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Response of *Capsicum* genotypes to the root-knot nematode *Meloidogyne enterolobii*

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Abstract: *Meloidogyne enterolobii* is a highly aggressive root-knot nematode (RKN) that causes substantial economic losses to *Capsicum* species and other crops. Resistant genotypes have been used as an alternative to chemical nematicides; however, available *Capsicum* cultivars are susceptible to this nematode. Hence, the objective of this study was to screen a Brazilian *Capsicum* germplasm collection, comprising germplasm from Embrapa and commercial cultivars to *M. enterolobii*, under greenhouse conditions. The treatments comprised 39 *C. chinense*, 22 *C. annuum*, and 2 tomato (*Solanum lycopersicum*) cultivars (checks). Individual plants were inoculated with 5,000 *M. enterolobii* eggs and second-stage juveniles (J2), and evaluations were carried out for the gall index, egg mass index, number of eggs per gram of roots, reproduction factor (RF), and reproduction index (RI) at 65 days post-inoculation. The results demonstrated that all plant genotypes exhibited susceptibility to this nematode. However, some genotypes exhibited a lower RF (0.01–4.9) than the tomato 'Nemadoro' (RF = 8.4–15.3), thus being classified as low susceptibility according to the RI concept. These findings are important for ongoing efforts to identify novel sources of resistance to RKN and contribute to safer, more sustainable agricultural practices.

Keywords: Bell pepper, chili pepper, guava root-knot nematode, resistance, Solanaceae

Résumé: *Meloidogyne enterolobii* est un nématode à galles qui provoque des pertes économiques substantielles chez *Capsicum* spp. et d'autres cultures. Des génotypes résistants ont été déployés comme alternative aux nématicides chimiques; cependant, aucun cultivar de *Capsicum* résistan à ce nématode n'a été. Par conséquent, l'objectif de cette étude était de sélectionner une collection brésilienne de germoplasmes de *Capsicum*, comprenant du germoplasme d'Embrapa et des cultivars commerciaux de *M. enterolobii* dans des conditions de serre. Les traitements comprenaient 39 *C. chinense*, 22 *C. annuum* et 2 cultivars de tomates (*Solanum lycopersicum*). Chaque plante a été inoculée avec 5000 œufs et juvéniles de deuxième stade (J2) de *M. enterolobii* et analysée 65 jours après l'inoculation. Des évaluations ont été effectuées pour indice de galle, indice de masse d'œufs, nombre d'œufs par gramme de racines, facteur de reproduction (RF) et indice de reproduction (RI). Les résultats ont montré que tous les génotypes de plantes étaient sensibles à ce nématode. Cependant, certains génotypes avaient un RF inférieur (0,01–4,9) par rapport à la tomate Nemadoro (RF = 8,4–15,3), étant classés comme peu sensibles selon le concept RI. Nos résultats contribuent aux objectifs d'identification de nouvelles sources de résistance et de pratiques agricoles plus durables.

Mots-clés: nématode à galles de la goyave, piment, poivron, réaction de l'hôte, Solanaceae

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Introduction

Capsicum species (peppers and chillies) are solanaceous vegetable plants that are cultivated worldwide for their socioeconomic and nutritional values. Consumption of these vegetables has increased recently, primarily due to their organoleptic characteristics and heightened public awareness of health benefits. Demand for these products is therefore increasing steadily, as they are consumed by more than a third of the global population. Furthermore, these plants are genetically diverse and versatile, with unique flavouring and high nutritional value, contributing to their daily consumption in fresh, dried, and processed forms. They are anti-carcinogenic and rich in provitamin A, vitamin C, carotenoids, antioxidants, minerals, and other bioactive compounds (De 2003; De Witt and Bosland 2009; Rodríguez-Burruezo et al. 2009; Hervert-Hernández et al. 2010; Mateos et al. 2013; Penella and Calatayud 2018; Parisi et al. 2020).

Capsicum crops are among the ten most widely cultivated vegetables worldwide, with an annual global production of over 41 million metric tons, cultivated across approximately 3.8 million hectares. China (16 million tons) and Mexico (2.3 million tons) top the list of global producers (FAO 2019). These crops also play a key role in vegetable production in Brazil due to their socioeconomic value, particularly for small-scale farmers. It is estimated that 280,000 tons are produced annually on 13 000 hectares (Ribeiro et al. 2015).

The cultivation of *Capsicum* crops can be limited by a number of factors, including climate and soil conditions, as well as diseases and pests. The most significant of these diseases are those caused by bacteria, fungi, and nematodes (Lima et al. 2017; Parisi et al. 2020). Among the diseases caused by plant-parasitic nematodes, those caused by the root-knot nematodes (RKN), such as *Meloidogyne* spp., e.g., *M. incognita* (Kofoid and White 1919) Chitwood 1949, and *M. arenaria* (Neal 1889) Chitwood 1949 are the most economically important in *Capsicum* and other crops, especially in the tropics, due to their high level of damage, aggressiveness, and difficulty of control in the field (Hunt and Handoo 2009; Lopes and Ferraz 2016; Wang et al. 2018; Pinheiro et al. 2020; Carneiro et al. 2024).

