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Effects of the *Mi-1* and the *N* root-knot nematode-resistance gene on infection and reproduction of *Meloidogyne enterolobii* on tomato and pepper cultivars

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Abstract: Meloidogyne enterolobii is widely considered to be an aggressive root-knot nematode species that is able to reproduce on root-knot nematode-resistant tomato and pepper cultivars. In greenhouse experiments, *M. enterolobii* isolates 1 and 2 from Switzerland were able to reproduce on tomato cultivars carrying the *Mi-1* resistance gene as well as an *N*-carrying pepper cultivar. Reproduction factors (Rf) ranged between 12 and 109 depending on the plant cultivar, with *M. enterolobii* isolate 2 being more virulent when compared to isolate 1. In contrast, *M. arenaria* completely failed to reproduce on these resistant tomato and pepper cultivars. Although some variability in virulence and effectiveness of root-knot nematode-resistance genes was detected, none of the plant cultivars showed Rf values less than 1 or less than 10% of the reproduction observed on the susceptible cv. 'Moneymaker' (Rf = 23-44) used to characterize resistance. The ability of *M. enterolobii* to overcome the resistance of tomato and pepper carrying the *Mi-1* and the *N* gene makes it difficult to manage this root-knot nematode species, particularly in organic farming systems where chemical control is not an option.
Key words: Capsicum annuum, resistance, root-knot nematodes, *Solanum lycopersicon*.

Meloidogyne enterolobii was first reported in Switzerland in 2008 (Kiewnick et al., 2008). Severe root galling was found on tomato rootstock cv. 'Maxifort' (*Solanum lycopersicum* L.) and on cucumber cv. 'Loustik' (*Cucumis sativus* L.) in two commercial greenhouses in Switzerland. All methods of identification confirmed the species *Meloidogyne enterolobii* (Yang and Eisenback, 1983). For further confirmation of the correct species identification, type material of *M. enterolobii* from the original host *Enterolobium contortisiliquum* (Vell.) Morong China was used for sequence data comparison. The compared sequences consisted of a fragment of cytochrome oxidase I (COI), internal transcribed spacer (ITS) region 1, 5.8s, ITS2, part of 26s, the mtDNA 63bp repeat region, and a fragment of the intergenic spacer region (Adam et al., 2007). All sequence data showed 100% homology and confirmed the identification as *M. enterolobii* (Kiewnick et al, 2008a, 2008b). Furthermore, additional comparative genomic studies based on COI, ITS and IGS regions with reference material from Brazil and Florida (Brito el al., 2004) of *M. mayaguensis*, a very closely related species (Rammah and Hirschmann, 1988), were conducted. The obtained sequence data revealed that the Swiss *M. enterolobii* populations were 100% identical to the Florida and Brazil populations of *M. mayaguensis* (Kiewnick et al., 2007, 2008b). These findings confirmed the recent suggestion that *M. enterolobii* is a senior synonym of *M. mayaguensis* (Xiu et al., 2004, Anonymous, 2008). Although *M. enterolobii* is not listed as a quarantine nematode, it is now considered to be one of the most pathogenic root-knot nematodes known. Due to its potential to become a quarantine pest, *M. enterolobii* was placed on the European and Mediterranean Plant Protection Organization (EPPO) alert list (Anonymous, 2008). The species *M. enterolobii* (syn. *M. mayaguensis*) is of great importance as it displayed virulence against several sources of root-knot nematode-resistance genes and is considered particularly aggressive. It has been reported in Africa, Central American and Caribbean countries, the United States, France, and China (Anonymous, 2008). Recently, Brito et al. (2007a) demonstrated that the Florida isolates of *M. mayaguensis* were able to overcome the resistance of tomato and pepper (*Capsicum annuum* L.) genotypes carrying the *Mi-1*, *N*, and *Tabasco* genes. These are all genes in tomato and pepper that confer resistance against the three most economically important root-knot nematode species: *M. incognita*, *M. javanica*, and *M. arenaria* (Williamson, 1999; Brito et al., 2007a; Thies et al., 2008). Furthermore, field and greenhouse studies revealed a wider host range, increased pathogenicity and higher reproductive potential of *M. mayaguensis* compared to other *Meloidogyn*e spp. (Cetintas et al., 2007, Brito et al., 2007b). The objectives of this study were to determine whether the two *M. enterolobii* populations present in Switzerland possess the same potential to overcome the *Mi-1* resistance gene in tomato and the *N* gene in the pepper, as well as to determine their virulence in root-knot nematode-resistant tomato and a pepper cultivar.

