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Search for sources of resistance to *Meloidogyne enterolobii* in commercial and wild tomatoes

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ABSTRACT

Meloidogyne enterolobii (=*M. mayaguensis*) is an emerging plant pathogen capable of inducing root galls and yield reduction in a wide range of host species. This pathogen has also been reported as a global threat for tomato (*Solanum lycopersicum*) crop production mainly due to its ability to overcome the resistance meditated by the *Mi-1* gene. Despite the potential importance of this nematode, sources of resistance to *M. enterolobii* are not yet available for breeding purposes. The main objective of the present work was to evaluate a large *Solanum* (section *Lycopersicon*) germplasm (comprising nine species and one botanic variety) aiming to identify useful sources of resistance to *M. enterolobii*. In the first screening assay, 101 accessions and the susceptible standard *S. lycopersicum* 'Santa Cruz' were inoculated and evaluated under controlled conditions. The phenotypic criteria used for evaluation were the number of root galls, gall index, number of eggs, and the reproduction factor. Plants of the 20 selected accessions were cultivated in 0.4 L pots filled with sterile soil. Inoculation procedures were identical to the first assay, but with higher inoculum pressure (3,300 eggs per plant). Three accessions with superior tolerance levels to *M. enterolobii* were identified viz. *S. lycopersicum* 'Yoshimatsu', *S. lycopersicum* 'CNPH 1246' and *S. Pimpinellifolium* CGO 7650 (= CNPH 1195). These accessions were re-evaluated against a distinct *M. enterolobii* population as well as against two other root-knot nematode species (*M. javanica* and one *M. incognita* race 1). Under higher inoculum pressure, 'Yoshimatsu' was found to be resistant to *M. javanica* and *M. incognita* race 1, but susceptible to *M. enterolobii* from guava. The other two sources displayed susceptibility to all three nematodes. Additional germplasm screening is needed since no source of stable genetic resistance to *M. enterolobii* was found so far.

Keywords: *Solanum* spp., germplasm, screening, root-knot nematode.

RESUMO

Busca por fontes de resistência a *Meloidogyne enterolobii* em tomateiros comerciais e selvagens

Meloidogyne enterolobii (=*M. mayaguensis*) é um patógeno de plantas capaz de induzir galhas e reduzir produtividade de uma vasta gama de espécies hospedeiras. Este patógeno tem sido também reportado como ameaça global para a cultura do tomateiro (*Solanum lycopersicum*), principalmente, por causa da sua habilidade de suplantar a resistência a algumas espécies de *Meloidogyne* mediada pelo gene *Mi-1*. Apesar da importância potencial deste nematoide, fontes de resistência a *M. enterolobii* ainda não estão disponíveis para fins de melhoramento. O principal objetivo do presente trabalho foi avaliar um amplo germoplasma de *Solanum* (seção *Lycopersicon*) composto por nove espécies e uma variedade botânica, objetivando identificar fontes de resistência a *M. enterolobii*. No primeiro ensaio, 101 acessos e a cultivar Santa Cruz, empregada como padrão de suscetibilidade, foram inoculados e avaliados sob condição controlada. As variáveis foram o índice de galhas, número de galhas e de ovos nas raízes e o fator de reprodução. Vinte acessos promissores quanto à reação de resistência a *M. enterolobii*, no primeiro ensaio, foram selecionados e testados no ensaio seguinte. Os acessos *S. lycopersicum* 'Yoshimatsu', *S. lycopersicum* 'CNPH 1246' e *S. Pimpinellifolium* CGO 7650 (= CNPH 1195) foram identificados com melhor comportamento de resistência a *M. enterolobii*. Estes acessos foram reavaliados contra uma população distinta de *M. enterolobii* e também contra *M. javanica* e *M. incognita* raça 1. Sob maior pressão de inóculo, 'Yoshimatsu' foi resistente a *M. javanica* e a *M. incognita* raça 1, mas, suscetível a *M. enterolobii*. Os outros dois acessos foram suscetíveis aos três nematoides. Germoplasmas adicionais devem ser avaliados uma vez que fontes de resistência a *M. enterolobii* ainda não foram encontradas.

Palavras-chave: *Solanum* spp., prospecção, nematoide-das-galhas, controle genético, melhoramento.

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Fruit quality and yield of cultivated tomato (*Solanum lycopersicum*) are severely affected by nematode species, especially in tropical and subtropical areas of the world (Moens *et al.*, 2009). *Meloidogyne* species are very difficult to control via chemical and cultural methods, being a very serious problem when a susceptible tomato crop is established in already infested soils (Elling, 2013) and, or under protected crop system.

