RESEARCH ARTICLE



Characterization of resistance responses to *Meloidogyne* enterolobii in Capsicum annuum landraces from Mexico

Rita J. Salazar-Mesta¹, José A. Carrillo-Fasio¹, Jesús E. Retes-Manjarrez², Raymundo S. García-Estrada¹, Josefina León-Félix¹, and Juan M. Tovar-Pedraza^{1*}

¹Centro de Investigación en Alimentación y Desarrollo, Coordinación Regional Culiacán, 80110, Culiacán, México. ²Fyffes, Finca El Oasis La Fragua, 19016, Zacapa, Guatemala.

*Corresponding author (juan.tovar@ciad.mx).

Received: 5 November 2023; Accepted: 30 December 2023, doi:10.4067/S0718-58392024000300301

ABSTRACT

Meloidogyne enterolobii is currently the most damaging nematode of the genus Meloidogyne due to its aggressiveness and ability to overcome existing sources of resistance; therefore, the search for genotypes with resistance in crops of high economic importance such as chili pepper (Capsicum annuum L. var. annuum) is one of the greatest challenges facing agricultural researchers. The aim of this study was to determine the level of resistance in C. annuum landraces from Mexico to different population densities of M. enterolobii. Five C. annuum landraces (UTC24, UTC25, UTC66, UTC67, and UTC90) and the commercial cv. Revelation were used. The experiment was conducted twice under greenhouse conditions with a randomized block design with four replicates per genotype and cultivar. Inoculation was performed on 21-d-old seedlings with inoculum doses of 0, 4500, 9000, and 13500 eggs plant⁻¹. The gall index, reproduction factor, and reproduction index were evaluated at 42 and 63 d after inoculation. Genotypes UTC66, UTC67, and UTC90 showed a higher level of resistance with a damage percentage lower than 50% compared to 'Revelation' (susceptible). Genotype UTC90 showed the lowest reproduction factor and index, so it was considered a highly resistant genotype to an inoculum dose of 4500 *M. enterolobii* eggs with a damage percentage of less than 10%, while, at a dose of 13 500 eggs, its resistance level was intermediate. The results of this study contribute to the search for sources of resistance to *M. enterolobii* in chili pepper landraces.

Key words: Gall index, landraces, plant parasitic nematode, reproduction factor, reproduction index, resistance.

INTRODUCTION

The genus *Capsicum* is native to the Americas and comprises about 30 species, of which five have been domesticated (*C. pubescens, C. chinense, C. frutescens, C. baccatum*, and *C. annuum*) (Votava et al., 2005). The species *C. annuum* was domesticated in Mexico and is considered the most economically important, as it is cultivated worldwide, and within it are most of the commercial peppers and chilies. In addition, this species includes semi-domesticated, landraces and wild genotypes that are widely distributed throughout the country (Votava et al., 2005; Carrizo-García et al., 2016).

About 3 086 742 tons of green chili peppers are produced annually in Mexico which is considered the 3rd largest pepper-exporting country with an economic profit of 1144 billion dollars (SIAP, 2022). However, the production of this crop is affected by soil-borne pathogens, including root-knot nematodes belonging to the genus *Meloidogyne* (Castagnone-Sereno, 2012).

For the species *M. incognita*, *M. arenaria*, and *M. javanica*, the *N*, *Me1*, *Me2*, *Me3*, *Me4*, *Me5*, *Me6*, *Me7*, *Mech1*, and *Mech2* genes associated with resistance have been efficient as a genetic control tool in several commercial cultivars containing them (Djian-Caporalino et al., 2001; Wang et al., 2009; Fazari et

al., 2012). However, *M. enterolobii* have been reported to successfully parasitize these cultivars with resistance genes to other *Meloidogyne* species (Brito et al., 2008; Velloso et al., 2022; Long et al., 2023).

The damage produced by *M. enterolobii* is greater than that of any of the other root-knot nematode species investigated so far (Castagnone-Sereno, 2012; Castillo and Castagnone-Sereno, 2020). To mitigate the damage in Solanaceae such as chili pepper, physical, chemical, and biological control methods are carried out. To date, there are no commercial chili pepper cultivars with resistance to *M. enterolobii*. The search for multiple resistance to several nematodes of different genera or species in commercial rootstocks is quite difficult to achieve in practice and constitutes one of the greatest challenges for researchers (Pinheiro et al., 2014). However, different studies have been carried out focused on searching for sources of resistance using plants of wild origin, which constitute the main source of genes with resistance to pathogens such as root-knot nematodes (Soares et al., 2018).

