southern Ripe’ and ‘Skyway 687’ infected with *M. enterolobii*, shoot fresh and dry weight and root fresh weight did not

significantly differ ( $P = 0.27$ ,  $P = 0.20$  and  $P = 0.57$ , respectively, Tables 2 and 3). Similarly, these growth parameters were not statistically significant among these cultivars infected with *M. javanica* ( $P = 0.44$  and  $P = 0.06$ , respectively). Numerically, cultivar ‘Mariana’ had the lowest shoot fresh and dry weight and root fresh weight among all tested cultivars (Tables 2 and 3).

*Late infection (at 56 DPI) of Meloidogyne enterolobii and M. javanica on tested cultivars*

For the susceptible cultivar ‘HM1823’, the gall index (GI) of *M. enterolobii* was significantly higher than that of *M. javanica*, whereas the number of eggs/root system and the reproduction factor (Rf) did not differ significantly ( $P = 0.17$  and  $P = 0.25$ ; respectively). Interestingly, eggs/g root for *M. enterolobii* were slightly but significantly lower than for *M. javanica* ( $P = 0.048$ ). For cultivar ‘Sanibel’, *M. enterolobii* also had a significantly higher GI than *M. javanica* ( $P = 0.01$ ), while eggs/root system, eggs/g root, and Rf were not significantly different between *M. enterolobii* and *M. javanica* ( $P = 0.31$ ,  $P = 0.079$ , and  $P = 0.54$ ; respectively). For cultivar ‘Southern Ripe’, the GI, eggs/root system, eggs/g root, and Rf were all significantly higher for *M. enterolobii* than *M. javanica* ( $P < 0.001$  for all parameters). For cultivar ‘Skyway 687’, GI, eggs/root system, eggs/g root, and Rf were all significantly higher in *M. enterolobii* than in *M. javanica* ( $P < 0.001$  for each). Similarly for cultivar ‘Mariana’, GI, eggs/root system, eggs/g root, and Rf were all significantly higher in *M. enterolobii* than in *M. javanica* ( $P < 0.001$  for GI, eggs/root system, and Rf;  $P = 0.02$  for eggs/g root, respectively) (Table 4).

All tested cultivars ‘HM1823’, ‘Sanibel’, ‘Southern Ripe’ and ‘Skyway 687’ were infected with *M. enterolobii* GI differed significantly ( $P = 0.02$ ) with cultivar ‘HM1823’ showing the highest GI (7.2) and cultivar ‘Sanibel’ the lowest (6.4). Also, the GI on these two cultivars differed significantly from each other, but not from other *Mi*-tomato cultivars. Eggs/root systems also varied significantly ( $P = 0.03$ ) in which cultivar ‘Southern Ripe’ had the lowest eggs/root system and significantly differed from the other three cultivars. However, eggs/g root and Rf were not significantly different among cultivars infected with *M. enterolobii* ( $P = 0.24$  and  $P = 0.13$ , respectively).

Table 3. Average shoot fresh and dry weight (g) of each tomato cultivar at 56 days post inoculation with 5000 eggs of *Meloidogyne enterolobii* (Me) or *M. javanica* (Mj). Values represent mean  $\pm$  standard error of means.

	Shoot fresh weight (g)		Shoot dry weight (g)		<i>p</i> value
	Me	Mj	Me	Mj	
HMI 823 (n = 10)	51.38 $\pm$ 2.77 aA	55.26 $\pm$ 6.49 aA	7.91 $\pm$ 0.76 aA	9.92 $\pm$ 0.98 aA	0.14
Mariana (n = 5)	47.52 $\pm$ 2.90 A	28.54 $\pm$ 5.52 B	6.76 $\pm$ 0.65 A	4.38 $\pm$ 0.98 A	0.12
Sanibel (n = 10)	58.0 $\pm$ 5.62 aA	63.92 $\pm$ 3.31 aA	8.65 $\pm$ 0.85 aA	8.39 $\pm$ 0.42 aA	0.84
Skyway 687 (n = 10)	59.79 $\pm$ 3.92 aA	63.98 $\pm$ 6.53 aA	9.23 $\pm$ 0.95 aA	9.52 $\pm$ 1.54 aA	0.83
Southern Ripe (n = 10)	51.20 $\pm$ 2.01 aA	51.97 $\pm$ 5.01 aA	7.07 $\pm$ 0.72 aA	8.05 $\pm$ 0.95 aA	0.43
<i>p</i> value	0.27	0.31	0.20	0.44	

Within row, treatment means with different uppercase letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

Within column, treatment means with different letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

Table 4. Average gall index, eggs/root system, eggs/g root and reproduction factor (Rf) on five tomato cultivars at 56 days post inoculation with 5000 eggs of *Meloidogyne enterolobii* (Me) and *M. javanica* (Mj). Values represent mean  $\pm$  standard error of means.