Material and Methods

Nematode sources: *Meloidogyne enterolobii* isolates were originally isolated from two greenhouse populations in Switzerland (Kiewnick et al., 2008). Isolate 1 was collected from cucumber roots from the Canton Aargau and isolate 2 was obtained from tomato root stock in the Canton Lucerne. The *M. arenaria* population was originally isolated from tomato from a greenhouse in the Canton Zurich. All isolates were reared on the susceptible tomato cultivar 'Moneymaker'.

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Greenhouse tests: The reproduction of *M. enterolobii* isolates 1 and 2 on the susceptible cultivar 'Moneymaker', as well as nine other tomato cultivars, including two root stocks, all carrying the *Mi-1* resistance gene, and one pepper rootstock 'Snooker' carrying the *N* gene (Table 1) were compared in six greenhouse experiments. For all experiments, 15 day old seedlings were transplanted into 13-cm-diam. plastic pots containing a pasteurized field-soil:sand mix (1:1,V:V). Afterwards, plants were transferred to a growth room with 23 ± 1°C, 12 hr light, and 75% relative humidity. After 15 days, each seedling was inoculated with 1000 eggs (experiments 1-4) of *M. enterolobii* isolate 1 or 2 by pipetting an egg suspension into four holes 2 cm deep around the plant base. For confirmation that the root-knot nematode resistance was effective in all the tomato and pepper cultivars, plants were also challenged with 1000 eggs of *M. arenaria* as a control treatment. In two additional experiments, five resistant tomato cultivars, the pepper cultivar 'Snooker', and the susceptible cultivar 'Moneymaker' were inoculated separately with 5000 eggs of *M. enterolobii* isolates 1 (experiment 5) or 2 (experiment 6). After 5 more days in the growth room, plants were transferred to a greenhouse with 25 ± 1°C, 75% relative humidity, and 12 hr supplemental light. Pots were arranged with 5 replicates in a completely randomized design on the greenhouse bench. Plants were watered daily as needed and fertilized every three weeks with 20 ml of 0.5% Wuxal solution (12,4,6; Maag, Switzerland). All experiments were evaluated 45 d after inoculation (DAI). Shoots were removed and weighed while root systems were harvested and carefully washed free of soil, weighed, and stained with 0.015% Phloxin B (FLUKA, Germany) solution (Hussey and Janssen, 2002). To assess the nematode's reproduction, the gall index (GI, 0 = no galls; 10 = dead plant), as described by Zeck (1971), and the numbers of egg masses per root were determined. To calculate the nematode reproduction factor (Rf = Pf/Pi), where Pi = initial inoculum level and Pf = newly produced eggs, the NaOCl method (Hussey and Janssen, 2002) was used to extract eggs from the entire root system. The gall index, the number of egg masses per root, the number of eggs per gram root, and the reproduction factor were used to determine the effectiveness of resistance genes on the reproduction of *M. enterolobii* and *M. arenaria*.

Statistical analysis: For experiments 1 through 4, data on shoot and root fresh weight were subjected to 2-way ANOVA using SPSS 15.0 (SPSS Inc., Chicago, Il.) with plant cultivar and *Meloidogyne* spp. as the main factors. For the GI, egg masses per root, eggs per gram root, and Rf parameters, only data from plants inoculated with *M. enterolobii* isolates 1 and 2 were subjected to ANOVA since no reproduction of *M. arenaria* could be found in all root-knot nematode-resistant plant cultivars. In the case of inhomogeneous variances, data were $\sqrt{x+1}$ transformed prior to ANOVA. Untransformed data are presented in tables. When ANOVA showed significant effects, mean separation was done using Tukey's HSD test ($P \leq 0.05$). As pooling of data from experiments 1 and 2 as well as 3 and 4 revealed inhomogeneous variances and significant interactions between the experiments, data for all experiments had to be analyzed separately.