Some plant species such as guava (*Psidium* spp.), acerola (*Malpighia emarginata*), sweet potato (*Ipomoea batatas*), and wild watermelon (*Citrullus amarus*) have been reported as possible candidates with resistance to *M. enterolobii* (Freitas et al., 2014; Santos et al., 2021; Schwarz et al., 2021; Waldo et al., 2022). In chili pepper, mainly the species *C. chinense, C. frutescens*, and *C. baccatum* have been reported as highly resistant to *M. enterolobii* (Gonçalves et al., 2014; Marques et al., 2019; 2020; Pinheiro et al., 2020); however, few studies have investigated the sources of resistance in *C. annuum* genotypes (Marques et al., 2019; Carrillo-Fasio et al., 2020; Pinheiro et al., 2020). In this sense, Carrillo-Fasio et al. (2020) found *C. annuum* landraces from Mexico with potential for resistance to *M. enterolobii* at population densities of 2000 eggs, but it is still necessary to investigate in depth the use of chili pepper landraces as a source of resistance to this nematode in order to generate information that can be incorporated into the integrated management of *M. enterolobii*. Therefore, the aim of this study was to characterize the level of resistance in *C. annuum* landraces from Mexico to different population densities of *M. enterolobii*.

MATERIALS AND METHODS

Plant material

Five landraces of *Capsicum annuum* L. var. *annuum* (UTC24, UTC25, UTC66, UTC67, and UTC90) previously reported by Carrillo-Fasio et al. (2020) were used. The commercial chili pepper 'Revelation' (Seminis, Oxnard, California, USA) was used as the susceptible control.

Inoculum production

A population of *Meloidogyne enterolobii* previously characterized by Salazar-Mesta et al. (2023) was used. The population was multiplied on 21-d-old tomato 'Aguamiel' (Vilmorin-Mikado, Santiago de Queretaro, Mexico) plants, individually transplanted into 2 kg pots with a mixture of sand, silt, and sterile plant substrate (2:1:1). Each plant was inoculated with 20 egg masses obtained from the population of *M. enterolobii*, with a total of 10 pots, and kept for 90 d under greenhouse conditions at temperatures ranging from 25 to 35 °C. Prior to inoculation, nematode eggs were extracted from infected tomato roots using the methodology described by Hussey and Barker (1973) and modified by using 0.5% NaOCl in a blender, instead of by manual shaking.

Resistance test

Two independent experiments were conducted under greenhouse conditions. The first experiment was conducted from March to June 2021 (mean temperature 22-36 °C) and the second experiment was from December 2021 to February 2022 (mean temperature 17-29 °C).

Seedlings of all chili pepper landraces and the commercial cultivar were produced in 128-cavity polystyrene trays with sterile plant substrate (Sogemix, Premier Tech, Rivière-du-Loup, Quebec, Canada). At 21 d after germination, plants were individually transplanted into 3 kg pots containing a mixture of sand, silt, and plant substrate (2:1:1) previously sterilized in an autoclave and kept under greenhouse conditions. Inoculation was carried out 7 d after transplanting and the inoculum doses used were 0, 4500, 9000, and 13500 eggs of *M. enterolobii* per plant.

The experimental design for all experiments consisted of a randomized block design, considering a pot with one plant as the experimental unit, with four replicates per genotype and per cultivar. The number of galls per root system was counted and eggs were extracted from the masses using the methodology indicated by Hussey and Barker (1973).

Data analysis

To determine the resistance of the chili pepper landraces, the gall index (GI), reproduction factor (RF), and reproduction index (RI) were evaluated at 42 and 63 d after inoculation (DAI), using the 1-to-5 gall index scale reported by Taylor and Sasser (1978), where: 0 = 0 galls, 1 = 1-2 galls, 2 = 3-10 galls, 3 = 11-30 galls, 4 = 31-100 galls, and 5 = more than 100 galls.

The reproduction factor (RF) was determined with the formula RF = Pf/Pi, where Pi is the initial nematode population at the time of inoculation and Pf is the final number of nematodes at the time of extraction of each root, and it was classified according to the Oostenbrink scale (Oostenbrink, 1966), where: An RF less than 1.0 is resistant (R), an RF greater than 1.0 is susceptible (S), and an RF equal to zero is immune (I). Finally, the reproduction index (RI) was calculated using the formula: 100 (Number of eggs per gram of root of each genotype/Average number of eggs per gram of root of the susceptible cultivar).

The resistance level of each genotype was established using the scale reported by Taylor (1967). It was classified as susceptible (S) when the RI value of the genotype was greater than 50% of the value obtained for the susceptible cultivar; it was classified as having low resistance (LR) when it was in the 26%-50% range, as having intermediate resistance (IR) when it was in the 11%-25% range, as being highly resistant (HR) when it had a value of 1%-10% and as being immune (I) when there was no reproduction. Data obtained were transformed to log (x + 1) to standardize the variance. The transformed means were compared using Fisher's LSD test (P < 0.05) with SAS software version 9.3 (SAS Institute, Cary, North Carlina, USA).