These nematodes damage plant roots, which inhibits proper water and nutrient uptake. They cause plant yellowing and decreased growth of the roots and shoots, ultimately leading to a reduced yield (Hunt and Handoo 2009; Lopes and Ferraz 2016). Furthermore, *Capsicum* plants infected by RKN are more prone to infections caused by other soil-borne bacterial and fungal pathogens (Soares et al. 2018).

Lately, the guava RKN *M. enterolobii* (Yang and Eisenback 1983) has been considered a threat to a number of crops, including *Capsicum* spp (Carneiro et al. 2006; Wang et al. 2018). Due to its widespread distribution and broad host range, virulence, and ability to parasitize plant genotypes resistant to other RKN species, this nematode is an emerging and aggressive pathogen (Carneiro et al. 2006; Cantu et al. 2009; Kiewnick et al. 2009; Shao et al. 2021; Ye et al. 2021; Pinto et al. 2023, 2024; Sikandar et al. 2023).

This nematode was first reported in Brazil in 2001, causing damage to guava (*Psidium guajava* L.) in the states of Pernambuco and Bahia (Carneiro et al. 2001). It was later reported in the state of São Paulo, parasitizing the bell pepper rootstock cv. Silver, which is resistant to *M. incognita* and *M. javanica* (Carneiro et al. 2006). Notably, this nematode has been reported to cause damage to a number of other crops in various regions worldwide, including tobacco, potato, tomato, *Capsicum* spp., eggplant, and scarlet eggplant, among others (Pinheiro et al. 2015; Ye et al. 2021; Ragassi et al. 2022; Sikandar et al. 2023). Therefore, it has been challenging to find promising sources of resistance against this nematode. Steady efforts must therefore be made to find effective control methods to reduce the significant economic impact caused by this important species of nematode.

Different methods and techniques have been employed to manage RKN, including biological control, crop rotation, cultural practices, grafting, and chemical nematicides (Hunt and Handoo 2009; Tanimola et al. 2017). However, the efficacy of these methods varies depending on climate conditions, soil types, nematode population levels, and plant genotypes. Furthermore, the use of certain chemical nematicides has been restricted or discontinued due to their harmful environmental and health effects.

Alternatively, using resistant varieties is the most effective and environmentally safe way to manage nematodes in the field. Several resistance genes have been identified and characterized in *Capsicum* species, including *N*, *Me1*, *Me2*, *Me3* (= *Me7*), *Me4*, *Me5*, *Me6*, *Mech1*, and *Mech 2* (Hendy et al. 1985; Djian-Caporalino et al. 2007; Wang et al. 2018). Most of these genes are found in *C. annuum* L., but none of them naturally occur in *C. chinense* Jacq. accessions (Wang and Bosland 2006; Naresh et al. 2019). Some of these resistance genes are specific to a particular RKN species, while others (e.g., *N*, *Me1*, and *Me3*) exhibit broad-spectrum resistance (e.g., *M. incognita* race 3, *M. javanica*, *M. arenaria* and *M. haplanaria* Eisenback, Bernard, Starr, Lee. & Tomaszewski, 2003 (Hajihassani et al. 2019). Conversely, a *C. annuum* rootstock harbouring both the *Me1* and *Me3* genes was found to be susceptible to *M. enterolobii* under field conditions (Pinheiro et al. 2015). Overall, the response of *Capsicum* spp. to nematode infection depends on the plant accession, the resistance gene, and the RKN species (Gisbert et al. 2013).

Sources of resistance to *M. arenaria, M. javanica*, and *M. hapla* Chitwood, 1949 have been identified in *C. chinense* germplasm (Thies and Fery 2001). However, no *Capsicum* cultivars resistant to *M. enterolobii* have been found in this germplasm. Previous studies have identified *C. chinense* accessions with low susceptibility levels; but none are resistant (Pinheiro et al. 2013, 2020). Although several resistance genes to RKN have been found in *C. annuum*, transferring these traits to *C. chinense* via conventional crosses has proved difficult due to levels of unilateral incompatibility (Onus and Pickersgill 2004). Furthermore, the lowland areas of the Amazon Basin are the main centres of *C. chinense* diversity (Pozzobon et al. 2015; Barboza et al. 2022). Therefore, identifying *C. chinense* accessions with high levels of durable resistance to RKN, especially *M. enterolobii*, is of great interest for breeding programs, particularly in neotropical regions (Pinto et al. 2025). Thus, the objective of this study was to screen a *C. chinense* and *C. annuum* germplasm collection (Embrapa, Brazil), mainly from the Amazon Basin Region, to search for genetic resistance against the nematode *M. enterolobii* under greenhouse conditions.