Tomato product HMI1823 (n = 10)	Gall index			Eggs/root system			Eggs/g root			Rf		
	Me	Mj	p value	Me <sup>i</sup>	Mj <sup>r</sup>	p value	Me <sup>i</sup>	Mj <sup>r</sup>	p value	Me <sup>i</sup>	Mj <sup>r</sup>	p value
	7.2 $\pm$ 0.1 aA	5.9 $\pm$ 0.2 aB	<0.001	901378 $\pm$ 26339 abA	112590 $\pm$ 22317 abA	0.17	5065 $\pm$ 1332 aB	7540 $\pm$ 1674 aA	0.05	18.0 $\pm$ 5.3 aA	22.5 $\pm$ 4.5 aA	0.25
Mariana (n = 5)	5.6 $\pm$ 0.3 A	0.4 $\pm$ 0.2 B	<0.001	146920 $\pm$ 13088 A	22480 $\pm$ 5788 B	<0.001	10277 $\pm$ 1373 A	3891 $\pm$ 1078 B	0.02	29.4 $\pm$ 2.6 A	4.5 $\pm$ 1.2 B	<0.001
Sanibel (n = 10)	6.4 $\pm$ 0.2 bA	5.6 $\pm$ 0.3 aB	0.01	125970 $\pm$ 31584 aA	114040 $\pm$ 19685 aA	0.31	7071 $\pm$ 1947 aA	8121 $\pm$ 1273 aA	0.08	25.2 $\pm$ 6.3 aA	22.8 $\pm$ 3.9 aA	0.54
Skyway 687 (n = 10)	6.8 $\pm$ 0.3 abA	0.7 $\pm$ 0.2 bB	<0.001	104508 $\pm$ 30545 abA	11169 $\pm$ 2495 cB	<0.001	6034 $\pm$ 1813 aA	893 $\pm$ 156 bB	<0.001	20.9 $\pm$ 6.1 aA	2.2 $\pm$ 0.5 bB	<0.001
Southern Ripe (n = 10)	6.7 $\pm$ 0.2 abA	0.5 $\pm$ 0.2 bB	<0.001	89528 $\pm$ 26223 bA	9083 $\pm$ 3339 dB	<0.001	5148 $\pm$ 1497 aA	874 $\pm$ 215 bB	<0.001	17.9 $\pm$ 5.2 aA	1.8 $\pm$ 0.7 bB	<0.001
p value	0.02	<0.001		0.03	<0.001		0.20	<0.001	0.05	0.13	<0.001	

z or <sup>r</sup>Data were fitted to a Poisson or Negative binomial respectively with a log link, and the means were back-transformed for presentation.

Within row, treatment means with different uppercase letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

Within column, treatment means with different letters indicate significant difference based on the Tukey-Kramer test ( $P \leq 0.05$ ). Data from two experiments were pooled before analysis.

For *M. javanica*, GI, eggs/root system, eggs/g root, and Rf were all significantly lower in ‘Skyway 687’, and ‘Southern Ripe’ than ‘HM1823’ and ‘Sanibel’ ( $P < 0.001$  for all parameters) (Table 4).

## DISCUSSION

Plant growth responses appeared to vary with cultivar background and RKN species. For the susceptible cultivar ‘HM1823’, plant height was significantly reduced more under *M. enterolobii* infection than *M. javanica*, whereas no such differences were observed for any of the *Mi*-tomato cultivars. The plum tomato cultivar ‘Mariana’ had the lowest shoot fresh and dry weight and root fresh weight, which was to be expected as this is a bushier and more compact cultivar as compared to the other cultivars. These results suggest that *Mi*-mediated resistance may compromise certain plant growth parameters under RKN pressure, which is a very common “growth-defense trade-off” phenomenon (He et al., 2022). Root fresh weight of all *Mi* cultivars was significantly higher when infected with *M. enterolobii* as compared to *M. javanica*. This is in line with the high degree of root galls observed with *M. enterolobii*, while all these cultivars (except ‘Sanibel’) provided good resistance and showed very few galls with *M. javanica*. Similar to previous studies by Regmi & Desaegeer (2020a), our study confirms good resistance of *Mi* cultivars ‘Southern Ripe’, ‘Skyway 687’, and ‘Mariana’ against *M. javanica*. Surprisingly, the *Mi* cultivar ‘Sanibel’ failed to protect against *M. javanica* despite having shown good resistance against the same *M. javanica* population in previous experiments (Regmi & Desaegeer, 2020a). Sanibel seed was purchased on two different occasions (once for each experiment) from the same supplier, which seems to indicate a mislabeled seed source from the supplier or possible contamination of this cultivar at the seed production field.