RESULTS

All chili pepper landraces and 'Revelation' analyzed in this study showed root gall symptoms in both experiments. The number of galls increased over time and the highest number of galls on the roots was observed at 63 DAI in all inoculated plants (Figure 1). However, 'Revelation' presented the highest number of galls at all *M. enterolobii* inoculum doses (4500, 9000, and 13500 eggs) during the three evaluation times. On the other hand, 'Revelation' showed a reduction in the growth of inoculated plants from 42 DAI onwards, while no growth reduction was observed in the genotypes during the three evaluation times.

The lowest number of galls on roots for the three inoculum doses was recorded in genotypes UTC66, UTC67, and UTC90, obtaining level 3 at a dose of 4500 eggs and level 4 at doses of 9000 and 13500 eggs at 63 DAI, respectively (Tables 1 and 2).

Reproduction factor (RF) values in the first experiment ranged from 0.73 to 16.2 at 42 DAI, and from 0.97 to 40.6 at 63 DAI, whereas, in the second experiment, RF values were significantly (P < 0.05) lower and ranged from 0.6 to 15.8 at 42 DAI and from 0.92 to 37.1 at 63 DAI. The RF value was significantly higher in 'Revelation' compared to the landraces, and in both experiments, the highest values were recorded with the dose of 13500 *M. enterolobii* eggs. Genotype UTC90 had the lowest nematode reproduction factor at all inoculum doses (in both experiments) and was significantly different from the rest of the genotypes; therefore, it was classified as resistant to an inoculum dose of 4500 eggs according to the Oostenbrink scale in the evaluations at 42 and 63 DAI. On the other hand, when the inoculum concentration increased to 9000 *M. enterolobii* eggs, the RF was < 1 in the evaluation corresponding to 42 DAI, whereas, at a density of 13500 eggs, the RF value was > 1 at 42 and 63 DAI, being classified as susceptible according to the Oostenbrink scale. The rest of the genotypes presented a reproduction factor > 1 in all evaluations and in both experiments (Tables 1 and 2).



Figure 1. Roots of chili pepper (*Capsicum annuum*) landraces and 'Revelation' showing galls, at 63 d after inoculation (DAI) with 4500 *Meloidogyne enterolobii* eggs. (A) 'Revelation'. (B) UTC25. (C) UTC24. (D) UTC67. (E) UTC66. (F) UTC90.

The results of the reproduction index (RI) indicated significant differences in the level of damage between the landraces with respect to 'Revelation'. Genotype UTC24 and UTC25, as well as 'Revelation' obtained an RI greater than 50% at all nematode inoculum doses (4500, 9000, and 13500 eggs plant⁻¹) in both experiments; therefore, they were classified as susceptible according to Taylor's scale (Taylor, 1967). Genotype UTC90 presented the lowest RI in both experiments for all nematode inoculum densities, being considered at a dose of 4500 *M. enterolobii* eggs as highly resistant, as was genotype UTC67. However, in both experiments, landrace UTC67 was not resistant according to its reproduction factor at any of the three inoculum doses. At the 9000 eggs plant⁻¹ dose, genotype UTC90 was highly resistant at 42 DAI and was classified as having intermediate resistance at 63

DAI, whereas genotype UTC67 presented intermediate resistance in both evaluations at a density of 9000 *M. enterolobii* eggs. At the 13500 eggs dose, genotype UTC90 was classified with intermediate resistance at both 42 and 63 DAI, whereas genotypes UTC67 and UTC66 were considered to have low resistance because their RIs were > 25% damage (Tables 1 and 2).

Table 1. Results of Experiment 1 according to the gall index (GI), reproduction factor (RF), and reproduction index (RI) of *Meloidogyne enterolobii* in *Capsicum annuum* landraces from Mexico. Mean values followed by different letters in the column indicate significant differences among treatments according to Fisher's LSD test (P < 0.05). T: Temperature range; DAI: days after inoculation; GI: gall index, the data were analyzed using the gall index scale from 1 to 5 (Taylor and Sasser, 1978), where: 0 = 0 galls, 1 = 1-2 galls, 2 = 3-10 galls, 3 = 11-30 galls, 4 = 31-100 galls and 5 = more than 100 galls; PD: population density (eggs g⁻¹ root); RF: reproduction factor; R: reaction (Oostenbrink, 1966) where: RF< 1.0 resistant, RF > 1.0 susceptible, and RF = 0 immune; RI: reproduction index; RN: resistance level, the data were analyzed using the scale of RI (Taylor, 1967), where: RI > 50% susceptible (S), RI: 26%-50% low resistance (LR). RI: 11%-25% intermediate resistance (IR), RI = 1%-10% highly resistant (HR) and RI = 0 immune (I).