Materials and methods

Plant genotypes

Sixty-one *Capsicum* genotypes, including 39 *C. chinense* and 22 *C. annuum*, were tested for host suitability to *M. enterolobii* (Table 1). The *Capsicum* germplasm was obtained from the public research sector (Embrapa Hortaliças). Tomato plants (*Solanum lycopersicum* L.) were also included in the experiments to demonstrate the inoculum viability and optimum growth conditions. The tomato 'Nemadoro' was used in the experiments as a resistant standard and to check the ability of *M. enterolobii* to parasitize this cultivar, as it is resistant to 13 species of *Meloidogyne*, but not *M. enterolobii* (Gabriel et al. 2020).

Nematode inoculum

The *Meloidogyne enterolobii* inoculum was obtained from a pure culture that was multiplied by periodic subculturing on tomato plants (*S. lycopersicum* cv. 'Santa Cruz'), which was previously identified as M2 (RM 0.7–0.9) using esterase phenotyping and SCAR PCR (Carneiro and Almeida 2001; Tigano et al. 2010), and maintained in a greenhouse (25–30°C). Nematode eggs and second-stage juveniles (J2) were extracted from infected roots according to Hussey and Barker (1973) and as modified by Boneti and Ferraz (1981). The roots were washed with tap water, and the nematode eggs in the egg masses were extracted using 0.5% sodium hypochlorite. The roots were sliced into small pieces (2 cm), covered with sodium hypochlorite, shaken for 30 s, washed with tap water, and then the eggs were collected using a 500-mesh screen. The total number of eggs per millilitre was quantified under a light microscope using a nematode counting slide (Peter's slide). *Capsicum* seedlings (25 days old) were inoculated with 5,000 eggs and J2s (Kiewnick et al. 2009; Pinheiro et al. 2020), three days after transplanting by placing the suspension into two holes around the stem base (Pinto et al. 2024).

Experimental site, design, and settings

The experiments were carried out in a greenhouse at Embrapa Hortaliças, Gama, DF, Brazil, over two seasons, from January to March 2023 (summer) and from May to July 2023 (autumn, winter). The average temperature in the first experiment was 26.7°C (49.9°C maximum and 18°C minimum), while in the second experiment, the average temperature was 26.6°C (49.7°C maximum and 14.2°C minimum).

The experiments were set out in a completely randomized design with 41 treatments and six replicates (39 *C. chinense* genotypes and two tomato genotypes) (Table 2) (experiments 1 and 2) and 24 treatments and six replicates (22 *C. annuum* genotypes and two tomato genotypes) (Table 3) (experiments 3 and 4). Each plant grown in 2 L pots filled with sterilized soil, sand, and Bioplant® organic compost constituted a single replicate.

Sample processing and statistical analysis

The roots of the plants were carefully removed from the soil and debris, washed with tap water, dried with a paper towel, and used for processing at the Nematology Laboratory (Embrapa Hortaliças). The fresh weight of the roots was determined at 65 days after inoculation. The roots were stained with Phloxine B (6 mg L^{-1}), and the nematode eggs + J2 were extracted from the infected roots and quantified as described

Table 1. *Capsicum chinense* and *C. annuum* accessions from Embrapa Vegetable Crops active germplasm Bank evaluated for resistance to *M. enterolobii.*