Also, our study provides evidence that *M. enterolobii* infected and reproduced on all four tested *Mi*-tomato cultivars ‘Sanibel’, ‘Southern Ripe’, ‘Skyway 687’, and ‘Mariana’. This confirms previous observations from North Carolina and Switzerland showing that *M. enterolobii* can overcome *Mi*-gene resistance in tomato (Philbrick et al., 2020). The ability of *M. enterolobii* to rapidly establish and complete its life cycle within *Mi*-tomato cultivars poses a significant threat to the

long-term durability of *Mi*-mediated resistance to RKN (Philbrick et al., 2020). The genetic and physiological mechanisms underlying *M. enterolobii* ability to bypass *Mi*-gene-mediated resistance remain incompletely understood. Studies have shown that effector gene variation, suppression of host immune signaling pathways, and enzymatic degradation of plant defense barriers are among the mechanisms by which *M. enterolobii* breaks down *Mi*-gene resistance (Castagnone-Sereno et al., 2013; Feng et al., 2024; Shi et al., 2025). Unraveling these mechanisms could inform molecular breeding programs aimed at developing resistance genes that remain effective against *M. enterolobii*. Until such breakthroughs are achieved, reliance on a single major resistance gene (*Mi*) represents a high-risk strategy, particularly in areas where *M. enterolobii* has been detected. Addressing this challenge also requires continued efforts to identify and incorporate novel resistance sources into breeding programs.

Early nematode infection at 14 DPI was more severe with *M. enterolobii* than *M. javanica*. This is consistent with previous findings showing that *M. enterolobii* can produce eggs as early as 15 days after inoculation, as compared to 20 days for *M. javanica*, highlighting its rapid life cycle and greater potential for population buildup (Collett et al., 2024). Similar findings were reported by Bui & Desaegeer (2022), where *M. enterolobii* caused greater damage and had higher reproduction than *M. javanica* on four cucurbit crops. The higher rates of early infection by *M. enterolobii* as compared to *M. javanica* are likely to contribute to its long-term reproductive success, particularly in most of the tested *Mi*-tomato cultivars. This also highlights the high damage potential of *M. enterolobii* relative to other RKN species (Cunha et al., 2025; Silva et al., 2019).

Root gall ratings after 56 DPI were higher with *M. enterolobii* than *M. javanica* for all cultivars, including the susceptible cultivar ‘HM1823’. However, egg counts and reproduction factors were only higher for the *Mi* cultivars, and not for the susceptible cultivar. The most likely explanation is that while both RKN species caused damage to the susceptible cultivar, *M. enterolobii* caused more severe early root damage, which negatively affected root health and reduced nematode-feeding sites later on.

The high virulence and host range of *M. enterolobii* is a concern for not only tomatoes

but also other vegetable crops in Florida, especially considering the high prevalence of *M. enterolobii* in Florida. In a recent survey in south-central Florida vegetable farms, *M. enterolobii* and *M. incognita* were the most common root-knot nematode species found (each 32% positive samples), followed by *M. javanica* (20%), *M. arenaria* (10%), and *M. hapla* (6%) (Riva et al., 2024). The high prevalence of *M. enterolobii* in Florida, as well as the increasing number of reports from other US states and countries, is cause for concern and emphasizes the need for more breeding efforts to find new sources of resistance. While some success in breeding for *M. enterolobii* resistance has been found in other crops like sweet potato (Rutter et al., 2021), this has not been the case in tomatoes and other fruiting vegetables.

*Mi* tomato cultivars ‘Southern Ripe’, ‘Skyway 687’, and ‘Mariana’ showed good resistance against a Florida population of *M. javanica*, but all cultivars were severely damaged by *M. enterolobii*. *Mi*-tomato cultivar ‘Sanibel’ was infected by both populations, likely due to a contaminated seed source. *Meloidogyne enterolobii* was more virulent and caused more severe damage than *M. javanica* on the non-*Mi* tomato cultivar ‘HM1823’. Our study underscores the urgent need to develop new resistant germplasm and implement broader nematode management strategies to help manage *M. enterolobii*.

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