Results

Two-factor ANOVA revealed significant effects by the "cultivar" factor on shoot and root fresh weight of tomato and pepper in experiments 1 through 4 after inoculation with *M. enterolobii* isolates 1 and 2, using *M. arenaria* as a control (data not shown). The *Meloidogyne* species used for inoculation (*M. enterolobii* vs. *M. arenaria*) did not affect the shoot and root fresh weight in experiments 1 through 3, but did so in experiment 4 (isolate 2). In this experiment only, a significant interaction between the factors "cultivar" and *Meloidogyne* spp. was found (data not shown).

In experiments 1 through 4, *M. arenaria* was able to reproduce well on the susceptible cultivar 'Moneymaker' with an average gall index of 3.5, 230 egg masses per root, 2300 eggs per gram root, and a reproduction

TABLE 1. Root-knot nematode resistant tomato (*Lycopersicon lycopersicum*) and pepper (*Capsicum annuum*) cultivars used in this study

	Cultivar	Use[a]	Seed source	Root-knot nematode resistance gene
Tomato	'Amaral'	F	Enza Zaden, Dannstadt, Germany	*Mi-1*
	'Balerina'	F	Enza Zaden, Dannstadt, Germany	*Mi-1*
	'Sakura'	F	Enza Zaden, Dannstadt, Germany	*Mi-1*
	'Savantas'	F	Enza Zaden, Dannstadt, Germany	*Mi-1*
	'Sparta'	F	Enza Zaden, Dannstadt, Germany	*Mi-1*
	'Foose F1'	F	Syngenta Seeds, Kleve, Germany	*Mi-1*
	'Devotion'[b]	F	Enza Zaden, Dannstadt, Germany	*Mi-1*
	'Brigeor'	RS	Enza Zaden, Dannstadt, Germany	*Mi-1*
	'Efialto'	RS	Enza Zaden, Dannstadt, Germany	*Mi-1*
Pepper	'Snooker'	RS	Syngenta Seeds, Kleve, Germany	*N*

[a]Commercial use: F = fruit production, RS = rootstock.
[b]Certified for organic production.

factor of 31 (data not presented). However, no reproduction of *M. arenaria* occurred on any of the root-knot nematode resistant tomato cultivars or the pepper cv. 'Snooker'. Therefore, only data on the reproduction of the *M. enterolobii* isolates 1 and 2 were further analysed.

In experiments 1 through 4, both *M. enterolobii* isolates reproduced well on the susceptible cultivar 'Moneymaker' as well as on all tested resistant cultivars (Tables 2 and 3). However, some differences in their response to *M. enterolobii* inoculation could be found. In experiment 1, none of the tomato cultivars or the pepper showed a significantly lower gall index compared to the susceptible control 'Moneymaker', but the cultivars 'Foose', 'Brigeor', and the pepper cv. 'Snooker' showed a significantly lower number of egg masses per root (Table 2). Cultivar 'Efialto' produced a significantly lower number of eggs per gram root compared to the susceptible cv. 'Moneymaker', but no significant differences in Rf values were found (Table 2). In experiment 2, similar results were obtained. There were no differences ($P > 0.05$) in GI values and no plant cultivar produced a number of egg masses significantly different from the susceptible cultivar 'Moneymaker' (Table 2). Differences in the number of eggs per gram root and the Rf values compared to the susceptible cultivar 'Moneymaker' were not significant (Table 2).

Isolate 2 of *M. enterolobii* also produced well on all tomato cultivars and the pepper cv. 'Snooker' (Table 3). In experiment 3, seven tomato cultivars and the pepper cv. 'Snooker' showed a significantly lower gall index when compared to the susceptible cultivar 'Moneymaker (Table 3). Conversely, in experiment 4, only the tomato cultivars 'Sparta' and 'Efialto' and the pepper cv. 'Snooker' showed a significantly lower gall index compared to cv. 'Moneymaker'. In experiments 3 and 4, isolate 2 produced similar numbers of egg masses per root. Only cv. 'Brigeor' showed a significantly lower number of egg masses compared to cv. 'Moneymaker' in experiment 4 (Table 3). In contrast to isolate 1, none of the plant cultivars inoculated with *M. enterolobii* isolate 2 produced numbers of eggs per root and Rf values that were significantly lower compared to the susceptible cv. 'Moneymaker' (Table 3). Based on Rf values, all root-knot nematode-resistant tomato cultivars and the pepper cv. 'Snooker' were susceptible to *M. enterolobii* isolate 1 and 2.