Accession code	Geographic origin	Morphoagronomic type
Capsicum chinense		
CNPH 15 348	Manaquiri – Amazon State	Habanero
CNPH 15 749	Brasília – DF (The Federal District)	Habanero
CNPH 55 001	Cultivar Pimenta de cheiro – Hortivale	Cheiro/aromatic, non-pungent
CNPH 55 002	Cultivar Pimenta de cheiro do Norte – Agristar	Cheiro/aromatic, non-pungent
CNPH 55 122	Santa Maria – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 123	Gama – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 129	Cultivar Pimenta de cheiro – Agristar	Cheiro/aromatic, non-pungent
CNPH 55 135	Rio Branco – Acre State	Cheiro/aromatic, non-pungent
CNPH 55 136	Rio Branco – Acre State	Cheiro/aromatic, non-pungent
CNPH 55 139	Rio Branco – Acre State	Cheiro/aromatic, non-pungent
CNPH 55 142	Taquara – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 148	Taquara – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 149	Taquara – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 155	Paranoá–DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 157	Cultivar Lupita – Feltrin	Cheiro/aromatic, non-pungent
CNPH 55 159	Ceilândia – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 160	Brasília – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 161	Ceilândia – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 162	Taquara – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 163	Taquara – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 55 201	Santa Maria – DF (The Federal District)	Cheiro/aromatic, non-pungent
CNPH 60 008–3	Manaquiri – Amazon State	Landrace of the Murupi-type
CNPH 60 008–4	Manaquiri – Amazon State	Landrace of the Murupi-type
CNPH 60 042–2	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 043–2	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 043–3	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 044–3	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 045–2	Manaquiri – Amazon State	Landrace of the Murupi-type
CNPH 60 046–1	Itacoatiara – Amazon State	Landrace of the Murupi-type
CNPH 60 047–5	Manaquiri – Amazon State	Landrace of the Murupi-type
CNPH 60 048–3	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 061	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 064	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 069	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 074	Manaus – Amazon State	Landrace of the Murupi-type
CNPH 60 078	Manaquiri – Amazon State	Landrace of the Murupi-type
CNPH 60 080	Itacoatiara – Amazon State	Landrace of the Murupi-type
CNPH 60 087	Manaquiri – Amazon State	Landrace of the Murupi-type
CNPH 60 090	Manaus – Amazon State	Habanero
BRS Nandaia	Commercial cultivar (Embrapa)	Habanero
Capsicum annuum		
CNPH 144 OR-2–2	Brasília – DF (The Federal District)	Ornamental pepper
CNPH 154 OR-1–4	Brasília – DF (The Federal District)	Ornamental pepper
CNPH 155-OR-2–1	Brasília – DF (The Federal District)	Ornamental pepper
CNPH 158 OR-1–1	Brasília – DF (The Federal District)	Ornamental pepper
CNPH 161 OR-5–1	Brasília – DF (The Federal District)	Ornamental pepper
CNPH 2781	India	Cayenne
CNPH 30 370	Brasília – DF (The Federal District)	Jalapeño
CNPH 30 371	Brasília – DF (The Federal District)	Jalapeño
CNPH 30 545–2	Brasília – DF (The Federal District)	Jalapeño
CNPH 30 647	Brasília – DF (The Federal District)	Jalapeño
CNPH 30 649	Brasília – DF (The Federal District)	Jalapeño
CNPH 3839	Commercial cultivar Vulcão – Feltrin	Ornamental pepper
CNPH 4134	Commercial cultivar Espaguetinho – Isla	Ornamental pepper
CNPH 4135	Cultivar Pirâmide – Commercial – Isla	Ornamental pepper
CNPH 50 316–2	Brasília – DF (The Federal District)	Cayenne
CNPH 50 317–2	Brasília – DF (The Federal District)	Cayenne

(*Continued*)

Table 1. (Continued.)

Accession code	Geographic origin	Morphoagronomic type
CNPH 50 318–1	Brasília – DF (The Federal District)	Cayenne
CNPH 50 318–4	Brasília – DF (The Federal District)	Cayenne
CNPH 50 319–3	Brasília – DF (The Federal District)	Cayenne
BRS ACARA	Commercial cultivar (Embrapa)	Rootstock pepper
BRS SARAKURA	Commercial cultivar (Embrapa)	Jalapeño
IKEDA	Commercial cultivar – Agristar	Bell pepper

above. The host reaction was measured by considering the fresh weight of the roots, the gall index (GI) (Bridge and Roberts 1981), the egg mass index (EMI) (MacGuidwin and Johnson 1982), the number of eggs + J2 per gram of roots [eggs + J2 (g root)$^{-1}$] = final population/fresh weight of roots, and the nematode reproduction factor (RF = final population/initial population) (Oostenbrink 1966).

Plant genotypes were rated according to their reaction to the nematode as either resistant or poor host (RF < 1) or susceptible or suitable host (RF > 1). The plant genotypes were also rated based on the nematode reproduction index (RI), as proposed by Taylor (1967), with ratings relative to a susceptible standard (genotypes CNPH55160 and CNPH50319–3): S = susceptible (RI > 50%), LS = low susceptibility (RI = 26–50%), MR = moderately resistant (RI = 11–25%), *R* = resistant (RI = 1–10%), HR = highly resistant (IR < 1%), and I = immune (RI = 0%).

The data were transformed using the formula $\sqrt{x} + 0.5$ for statistical analysis, i.e., normality test, analysis of variance, and Scott-Knott test ($p < 0.05$). The data were then back-transformed to present the original values. As there were significant interactions between experiments and genotypes ($p < 0.05$), the data sets from each experiment were analysed separately.

Results

The genotypes reacted differently to *M. enterolobii* as inferred by the GI, EMI, eggs + J2 (g root)$^{-1}$, RF and RI parameters (Tables 2 and 3). The RF and RI measure the effects of the plant genetic background on nematode reproduction. Plant genotypes were rated according to their reaction to the nematode as resistant or poor host (RF < 1, R) or, susceptible or suitable host (RF > 1, S), and immune (RF = 0, I).