		Experiment 1 (March-May 2021)													
		42 DAI							63 DAI						
Eggs	Genotype/	T = 22-30 °C						T = 25-36 °C							
plant ⁻¹	cultivar	GI			RI	RN	GI	PD	RF	R	RI	RN			
4500	UTC24	3	2 968°	6.0°	S	S 53.4 S		4	4 838 ^b	19.5 ^b	S	55.6	S		
	UTC25	3	3 181ь	6.9 ^b	s	57.2	S	4	7 299°	19.7°	S	83.9	s		
	UTC66	2	620 ^d	1.7^{d}	S	11.1	IR	3	992 ^d	4.1 ^d	S	11.3	IR		
	UTC67	2	438°	1.2ª	S	7.8	HR	3	699e	2.7°	S	8.0	HR		
	UTC90	2	172 ^f	0.7^{f}	R	3.0	HR	3	301 ^f	0.9 ^f	R	3.4	HR		
	Revelation	3	5 554ª	9.6ª	s	*	S	4	8 692ª	25.5ª	S	*	s		
9000	UTC24	3	6 867°	7.3°	s	69.6	S	5	9 358°	17.8°	s	79.7	S		
	UTC25	3	8 061 ^b	8.5 ^b	s	70.3	S	5	11 128 ^b	20.1 ^b	s	94.8	S		
	UTC66	3	2 683ª	2.8 ^d	s	27.2	IR	4	3 202 ^d	8.2 ^d	S	27.3	LR		
	UTC67	3	1 841°	1.8°	s	18.6	IR	4	2 217ª	4.2°	S	18.9	IR		
	UTC90	3	979 ^f	0.9 ^f	R	9.9	HR	4	1 313 ^f	2.2 ^f	s	11.1	IR		
	Revelation	4	9 855ª	11.8ª	s	*	S	5	11 731ª	29.1ª	S	*	S		
13500	UTC24	4	13 097°	11.2°	s	76.2	S	5	17 689°	20.6°	S	82.4	S		
	UTC25	4	13 410 ^b	12.5 ^b	s	78.1	S	5	21 280ь	24.0 ^b	S	99.2	S		
	UTC66	4	5 644ª	5.6 ^d	S	32.8	LR	4	7 532ª	10.1^{d}	S	35.1	LR		
	UTC67	3	4 434e	4.1ª	S	25.8	IR	4	6 017ª	8.8°	S	28.0	LR		
	UTC90	3	$2\ 452^{f}$	2.3 ^f	S	14.2	IR	4	$4\ 134^{\mathrm{f}}$	4.8 ^f	S	19.2	IR		
	Revelation	4	17 168ª	16.2ª	S	*	S	5	21 443ª	40.6ª	S	*	S		

Table 2. Results of Experiment 2 according to the gall index (GI), reproduction factor (RF), and reproduction index (RI) of *Meloidogyne enterolobii* in *Capsicum annuum* landraces from Mexico. Mean values followed by different letters in the column indicate significant differences among treatments according to Fisher's LSD test (P < 0.05). T: Temperature range; DAI: days after inoculation; GI: gall index, the data were analyzed using the gall index scale from 1 to 5, (Taylor and Sasser, 1978), where: 0 = 0 galls, 1 = 1-2 galls, 2 = 3-10 galls, 3 = 11-30 galls, 4 = 31-100 galls and 5 = more than 100 galls; PD: population density (eggs g⁻¹ root); RF: reproduction factor; R: reaction (Oostenbrink, 1966) where: RF< 1.0 resistant, RF > 1.0 susceptible, and RF = 0 immune; RI: reproduction index; RN: resistance level, the data were analyzed using the scale of RI (Taylor, 1967), where: RI > 50% susceptible (S), RI: 26%-50% low resistance (LR). RI: 11%-25% intermediate resistance (IR), RI = 1%-10% highly resistant (HR) and RI = 0 immune (I).