Meloidogyne enterolobii is a new invasive root-knot nematode species with an extremely wide host range, which includes the original host pacara earpod tree (*Enterolobium contortisiliquum*) as well as guava (*Psidium guajava*),

acerola (*Malpighia glabra*), weed and ornamental plants, tomato (*Solanum lycopersicum*) and many vegetable crops (Yang & Eisenback, 1983; Carneiro *et al*., 2001). An earlier confirmation of *M. enterolobii* as a new species was delayed since it was much likely misidentified as *M. incognita* (Elling, 2013).

Symptoms of *M. enterolobii* in many host plants include overall chlorosis and stunting associated with the presence of large root galls and root necrosis (Elling, 2013). This nematode has been already reported occurring in Asia (China and Vietnam), Europe (France and Switzerland); Central America (Puerto Rico), South America (Brazil) and North America (Florida) as well as in the African continent (Elling, 2013). In Brazil, *M. enterolobii* (initially described as *M. mayaguensis*) was first reported causing severe yield losses in guava orchards in Pernambuco and Bahia States (Carneiro *et al*., 2001). After this initial report, *M. enterolobii* was reported in virtually all geographic areas of the country (Siqueira *et al.*, 2009), affecting also tomatoes and bell peppers (*Capsicum annuum*) under protected crop systems in Southeast Brazil.

So far, the employment of cultivars and rootstocks with genetic resistance has been the major strategy to control the damages caused by root-knot nematodes in tomato. Sources of resistance to *Meloidogyne* species in the genus *Solanum* (section *Lycopersicon*) were first identified in *S. peruvianum* accessions and a single, dominant gene (*Mi-1*) was successfully introgressed into *S. lycopersicum* via interspecific crosses and embryo rescue techniques. The *Mi-1* gene confers large-spectrum resistance, being effective against isolates and races of three root-knot nematode species (*M. incognita*, *M. javanica*, and *M. arenaria*). The resistance of the *Mi-1* gene was mapped to the top region of the chromosome 6 and it was already cloned and characterized. Introgression of the *Mi-1* gene into commercial tomato cultivars was a very important breeding achievement, avoiding yield and quality losses caused mainly by mixed infections of *M. incognita* and *M. javanica*, a common feature observed in many producing areas of the world. However, this gene is not effective to *M. hapla* and also against isolates of *M. brasiliensis* (Charchar *et al.*, 2010). In fact, *M. enterolobii* has been reported as a potential threat for tomato crop in tropical and subtropical areas, especially due to its ability to overcome the resistance meditated by the *Mi-1* gene (Yang & Eisenback, 1983). In tomato cultivars and rootstocks (with and without the *Mi-1* gene), *M. enterolobii* is able to induce stunting and extensive root galling, which might result in drastic yield and quality losses (Pinheiro *et al.*, 2009).

In addition to the *Mi-1*, new resistance genes/alleles to *Meloidogyne* species (named as *Mi-2* up to *Mi-9*) have been reported in *Solanum* accessions and some of these genetic factors have been also located in the chromosome 6 as well as in the chromosome 12 (Jablonska *et al*., 2007). Some of these genes as well as other not yet fully characterized loci can confer resistance to *M. hapla* and, or can be effective under high temperature or against some resistance-breaking *M. incognita* isolates (Veremis & Roberts, 1996). However, there is so far no information about the reaction of these new sources of resistance to *M. enterolobii*. In addition, there is yet an unexplored genetic variability in *Solanum* (*lycopersicon*) for *M. enterolobii* resistance and this pathogen opens the opportunity to discover alternative resistance genes/alleles in this rich germplasm (Pinheiro *et al*., 2009; Melo *et al*., 2011).

Even though considered yet as a potential threat to the tomato crop, preemptive breeding to *M. enterolobii* resistance will be an important component aiming to minimize potential worldwide damages. In this context, the identification and incorporation into elite germplasm of broad spectrum resistance factors to *Meloidogyne* species (including *M. enterolobii*) is highly desirable, especially in tropical and subtropical regions where tomato is cultivated under high nematode inoculum pressure. We aimed to search for sources of stable genetic resistance to *M. enterolobii* exploring a large *Solanum* (section *Lycopersicon*) germplasm collection, comprising accessions of the cultivated and wild species.

MATERIAL AND METHODS

Experimental location and conditions

The experiments were carried out in a greenhouse system belonging to the Laboratory of Plant Nematology, Agronomy Department, Universidade Federal Rural de Pernambuco (UFRPE), Recife, Pernambuco State, Brazil (8°01'02''S, 34°56'41''W). The *Solanum* (section *Lycopersicon*) accessions evaluated in the present work are part of the germplasm collection maintained at Embrapa Hortaliças located in Brasilia-DF, Brazil. This germplasm collection comprised accessions classified into nine species and one botanic variety viz. *S. lycopersicum*, *S. lycopersicum* var. *cerasiforme*, *S. pimpinellifolium*, *S. peruvianum*, *S. chilense*, *S. habrochaites*, *S. pennellii*, *S. corneliomulleri*, *S. neorickii*, and *S. chmielewski* (Full accession list in supplementary table).