In this study, the RF value of the susceptible control tomato 'Rutgers' was considered high (14.8 - 20.8), indicating good inoculum viability and suitable conditions for nematode development (Tables 2 and 3). Overall, all genotypes evaluated were rated as susceptible (RF > 1) to *M. enterolobii*, including the tomato 'Nemadoro', a resistant control for other *Meloidogyne* spp. (RF = 8.4–15.3). The fact that 'Nemadoro' is susceptible here confirms the exclusive presence of *M. enterolobii* in our assays, as it would have exhibited resistance to infection if other species were present.

Nonetheless, it is worth mentioning that some genotypes had a lower RF than the tomato 'Nemadoro', e.g., *C. chinense* genotypes CNPH15749, CNPH60064, CNPH55129, CNPH60078, CNPH60058, CNPH60046, CNPH60061, CNPH6661, CNPH60087, CNPH55155, BRS Nandaia, and CNPH55201, which had RF values ranging from 1.7 to 5.6 (Table 2), and *C. annuum* genotypes CNPH158OR–1–1, CNPH30647, CNPH155-OR -2–1, CNPH50316–2, CNPH2781, and CNPH50317–2, with RF ranging from 0.01 to 4.9 (Table 3), indicating lower susceptibility. Indeed, these trends are corroborated by Taylor's (1967) RI classification, in which the genotypes listed above were rated as having lower susceptibility (LS) compared to the susceptible controls CNPH55160 and CNPH50319–3 (Tables 2 and 3). However, according to Taylor's concept, none of the genotypes were rated as resistant. In experiment 3, genotype CNPH 158 OR-1–1 was rated as resistant (RF < 1) and highly resistant according to Taylor's concept (RF = 0.01); however, in experiment 4, it was rated S/MR (Table 3).

The GI and EMI indices provide supporting parameters for analysing genotype responses to RKN infection. Typically, there is a positive correlation between these indices and the RF, i.e., the higher the RF, the higher the GI and EMI. Overall, these trends are seen in Tables 2 and 3.

Discussion

Genetic resistance in *Capsicum* spp. has been used against *Meloidogyne* species other than *M. enterolobii* (e.g., *M. incognita*, *M. javanica*, *M. arenaria*, *M. hapla, M. floridensis* Handoo, Nyczepir, Esmenjaud, van der Beek, Castagnone-Sereno, Carta, Skantar and Higgins

Table 2. Host reaction of *Capsicum chinense* genotypes inoculated with *Meloidogyne enterolobii* under greenhouse conditions at 65 days post- inoculation. Gall index (GI), egg mass index (EMI), eggs and second-stage juveniles (J2) per (g root)$^{-1}$, nematode reproduction factor (RF) and reproduction index (RI).