		Experiment 2 (December 2021-February 2022													
		42 DAI							63 DAI						
	Genotype/	T = 17-24 °C						T = 25-29 °C							
Eggs plant ⁻¹	cultivar	GI	PD	RF	R	RI	RN	GI	PD	RF	R	RI	RN		
4500	UTC24	2	2 052b	3.8 ^b	S	51.3	S	3	4 011 ^b	14.2 ^b	S	56.2	S		
	UTC25	2	2 186 ^b	3.9 ^b	S	54.7	S	3	4 502 ^b	15.7 ^b	S	63.0	S		
	UTC66	2	485°	1.6°	S	12.1	IR	3	653°	2.9°	S	14.1	IR		
	UTC67	2	314 ^{cd}	1.1c	S	7.8	HR	3	408 ^{cd}	1.4 ^{cd}	S	8.5	HR		
	UTC90	2	204 ^d	0.6 ^d	R	5.1	HR	3	290 ^d	0.9 ^d	R	5.3	HR		
	Revelation	2	3 992ª	8.5ª	S	٠	S	4	7 137ª	22.1ª	S	•	S		
9000	UTC24	2	5 738⁰	6.1 ^b	S	62.8	S	4	9 332 ^b	16 ^b	S	67.5	S		
	UTC25	2	5 946 ^b	6.2 ^b	S	65.1	S	4	9 552ªb	16.2 ^b	S	69.1	S		
	UTC66	2	1 907c	2.0c	S	20.8	IR	3	2 944°	7.6°	S	27.3	LR		
	UTC67	2	1 394 ^{cd}	1.3 ^{cd}	S	15.2	IR	3	2 510c	4.7c	S	18.9	IR		
	UTC90	2	951ª	0.9 ^d	R	10.4	HR	3	1 548 ^d	2.6 ^d	S	11.2	IR		
	Revelation	2	9 130ª	10.9ª	S	•	S	4	11 408ª	28.3ª	S	•	S		
13500	UTC24	4	11 310 ^b	10.8 ^b	S	71.8	S	4	14 452 ^b	18.5 ^b	S	73.7	S		
	UTC25	4	11 909 ^b	11.4 ^b	S	75.6	S	4	14 529 ^b	18.9 ^b	S	74.1	S		
	UTC66	3	4 843c	4.8c	S	30.7	LR	4	7 054°	8.2c	S	35.9	LR		
	UTC67	3	3 784°	3.7c	S	24.0	IR	4	5 116°	6.5°	S	26.1	LR		
	UTC90	3	1 931 ^d	1.8 ^d	S	12.2	IR	4	2 919 ^d	3.4 ^d	S	14.8	IR		
	Revelation	4	15 740ª	15.8ª	S	•	S	5	19595ª	37.1ª	S	•	S		

Finally, an effect of temperature was observed on the gall index (GI), reproduction factor (RF), and reproduction index (RI), mainly in the genotype UTC25, which showed a greater number of nematode eggs in its roots and the reproduction index of the nematode increased more than 20% when temperatures were above 30 °C. For the rest of the genotypes, in the first experiment where temperatures ranged from 22 to 36 °C, a higher number of *M. enterolobii* eggs was recorded for all inoculum doses compared to the second experiment when the average temperatures ranged from 17 to 29 °C.

DISCUSSION

Resistance is defined as the ability of a plant to inhibit the reproduction of a nematode species compared to the reproduction of the nematode in a plant lacking such trait, i.e., compared to a susceptible plant. In addition, the response of the same plant to parasitism by the nematode differs from the ability of the plant to support nematode reproduction because the nematode can invade the plant, but it will have difficulty completing its development and reproduction (Cook and Evans, 1987).

In this research, the resistance levels determined based on the reproduction factor (RF), reproduction index (RI), and gall index (GI) provided more precise information to characterize the resistance of *C. annuum* landraces from Mexico to the nematode *M. enterolobii*. Only genotype UTC90 was considered highly resistant according to its RF and RI at a dose of 4500 eggs plant⁻¹; however, according to the gall scale, it was located at the same level (3) as genotypes UTC24, UTC25, UTC66, and UTC67. Therefore, this last variable did not show sufficient information to discriminate between genotypes in relation to their resistance level.

In other research, it has been concluded that the root-gall index is not a reliable and adequate criterion for the selection of resistant cultivars (López-Gómez et al., 2015; Hallmann and Kiewnick, 2018) since the formation of galls on the roots indicates the presence of the nematode but does not ensure its development or reproduction. On the contrary, the formation of egg masses on the roots is considered a reliable and adequate indicator since it correlates with nematode reproduction and is determined by the RF and RI (Bellafiore et al., 2015; Mantelin et al., 2017; Cabasan et al., 2018; Hallmann and Kiewnick, 2018).

Plant resistance to nematodes can be influenced by several parameters, from the species or population of the nematode to environmental effects. In the trials carried out in this study, it was observed that genotype UTC25 was more susceptible to *M. enterolobii* at all inoculum doses when the temperature was above 30 °C. In this sense, it is known that temperature affects nematode reproduction and plant resistance, and the instability of resistance genes at high soil temperatures has been reported, as in the case of the *Mi-1* gene in tomato and the *N* gene in pepper, limiting their usefulness for managing *M. enterolobii* in vegetables in hot climates, due to the loss of their ability at temperatures above 28 °C (Haroon et al., 1993; Brito et al., 2007).

In this study, the results of our second resistance trial showed a lower RF at temperatures < 25 °C. In contrast, in the first experiment with temperatures > 25 °C, there was an increase in nematode reproduction, and this was higher when the temperature was equal to or higher than 30 °C. It has been reported that the adaptability of *M. enterolobii* to different temperatures gives it greater aggressiveness, and this nematode is capable of completing its life cycle at temperatures above 30 °C in vegetables, whereas, when at temperatures below 25 °C, a delay in the infection process is observed due to the reduced penetration and development of infective juveniles (J₂) (Velloso et al., 2022; Salazar-Mesta et al., 2023). Similarly, Brito et al. (2007) concluded that populations of *M. enterolobii* were able to reproduce successfully at temperatures of 22 and 33 °C, but with a lower RF when the temperature was 22 °C in tomato cultivars containing the *Mi-1* genes, as well as in chili pepper cultivars with *N* and *Tabasco* genes.