On average, *M. enterolobii* isolate 2 seemed more virulent than isolate 1, producing higher Rf values on the susceptible cv. 'Moneymaker' and all plant cultivars tested, with the exception of tomato cv. 'Foose' in experiment 1 (Tables 2 and 3). In the experiments 5 and 6, with the higher inoculum level of 5000 eggs per plant, GI values ranged from 3.6 on pepper cv. 'Snooker' to

TABLE 2. Galling index (GI), number of egg masses per root, eggs per gram of root and reproduction factor (Rf) of *Meloidogyne enterolobii* (isolate 1) on the susceptible cultivar 'Moneymaker', root-knot nematode resistant tomatoes, and a pepper cultivar in two separate experiments

	Cultivar	GI[a]	Egg masses/root	Eggs/g root	Rf[b]
Experiment 1					
Tomato	'Moneymaker'	3.2 ab	110.4 a	3899.6 a[c]	29.5 bc
	'Amaral'	3.0 ab	100.0 ab	2876.7 a	38.2 bc
	'Balerina'	3.2 ab	69.6 ab	2615.5 a	36.8 bc
	'Sakura'	4.2 a	92.2 ab	3732.6 a	42.1 bc
	'Savantas'	2.8 b	66.4 ab	2574.7 a	38.2 bc
	'Sparta'	3.2 ab	108.4 ab	3444.0 a	42.6 bc
	'Foose'	3.8 ab	19.2 d	2290.4 a	109.1 a
	'Devotion'	3.2 ab	113.6 a	3318.8 a	36.4 bc
	'Brigeor'	2.8 b	53.8 bcd	2249.5 a	13.0 c
	'Efialto'	3.2 ab	68.4 ab	579.1 b	12.2 c
Pepper	'Snooker'	3.6 ab	52.0 cd	1953.9 a	66.0 ab
Experiment 2					
Tomato	'Moneymaker'	3.2	94.6 abc	2517.8 ab	23.5 b
	'Amaral'	3.6	112.2 ab	2542.8 ab	35.0 ab
	'Balerina'	2.6	71.4 bc	1515.3 b	21.4 b
	'Sakura'	3.6	83.6 bc	2522.8 ab	33.9 ab
	'Savantas'	3.4	85.2 bc	2926.5 ab	41.5 ab
	'Sparta'	3.4	92.4 abc	3986.6 a	55.1 a
	'Foose'	2.6	103.4 abc	2426.9 ab	33.9 ab
	'Devotion'	3.9	94.2 abc	2924.4 ab	31.2 b
	'Brigeor'	2.6	55.0 c	3265.5 ab	24.4 b
	'Efialto'	3.6	75.2 bc	1169.5 b	23.8 b
Pepper	'Snooker'	4.0	143.6 a	3310.5 ab	28.3 b
		n.s.[d]			

[a]Gall index: 0-10 scale where 0= no galls and 10= dead plant (Zeck, 1971).
[b]Rf = final population/initial population.
[c]Data on eggs per gram of root from experiment 1 were transformed with $\sqrt{x+1}$ before analysis, and untransformed data are presented in the table. Means within a column followed by the same letters are not significantly different at $P \leq 0.05$ according to Tukey's HSD Test.
[d]n.s.= not significant.