	GI[a,b]		EMI[c]		Eggs+J2/(g root)$^{-1(d)}$		RF[e]/Reaction[f]/Classification[g]	
Genotypes	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
CNPH 55 160[h]	5.0	4.0	5.0	4.0	1932 a A	3008 a A	11.8 a A S/S	9.7 a A S/S
CNPH 60 042–2	5.0	4.5	5.0	4.5	2554 a B	7786 a A	10.6 a A S/S	8.7 a A S/S
CNPH 55 161	5.0	4.2	5.0	4.2	2144 a A	1748 a A	10.3 a A S/S	8.9 a A S/S
CNPH 60 074	5.0	4.2	5.0	3.7	2444 a A	2836 a A	10.5 a A S/S	5.5 c B S/S
CNPH 55 159	4.7	4.5	4.7	4.5	2592 a A	2179 a A	10.1 a A S/S	7.3 b A S/S
CNPH 60 045–2	5.0	4.5	5.0	4.5	2335 a A	1121 b B	9.7 a A S/S	5.3 c B S/S
CNPH 60 080	5.0	4.7	5.0	4.7	3328 a A	1986 a B	9.6 a A S/S	5.1 c B S/S
CNPH 55 139	5.0	4.7	5.0	4.7	2136 a A	2165 a A	9.4 a A S/S	10.6 a A S/S
CNPH 55 001	5.0	5.0	5.0	5.0	1478 b A	1326 b A	9.1 a A S/S	7.4 b A S/S
CNPH 60 090	5.0	5.0	5.0	4.7	2306 a A	1085 b B	9.1 a A S/S	4.0 c B S/LS
CNPH 15 348	4.7	3.5	4.7	3.5	1512 b A	2799 a A	8.9 a A S/S	12.3 a A S/S
CNPH 55 157	4.2	4.0	4.2	4.2	3401 a A	1640 a B	8.6 a A S/S	11.7 a A S/S
CNPH 60 043–2	4.7	4.5	4.7	4.5	2166 a A	2534 a A	8.4 a A S/S	6.0 b A S/S
CNPH 60 047–5	4.5	3.7	4.5	3.7	1763 a A	1457 b A	8.2 a A S/S	5.4 c A S/S
CNPH 55 163	4.7	4.0	4.7	4.0	2014 a A	1232 b A	8.2 a A S/S	4.2 c B S/LS
CNPH 55 123	4.7	4.5	4.7	4.2	1531 b A	1593 a A	8.0 a A S/S	6.0 b A S/S
CNPH 55 149	4.5	3.7	4.7	3.7	1373 b A	878 c A	7.9 a A S/S	4.1 c B S/LS
CNPH 55 135	4.7	4.2	4.7	4.5	2172 a A	1091 b B	7.7 a A S/S	3.0 d B S/LS
CNPH 55 136	4.2	4.0	4.2	4.0	2224 a A	606 c B	7.4 a A S/S	3.9 c B S/LS
CNPH 55 162	4.2	4.7	4.2	4.7	2027 a A	1144 b A	7.3 a A S/S	6.9 b A S/S
CNPH 55 122	4.7	4.5	4.7	4.5	1149 b A	1328 b A	7.0 a A S/S	5.5 c A S/S
CNPH 55 148	4.0	3.7	4.0	3.7	1401 b A	1391 b A	6.4 b A S/S	5.9 b A S/S
CNPH 60 069	4.0	5.0	4.0	5.0	2555 a A	1448 b A	6.1 b A S/S	5.1 c A S/S
CNPH 15 749	4.5	3.7	4.5	3.7	1573 b A	1203 b A	5.6 b A S/LS	3.3 d A S/LS
CNPH 60 064	4.2	3.5	4.2	3.5	2110 a A	984 b B	5.3 b A S/LS	1.9 d B S/MR
CNPH 60 008–3	4.0	4.2	4.0	4.2	2004 a A	2239 a A	5.2 b A S/LS	7.2 b A S/S
CNPH 60 008–4	3.5	3.7	3.5	3.7	809 b A	1571 b A	5.2 b A S/LS	8.1 b A S/S
CNPH 55 129	4.0	3.7	4.0	3.7	1791 a A	571 c B	5.1 b A S/LS	1.85 d B S/MR
CNPH 55 142	4.0	4.5	4.0	4.5	1953 a A	1400 b A	5.0 b A S/LS	5.9 b A S/S
CNPH 60 044–3	4.0	4.7	4.0	4.7	1416 b A	1576 b A	4.9 b B S/LS	7.8 b A S/S
CNPH 60 078	3.5	4.0	3.5	3.7	1323 b A	1049 b A	4.7 b A S/LS	2.8 d A S/LS
CNPH 60 048–3	3.5	4.0	3.5	4.0	1180 b A	1265 b A	4.5 b A S/LS	4.1 c A S/LS
CNPH 60 046–1	3.0	4.2	3.0	4.0	1813 a A	1705 a A	4.4 b A S/LS	3.3 d A S/LS
CNPH 60 061	4.0	4.7	4.0	4.7	1030 b A	1201 b A	4.3 b A S/LS	3.9 c A S/LS
CNPH 55 002	5.0	4.7	5.0	4.7	1135 b A	1538 b A	4.3 b A S/LS	5.0 c A S/S
CNPH 60 087	4.0	5.0	4.0	4.7	916 b A	1419 b A	4.0 b A S/LS	4.7 c A S/LS
CNPH 55 155	4.2	4.5	4.2	4.5	852 b A	414 c A	3.9 b A S/LS	2.7 d A S/LS
BRS Nandaia	3.5	3.7	3.5	3.7	1028 b A	1849 a A	3.8 b A S/LS	4.0 c A S/LS
CNPH 55 201	2.7	2.2	2.7	2.2	777 b A	340 c A	3.2 b A S/LS	1.7 d A S/MR
Average	4.3	4.2	4.4	4.2	1801	1659	7.02	5.67
Tomato Rutgers[i]	5.0	5.0	5.0	4.5	2555	2788	20.8	14.6
Tomato Nemadoro	5.0	5.0	5.0	4.7	2656	3758	15.3	10.0
CV (%)[j]	6.4	7.0	6.4	7.3	21.4	21.7	15.4	18.1

Note: [a]All data presented in the table were $\sqrt{x} + 0.5$ transformed for statistical analysis. Original data set shown. Means ($n = 6$) followed by different lower-case letters within a column are significantly different according to Scott-Knott´s test ($p < 0.05$) and by different uppercase letters within a line are significantly different according to the joint analysis of variance.

[b]GI: gall index (scale 1–5) according to Taylor & Sasser (1978);

[c]EMI: egg mass index (scale 1–5) according to Taylor & Sasser (1978);

[d]Eggs + J2: eggs + juveniles per (g roots)$^{-1}$;

[e]RF: nematode reproduction factor = final population/5,000 eggs of *M. enterolobii*;

[e]Susceptible (RF > 1); resistant (RF < 1), immune (RF = 0);

[g]Classification according to reproduction index (RI) criterion proposed by Taylor (1967) with modifications, where S = susceptible (RI > 51%); LS = low susceptibility (RI 26%-50%); MR = moderately resistant (RI 11%-25%); *R* = resistant (1%-10%); HR = highly resistant (RI < 1%) and I = immune (RI = 0);

[h]Susceptible control used in the RI classification;

[i]Tomato 'Rutgers' is a standard susceptible; tomato 'Nemadoro' is resistant to other *Meloidogyne* species;

[j]CV = coefficient of variation.