Another important parameter to consider in resistance trials is the nematode inoculum density, i.e., the initial population of a *Meloidogyne* species used in a trial directly influences the severity of plant damage (Débia et al., 2021; Padilla-Hurtado et al., 2022). In our research, increasing the nematode inoculum density modified the resistance response in the landraces evaluated based on the criteria of RF and RI, since genotype UTC90 was resistant to an inoculum density of 4500 eggs for both criteria, but at doses of 9000 and 13500 eggs, it was considered as susceptible according to the RF and with intermediate resistance based on the RI. Similarly, Carrillo-Fasio et al. (2020) determined that genotype UTC90 was resistant to a dose of 2000 *M. enterolobii* eggs. In contrast, Marques et al. (2019) concluded that increasing the inoculum levels of *M. enterolobii* did not modify the resistance or susceptibility behavior of *Capsicum* spp. genotypes based on the RF with doses of 2000, 4000, and 8000 eggs. On the other hand, Gonçalves et al. (2014) determined the resistance level of *Capsicum* spp. accessions towards *M. enterolobii* according to the nematode RF and index criteria, and found that all *C. annuum* accessions were susceptible, and only one *C. chinense* accession was considered resistant based on a single inoculum dose (500 eggs) of the nematode.

So far, there are no reports of *C. annuum* genotypes with resistance to initial inoculum densities greater than 8000 *M. enterolobii* eggs such as those used in our study. Likewise, in most of the studies, the resistance of *Capsicum* spp. landraces to *M. enterolobii* was evaluated with a single inoculum dose of the nematode, and the results are compared with a single criterion or resistance scale, so it is necessary to

carry out more studies that allow knowing the behavior of *Capsicum* spp. landraces with different resistance evaluation parameters such as those obtained in this research.

CONCLUSIONS

The results of this study provide relevant information regarding chili pepper landraces resistant to *Meloidogyne enterolobii*. Genotypes UTC66, UTC67, and UTC90 showed a higher level of resistance with a damage percentage lower than 50% compared to 'Revelation' (susceptible). Genotype UTC90 showed the lowest reproduction factor and index, so it was considered a highly resistant genotype to an inoculum dose of 4500 *M. enterolobii* eggs.

Author contribution

Conceptualization: J.A.C.F., J.M.T.P. Methodology: J.E.R.M., J.A.C.F. Validation: R.J.S.M. Formal analysis: R.J.S.M. Investigation: R.J.S.M., Resources: R.S.G.E., J.M.T.P. Writing-original draft: R.J.S.M. Writing-review & editing: J.M.T.P. Supervision: J.L.F. Funding acquisition: J.M.T.P. All co-authors reviewed the final version and approved the manuscript before submission.