TABLE 3. Galling index (GI), number of egg masses per root, eggs per gram of root, and reproduction factor (Rf) of *Meloidogyne enterolobii* (isolate 2) on the susceptible cultivar 'Moneymaker', root-knot nematode resistant tomatoes and a pepper cultivar in two separate experiments

	Cultivar	GI[a]	Egg masses/root	Eggs/g root	Rf[b]
Experiment 3					
Tomato	'Moneymaker'	5.4 a	164.8	4598.9 abcd[c]	37.9 ab[c]
	'Amaral'	4.0 b	144.8	2881.3 abcd	42.2 ab
	'Balerina'	4.0 b	125.4	1924.4 d	27.0 ab
	'Sakura'	4.4 ab	190.2	6053.7 a	63.7 a
	'Savantas'	3.8 b	219.4	3919.6 abcd	60.0 ab
	'Sparta'	4.0 b	166.4	5856.5 ab	62.5 ab
	'Foose'	3.8 b	135.6	3766.4 abcd	52.7 ab
	'Devotion'	4.8 ab	214.6	5065.2 abc	67.3 a
	'Brigeor'	4.2 b	143.6	3440.2 abcd	24.1 b
	'Efialto'	3.0 bc	141.6	2817.9 bcd	49.6 ab
Pepper	'Snooker'	2.2 c	142.0 n.s.[d]	2557.9 cd	24.9 b
Experiment 4					
Tomato	'Moneymaker'	5.4 abc[c]	182.2 ab	3840.9 bcd	44.4 b
	'Amaral'	5.8 abc	138.2 abc	2487.1 cd	51.0 ab
	'Balerina'	6.0 ab	201.2 a	2816.3 bcd	61.7 ab
	'Sakura'	6.0 ab	196.2 a	4021.6 bc	67.5 ab
	'Savantas'	5.6 abc	151.0 abc	3758.6 bcd	67.3 ab
	'Sparta'	4.8 bc	153.0 abc	4295.7 b	70.2 ab
	'Foose'	5.6 abc	189.2 a	3108.9 bcd	66.3 ab
	'Devotion'	6.4 a	130.6 abc	3944.1 bc	70.1 ab
	'Brigeor'	5.6 abc	94.4 c	2475.5 cd	34.8 b
	'Efialto'	4.8 c	116.0 bc	2234.0 d	43.5 b
Pepper	'Snooker'	3.0 d	133.2 abc	6311.8 a	81.5 a

[a]Gall index: 0-10 scale where 0= no galls and 10= dead plant (Zeck, 1971).
[b]Rf = final population/initial population.
[c]Data on eggs per gram of root and reproduction factor from experiment 1 and gall index from experiment 2 were transformed with $\sqrt{x+1}$ before analysis, and untransformed data are presented in the table. Means within a column followed by the same letters are not significantly different at $P \leq 0.05$ according to Tukey's HSD Test.
[d]n.s.= not significant.

5.0 on tomato cv. 'Sparta' for isolate 1 and from 4.0 on cv. 'Snooker' to 6.0 on cv. 'Sakura' for isolate 2 (Table 4). Only on the pepper cultivar inoculated with isolates 1 and 2 and for tomato cv. 'Brigeor' inoculated with isolate 2 was the gall index significantly lower when compared to the susceptible cv. 'Moneymaker' (Table 4). For isolate 1, all plant cultivars except tomato cv. 'Foose' and pepper cv. 'Snooker' produced significantly higher egg mass numbers compared to cv. 'Moneymaker' (Table 4). For isolate 2, all plant cultivars tested produced similar numbers of egg masses ($P > 0.05$) ranging from 127 on cv. 'Brigeor' to 236 on cv. 'Efialto' (Table 4).

DISCUSSION

The two isolates of *M. enterolobii* from Switzerland were able to overcome the *Mi-1* resistance in nine tomato cultivars, including two root stocks, and the *N* gene in the pepper rootstock 'Snooker'. These genes

TABLE 4. Galling index (GI) and number of egg masses per root of *Meloidogyne enterolobii* (isolates 1 and 2) on the susceptible cultivar 'Moneymaker', root-knot nematode resistant tomatoes, and a pepper cultivar in two separate experiments