Table 3. Host reaction of *Capsicum annuum* genotypes inoculated with *Meloidogyne enterolobii* under greenhouse conditions at 65 days post- inoculation. Gall index (GI), egg mass index (EMI), eggs and second-stage juveniles (J2) per (g root)$^{-1}$, nematode reproduction factor (RF) and reproduction index (RI).

	GI[a,b]		EMI[c]		Eggs+J2/(g root)$^{-1}$[(d)]		RF[e]/Reaction[f]/Classification[g]	
Genotypes	Experiment 3	Experiment 4	Experiment 3	Experiment 4	Experiment 3	Experiment 4	Experiment 3	Experiment 4
CNPH 50 319–3[h]	4.5	4.5	4.5	4.5	5940 a A	6675 a A	10.9 a B S/S	19.0 a A S/S
CNPH 50 318–1	4.7	4.0	4.7	4.0	4917 a A	2007 c B	9.8 a A S/S	6.0 c B S/LS
BRS ACARA	3.7	4.0	3.7	3.7	4256 b A	2033 c B	6.5 b A S/S	5.2 c A S/LS
CNPH 144 OR-2–2	4.0	3.5	4.0	3.5	5020 a A	1398 c B	6.3 b A S/S	4.4 c A S/MR
CNPH 3839	3.7	3.2	4.0	3.2	2342 c A	3180 c A	5.9 b A S/S	8.3 b A S/LS
CNPH 161 OR-5–1	4.5	3.0	4.2	3.0	5179 a A	1488 c B	5.7 b A S/S	2.5 c B S/MR
IKEDA	4.0	4.0	4.0	3.2	3875 b A	2002 c A	5.2 b A S/LS	5.2 c A S/LS
BRS SARAKURA	3.3	3.5	3.3	3.5	1764 c B	3886 b A	5.1 b B S/LS	10.3 b A S/S
CNPH 4134	3.0	3.5	3.0	3.5	1921 c A	2257 c A	5.0 b A S/LS	8.3 b A S/LS
CNPH 50 318–4	3.7	4.2	3.7	4.2	2160 c B	5742 a A	4.7 b B S/LS	12.2 a A S/S
CNPH 50 317–2	4.0	3.5	3.7	3.5	1558 c A	1583 c A	4.5 b A S/LS	4.4 c A S/MR
CNPH 154 OR-1–4	3.2	3.2	3.2	3.2	3430 b B	7781 a A	4.5 b A S/LS	8.3 b A S/LS
CNPH 30 371	4.0	3.2	4.0	3.2	950 c B	2805 c A	4.5 b A S/LS	8.1 b A S/LS
CNPH 2781	3.5	3.2	3.5	3.2	1398 c A	1563 c A	4.4 b A S/LS	4.9 c A S/LS
CNPH 30 370	4.2	2.7	4.2	2.7	1394 c A	3871 c A	3.9 c A S/LS	9.8 b A S/S
CNPH 50 316–2	3.0	3.7	2.5	3.7	1149 c A	1556 c A	3.8 c A S/LS	3.5 c A S/MR
CNPH 30 649	3.7	3.5	3.7	3.2	1475 c A	2403 c A	3.6 c A S/LS	5.3 c A S/LS
CNPH 30 545–2	4.2	3.5	4.0	3.7	1564 c B	4548 b A	3.4 c A S/LS	6.8 b A S/LS
CNPH 155-OR-2–1	3.7	2.2	3.7	2.2	3644 b A	1440 c B	3.2 c A S/LS	2.6 c A S/MR
CNPH 4135	5.0	4.7	5.0	4.7	1055 c B	3651 a A	3.0 c B S/LS	12.7 a A S/S
CNPH 30 647	4.0	3.0	4.0	2.7	822 c A	1479 c A	2.4 c A S/LS	3.0 c A S/MR
CNPH 158 OR-1–1	1.0	3.0	1.0	3.0	13 d B	1572 c A	0.01 d B R/HR	3.4 c A S/MR
Average	3.8	3.5	3.7	3.4	2537	2951	4.85	7.04
Tomato Rutgers[i]	5.0	5.0	5.0	5.0	3052	3161	15.5	17.0
Tomato Nemadoro	4.7	4.7	4.5	4.7	1322	2537	8.4	12.4
CV (%)[j]	11.4	7.2	10.9	8.5	21.3	28.5	14.1	29.3