References

- Bellafiore, S., Jougla, C., Chapuis, É., Besnard, G., Suong, M., Vu, P.N., et al. 2015. Intraspecific variability of the facultative meiotic parthenogenetic root-knot nematode (*Meloidogyne graminicola*) from rice fields in Vietnam. Comptes Rendus Biologies 338:471-483. doi:10.1016/j.crvi.2015.04.002.
- Brito, J.A., Kaur, R., Cetintas, R., Stanley, J.D., Mendes, M.L., McAvoy, E.J., et al. 2008. Identification and isozyme characterization of *Meloidogyne* spp. infecting horticultural and agronomic crops, and weed plants in Florida. Nematology 10(5):757-766. doi:10.1163/156854108785787253
- Brito, J.A., Stanley, J.D., Kaur, R., Cetintas, R., Di Vito, M., Thies, J.A., et al. 2007. Effects of the *Mi-1*, *N* and *Tabasco* genes on infection and reproduction of *Meloidogyne mayaguensis* on tomato and pepper genotypes. Journal of Nematology 39(4):327-332.
- Cabasan, M.T.N., Kumar, A., De Waele, D. 2018. Evaluation of resistance and tolerance of rice genotypes from crosses of *Oryza glaberrima* and *O. sativa* to the rice root-knot nematode, *Meloidogyne graminicola*. Tropical Plant Pathology 43:230-241. doi:10.1007/s40858-018-0210-8.
- Carrillo-Fasio, J.A., Martínez-Gallardo, J.A., Ayala-Tafoya, F., López-Orona, C.A., Allende-Molar, R., Retes-Manjarrez, J.E. 2020. Screening for resistance to *Meloidogyne enterolobii* in *Capsicum annuum* landraces from Mexico. Plant Disease 104:817-822. doi:10.1094/PDIS-04-19-0718-RE.
- Carrizo-García, C., Barfus, M.H.J., Serh, E.M., Barbosa, G.E., Samuel, R., Moscone, E.A., et al. 2016. Phylogenetic relationships, diversification and expansion of chili Peppers (*Capsicum*, Solanaceae). Annals of Botany 118:35-51. doi:10.1093/aob/mcw079.
- Castagnone-Sereno, P. 2012. *Meloidogyne enterolobii* (=*M. mayaguensis*): Profile of an emerging highly pathogenic, root- knot nematode species. Nematology 14:133-138. doi:10.1163/156854111X601650.
- Castillo, P., Castagnone-Sereno, P. 2020. *Meloidogyne enterolobii* (Pacara earpod tree root-knot nematode). Invasive Species Compendium. CABI, Wallingford, UK. doi:10.1079/ISC.33238.20210200738.
- Cook, R., Evans, K. 1987. Resistance and tolerance. p. 179-231. In Brown, R.H., Kerry, B.R. (eds.) Principles and practice of nematode control in crops. Academic Press, New York, USA.
- Débia, P.J.G., Barros, B.C.B., Puerari, H.H., Ferreira, J.C.A., Dias-Arieira, C.R. 2021. Induced systemic resistance in beet plants infected with *Meloidogyne javanica*. Chilean Journal of Agricultural Research 81(1):70-79. doi.org/10.4067/S0718-58392021000100070.
- Djian-Caporalino, C., Pijarowski, L., Fazari, A., Samson, M., Gaveau, L., O'Byrne, C., et al. 2001. High-resolution genetic mapping of the pepper (*Capsicum annuum* L.) resistance loci *Me*₃ and *Me*₄ conferring heat-stable resistance to root-knot nematodes (*Meloidogyne* spp.) Theorical and Applied Genetics 103:592-600. doi:10.1007/PL00002914.
- Fazari, A., Palloix, A., Wang, L., Hua, M.Y., Palloix, A.M.S., Zhang, B.X., et al. 2012. The root-knot nematode resistance *N*-gene co-localizes in the *Me*-genes cluster on the pepper (*Capsicum annuum* L.) P9 chromosome. Plant Breeding 131:665-673. doi:10.1111/j.1439-0523.2012.01994.x.
- Freitas, V.M., Correa, V.R., Motta, F.C., Sousa, M.G., Gomes, A.C.M.M., Carneiro, M.D.G., et al. 2014. Resistant accessions of wild *Psidium* spp. to *Meloidogyne enterolobii* and histological characterization of resistance. Plant Pathology 63:738-746. doi:10.1111/ppa.12149.