		GI[a]		Egg masses/root	
	Cultivar	Isolate 1	Isolate 2	Isolate 1	Isolate 2
Tomato	'Moneymaker'	4.6 a	5.4 a	323.6 c	145.6
	'Sakura'	4.6 a	6.0 a	557.0 a	199.0
	'Sparta'	5.0 a	5.8 a	498.0 ab	208.8
	'Foose'	4.2 ab	5.2 ab	382.0 bc	218.6
Root-stock	'Brigeor'	4.2 ab	4.0 b	541.8 ab	127.4
	'Efialto'	4.8 a	5.6 a	503.6 ab	236.4
Pepper	'Snooker'	3.6 b	4.0 b	475.0 abc	190.0 n.s.[b]

[a]Gall index: 0-10 scale where 0= no galls and 10= dead plant (Zeck, 1971).
[b]n.s.= not significant. Means within a column followed by the same letters are not significantly different at $P \leq 0.05$ according to Tukey's HSD Test.

confer resistance to the tropical species *M. incognita*, *M. javanica* and *M. arenaria*. These results confirm the findings by Brito et al. (2007a) who showed that the Florida populations of *M. mayaguensis* (junior synonym of *M. enterolobii*) were able to reproduce on tomato and pepper genotypes carrying the *Mi-1*, *N*, and *Tabasco* genes. They also showed that the *Mi-1* gene was instable to *M. incognita* at high temperatures. In our studies, growth room and green house temperatures were kept at 23°C and 25°C ± 1°C, respectively, to ensure effectiveness of resistance in all plant cultivars tested. Isolates 1 and 2 of *M. enterolobii* reproduced well on root-knot nematode-resistant tomato cultivars and the pepper cv. 'Snooker', whereas *M. arenaria* did not reproduce. In most cases, Rf values for isolates 1 and 2 were equal or higher compared to the susceptible control cv. 'Moneymaker' which contrasts with the findings of Brito et al. (2007a) who found, depending on the isolate used, reduced reproduction rates on tomato genotypes carrying the *Mi-1* gene. In our studies, the tomato root-stocks 'Brigeor' and 'Efialto' showed lower reproduction for *M. enterolobii* isolate 1, but not for isolate 2, at the low inoculum level. This indicates some differences in virulence of the two isolates, which might be due the intensive use of resistant root stock cultivars such as 'Maxifort' and 'Beaufort' (De Ruiter Seeds) on the organic farm where isolate 2 was obtained from (Kiewnick et al., 2008). Although it expressed lower GI values, the *M. enterolobii* isolate 1 produced twice the number of egg masses per root when compared to isolate 2 at the higher inoculum level. In two out of six experiments, the root stock cv. 'Brigeor' showed lower GI and Rf values compared to the cv. 'Moneymaker'. Cordata et al. (2008) described this cultivar as highly resistant to *M. javanica*. However, the observed effects on *M. enterolobii* reproduction were based on a significantly smaller root system, which was not able to support higher reproduction rates. In four out of six experiments the pepper root stock 'Snooker' showed lower GI values compared to the control cv. 'Moneymaker' but produced high numbers of egg masses and Rf values with both *M. enterolobii* isolates. Similar effects were shown by Brito et al. (2007a) with *M. mayaguensis* on the resistant Bell pepper 'Charleston Belle'. *Meloidogyne arenaria* was not able to reproduce on cv. 'Snooker' which is in contrast to the findings by Oka et al. (2004), who described this root stock as only moderately resistant to *M. incognita* and *M. javanica*.

The differences in the ability of the two *M. enterolobii* isolates to reproduce on the plant cultivars tested might indicate variability in virulence and the effectiveness of root-knot nematode-resistance genes. However, none of these plant cultivars expressed Rf values less than 1 or less than 10% of the reproduction observed on the susceptible cv. 'Moneymaker', which would characterize resistance (Hussey and Janssen, 2002; Brito et al., 2007a; Cortada et al., 2008). So far, no effective resistance mechanism against *M. enterolobii* is available in tomato or pepper, which makes it particularly difficult to manage this root-knot nematode species in organic farming systems where chemical control is not available. Recently, resistance against *M. mayaguensis* was found in Guava (*Psidium* spp.) in Brazil (Carneiro et al., 2007), which indicates that sources of resistance exist. However, further testing is needed to determine whether tomato or pepper genotypes exist which could be useful in effectively controlling the Swiss *M. enterolobii* populations.

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