Note: [a]All data presented in the table were $\sqrt{x} + 0.5$ transformed for statistical analysis. Original data set shown. Means ($n = 6$) followed by different lower-case letters within a column are significantly different according to Scott-Knott´s test ($p < 0.05$) and by different uppercase letters in the lines are significantly different according to the joint analysis of variance.
[b]GI: gall index (scale 1–5) according to Taylor & Sasser (1978);
[c]EMI: egg mass index (scale 1–5) according to Taylor & Sasser (1978);
[d]Eggs + J2: eggs + juveniles per (g roots)$^{-1}$;
[e]RF: nematode reproduction factor = final population/5,000 eggs of *M. enterolobii*;
[f]Susceptible (RF > 1); resistant (RF < 1), immune (RF = 0);
[g]Classification according to reproduction index (RI) criterion proposed by Taylor (1967) with modifications, where S = susceptible (RI > 51%); LS = low susceptibility (RI 26%-50%); MR = moderately resistant (RI 11%-25%); *R* = resistant (RI 1%-10%); HR = highly resistant (RI < 1%) and I = immune (RI = 0);
[h]Susceptible control used in the RI classification;
[i]Tomato 'Rutgers' is a standard susceptible; tomato 'Nemadoro' is resistant to other *Meloidogyne* species;
[j]CV = coefficient of variation

2004). At least ten resistance genes have been isolated and characterized in *Capsicum* spp., including the NBS-LRR *N*, *Me1* to *Me7*, *Mech1* and *Mech2* genes. Some of these are thermostable and highly specific, while others exhibit a broad spectrum of resistance to major RKN nematodes (Djian-Caporalino et al. 2011; Fazari et al. 2012). However, several studies have shown that *Capsicum* genotypes harbouring these genes are susceptible to *M. enterolobii* (Carrillo-Fasio et al. 2020).

In our study, we screened 39 *C. chinense* and 22 *C. annuum* genotypes to search for resistance to *M. enterolobii*. While none of the genotypes were rated as resistant, some of them exhibited relatively low RF values compared to susceptible controls, such as the tomato 'Rutgers' and *Capsicum* genotypes CNPH55160, CNPH50319–3, indicating a lower susceptibility to this nematode. Additionally, the tomato 'Nemadoro' (which carries the *Mi* resistance gene and is resistant to other *Meloidogyne* species), was found to be susceptible to *M. enterolobii*, which is consistent with the findings of other studies (Pinheiro et al. 2020; Pinto et al. 2024).

Similarly, Soares et al. (2018) evaluated the resistance of *Capsicum* genotypes to *M. incognita* race 3, *M. javanica* and *M. enterolobii* under greenhouse conditions.

They reported three *C. annuum* genotypes, CNPH185, CNPH187 and CNPH680, as being resistant to both *M. incognita* race 3 and *M. javanica*. One line of *C. frutescens* L., meanwhile, was found to be resistant to these RKN species, as well as to *M. enterolobii*. Hence, these genotypes are valuable sources for the development of future breeding programs.

Early studies on *Capsicum* resistance to RKN have reported low susceptibility or moderate resistance to *M. enterolobii* (Melo et al. 2011; Pinheiro et al. 2013; Gonçalves et al. 2014). For instance, Melo et al. (2011) identified accessions of *C. chinense* and *C. annuum* with low susceptibility (RF = 1–2.5), and Pinheiro et al. (2020) obtained similar results (RF = 1.2–3) with other *Capsicum* genotypes; however, none were classified as fully resistant. Further investigation of these genotypes with reduced susceptibility is warranted to elucidate the genetic and molecular basis of their partial resistance, as they could serve as valuable sources for breeding programs aiming to develop *M. enterolobii*-resistant cultivars.

An alternative approach to managing RKN nematodes in the field is to use resistant *Capsicum* rootstocks, since grafting is widely used in vegetable cultivation as it improves resistance to soil-borne pathogens, salt, drought, and other stresses, resulting in higher yields and better quality (Shi et al. 2024). However, grafting is time-consuming and can increase cropping-associated costs (Pinheiro et al. 2015). Moreover, some available rootstocks are also susceptible to *M. enterolobii* (Pinheiro et al. 2015, 2020). Therefore, it is crucial to conduct further studies to screen a wide range of *Capsicum* genotypes in order to identify novel sources of genetic resistance to major RKN nematodes, including *M. enterolobii*, given the significance of this pathogenic nematode to *Capsicum* cultivation.

In conclusion, our research identified 39 *Capsicum chinense* and 22 *C. annuum* genotypes that were susceptible to *M. enterolobii* under greenhouse conditions. However, three *C. chinense* genotypes (CNPH 55 201, CNPH 55 129, and CNPH 60 064) exhibited a relatively low level of susceptibility despite being considered hosts to *M. enterolobii*, contrasting with other *C. chinense* genotypes that were evaluated.

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