- Gonçalves, L.S.A., Gomes, V.M., Robaina, R.R., Valim, R.H., Rodrigues, R., Aranha, F.M. 2014. Resistance to rootknot nematode (*Meloidogyne enterolobii*) in *Capsicum* spp. accessions. Revista Brasileira de Ciências Agrárias 9(1):49-52. doi:10.5039/agraria.v9i1a3496.
- Hallmann, J., Kiewnick, S. 2018. Virulence of *Meloidogyne incognita* populations and *Meloidogyne enterolobii* on resistant cucurbitaceous and solanaceous plant genotypes. Journal of Plant Diseases and Protection 125:415-424. doi:10.1007/s41348-018-0165-5.
- Haroon, S.A., Baki, A.A., Huettel, R.N. 1993. An *in vitro* test for temperature sensitivity and resistance to *Meloidogyne incognita* in tomato. Journal of Nematology 25:83-88.
- Hussey, R.S., Barker, K.R. 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. Plant Disease Reporter 57:1025-1028.
- Long, H., Sun, Y., Chen, Y., Pei, Y., Feng, T., Che, H. 2023. Occurrence of root-knot nematodes (*Meloidogyne* spp.) on peppers in Hainan, China, and resistance of field cultivars to *M. enterolobii* and *M. incognita*. Plant Disease 107(10):3148-3154. doi:10.1094/PDIS-02-23-0281-RE.
- López-Gómez M., Flor-Peregrín E., Talavera M., Verdejo-Lucas S. 2015. Suitability of zucchini and cucumber genotypes to populations of *Meloidogyne arenaria*, *M. incognita*, and *M. javanica*. Journal Nematology 47(1):79-85.
- Mantelin, S., Bellafiore, S., Kyndt, T. 2017. *Meloidogyne graminicola*: A major threat to rice agriculture. Molecular Plant Pathology 18(1):3-15. doi:10.1111/mpp.12394.
- Marques, M.L.S., Chadud, J.V.G., Oliveira, M.F., Nascimiento, A.R., Rocha, M.R. 2019. Identification of chili pepper genotypes (*Capsicum* spp.) resistant to *Meloidogyne enterolobii*. Journal of Agricultural Science 11(8):165. doi:10.5539/jas.v11n8p165.
- Marques, M.L.S., Oliveira, M.F., Pereira, P.S., Rocha, M.R. 2020. Penetration and development of *Meloidogyne enterolobii* in resistant and susceptible *Capsicum* spp. European Journal of Horticultural Science 85(2):86-91. doi:10.17660/eJHS.2020/85.2.2.
- Oostenbrink, M. 1966. Major characteristics of the relation between nematodes and plants. Mededelingen van de Landbouwhogeschool, Wageningen 66:1-46.
- Padilla-Hurtado, B., Morillo-Coronado, Y., Tarapues, S., Burbano, S., Soto-Suárez, M., Urrea, R., et al. 2022. Evaluation of root-knot nematodes (*Meloidogyne* spp.) population density for disease resistance screening of tomato germplasm carrying the gene *Mi-1*. Chilean Journal of Agricultural Research 82:157-166. doi.org/10.4067/S0718-58392022000100157.
- Pinheiro, J.B., Reifschneider, F.J., Pereira, R.B., Moita, A.W. 2014. Reação de genótipos de *Capsicum* ao nematoidedas-galhas. Horticultura Brasileira 32(3):371-375. doi:10.1590/S0102-05362014000300022.
- Pinheiro, J.B., Silva, G.O., Macêdo, A.G., Biscaia, D., Ragassi, C.F., Ribeiro, C.S.C., et al. 2020. New resistance sources to root-knot nematode in *Capsicum* pepper. Horticultura Brasileira 38:33-40. doi:10.1590/S0102-053620200105.
- Salazar-Mesta, R.J., Carrillo-Fasio, J.A., Retes-Manjarrez, J.E., García-Estrada, R.S., León-Félix, J., Mora-Romero, G.A., et al. 2023. Characterization, pathogenicity, and reproduction of *Meloidogyne enterolobii* populations parasitizing vegetables in Sinaloa, Mexico. Tropical Plant Pathology 48:394-407. doi:10.1007/s40858-023-00576-7.
- Santos, J.L.F.D., Souza, F.D.F., Borel, J.C., Castro, J.M.D.C.E., Hood, A.S. 2021. Identification of sources of resistance to *Meloidogyne enterolobii* in acerola. Revista Caatinga 34(4):879-886. doi:10.1590/1983-21252021v34n415rc.
- Schwarz, T.R., Li, C., Yencho, G.C., Pecota, K.V., Heim, C.R., Davis, E.L. 2021. Screening sweet potato genotypes for resistance to a North Carolina Isolate of *Meloidogyne enterolobii*. Plant Disease 105(4):1101-1107. doi:10.1094/PDIS-02-20-0389-RE
- SIAP. 2022. Panorama Agroalimentario 2022. Servicio de Información Agroalimentaria y Pesquera (SIAP), Ciudad de Mexico. Available at https://www.gob.mx/siap (accessed 4 June).
- Soares, R.S., Silva, E.H.C., Vidal, R.L., Candido, W.D., Franco, C.A., Reifschneider, F.J.B., et al. 2018. Response of *Capsicum annuum* L. var. *annuum* genotypes to root-knot nematode infection. Chilean Journal of Agricultural Research 78:78-85. doi:10.4067/S0718-58392018000100078.
- Taylor, A.L. 1967. Introduction to research on plant nematology: an FAO guide to the study and control of the plantparasitic nematodes. FAO, Rome, Italy.
- Taylor, A.L., Sasser, J.N. 1978. Biology, identification, and control of root-knot nematodes (*Meloidogyne* spp.). Cooperative Publication. Department of Plant Pathology, North Carolina State University, and U.S. Agency for International Development, Raleigh, North Carolina, USA.

- Velloso, J., Maquilan, M., Campos, V., Brito, J., Dickson, D. 2022. Temperature effects on development of *Meloidogyne* enterolobii and M. floridensis. Journal of Nematology 54(1):e2022-1. doi:10.2478%2Fjofnem-2022-0013.
- Votava, E.J., Baral, J.B., Bosland, P.W. 2005. Genetic diversity of chile (*Capsicum annuum* var. annuum L.) landraces from northern New Mexico, Colorado, and Mexico. Economic Botany 59:8-17. doi:10.1663/0013-0001(2005)059[0008:GDOCCA]2.0.CO;2
- Waldo, B., Branham, S., Levi, A., Wechter, W., Rutter, W. 2022. Distinct genomic loci underlie quantitative resistance to *Meloidogyne enterolobii* galling and reproduction in *Citrullus amarus*. Plant Disease 107(7):2126-2132. doi:10.1094/PDIS-09-22-2228-RE.
- Wang, L.H., Gu, X.H., Hua, M.Y., Mao, S.L., Zhang, Z.H., Peng, D.L., et al. 2009. A SCAR marker linked to the N gene for resistance to root knot nematodes (*Meloidogyne* spp.) in pepper (*Capsicum annuum* L.) Scientia Horticulturae 122:318-322. doi:10.1016/j.scienta.2009.04.011.