First screening assay: *Meloidogyne enterolobii* population and inoculum preparation

The *M. enterolobii* population employed in the present work was initially obtained from infected guava plants and then cultured on *S. lycopersicum* 'Santa Cruz' under greenhouse conditions (UFRPE). Eggs of *M. enterolobii* employed as inoculum in all assays were collected according to the technique of Hussey & Barker (1973) with minor modifications introduced by Boneti & Ferraz (1981). In short, roots with galls and egg masses were washed free of soil and cut into 2-cm pieces and dipped into a diluted sodium hypochlorite solution. Root segments were then triturated for 30 s at 200 rpm in a blender. Eggs were separated from plant and soil debris by pouring the suspension through a series of sieves and collecting them on a 38 µm-pore mesh.

First screening assay: Evaluation

of 101 *Solanum* (*Lycopersicum*) accessions to one *M. enterolobii* population

One hundred and one *Solanum* (section *Lycopersicon*) accessions were evaluated in the first experiment. Seedlings were produced in polystyrene trays (68x34 cm / 128 cells / 40 mL/cell) filled with commercial solid substrate (Basaplant®). The experiment was conducted only in polystyrene trays. The assay was set up in a randomized block design with two replications (two lines with eight plants of each tomato genotype were evaluated). Only a single plant was allowed to grow in each tray cell. One tray line (with eight plants each) of the susceptible tomato 'Santa Cruz' was included as internal control in each tray in order to monitor the inoculum viability. The trays were kept in a greenhouse free of insect infestation with daily irrigation and without pesticide applications. Temperature range during the assay was 21.6 to 31.7°C and relative air humidity range was 54.8 to 91.3%. Substrate infestation was carried out 20 days after sowing with an egg suspension (adjusted to 710 *M. enterolobii* eggs/mL). Inoculum was placed at crown area around the stem of each plant (1 mL of the inoculum suspension/plant) with the aid of a disposable syringe. Presence of root galls in the susceptible control was checked weekly. The most adequate time to carry out the germplasm evaluation was established when profuse gall formation was observed (around 45 days after inoculation) in the susceptible control.

The phenotypic criteria used for evaluation of each individual plant were number of galls, gall index, number of eggs, and the reproduction factor. The number of galls was visually estimated in roots immersed in water in order to remove the substrate. The gall index was assessed using the scale of Carvalho Filho *et al*. (2011) [1= few visible (<10 galls) and small (<1 mm) galls; 2= few visible galls, but with intermediate size (1 to 3 mm); 3= intermediate number of visible galls (10 to 30 galls), standard size, with some large galls (>3 mm); 4= many visible (>30 galls) predominantly large (>3 mm) galls, with few of intermediate size, some galls already coalescing; 5= high number (>30 galls) of large, conspicuous galls, many of them already coalescing]. The levels of resistance/susceptibility were grouped according to Boiteux & Charchar (1996) (grades between 1.0 and 1.6 were classified as highly resistant; from 1.7 to 2.3 = resistant; from 2.4 to 3.0 = intermediate; from 3.1 to 4.0 = susceptible; from 4.1 to 5.0 = highly susceptible). The number of nematode eggs in the root system of each accession was determined by counting the eggs under a dissecting stereomicroscope after extraction employing the technique described by Hussey & Barker (1973) with modifications introduced by Boneti & Ferraz (1981) and then counted using a microscope. The reproduction factor (RF) was calculated as the number of eggs observed in each inoculated plant [= final nematode population (FP)] divided by number of eggs used for inoculation of each plant [= initial nematode population (IP)] (Oostenbrink, 1966).

Second screening assay: Re-evaluation of 20 selected *Solanum* (*Lycopersicum*) accessions against *M. enterolobii*

Twenty accessions with the lowest values for gall index, gall number, number of eggs, and reproduction factor in the first assay were selected for a subsequent assay. The cultivars Santa Cruz and Yoshimatsu (*S. lycopersicum*) (previously identified as a promising resistant material) were included in this second assay as susceptible and resistant standards, respectively. The second assay was set up in a randomized block design with three replications. The experimental plots were composed by three 0.4-L plastic pots (one plant/pot) filled with sterile soil. The cultivation in large pots was carried out in order to allow a better root development when compared to the first assay (conducted in polystyrene trays). Temperature ranged between 23.6 and 33.6°C and relative air humidity range was 55.8 to 92.8%. Substrate infestation was carried out 20 days after sowing (straight in the soil) with a nematode egg suspension (adjusted to 1,100 eggs/mL). Inoculum was placed at the crown area around the stem of each plant (3 mL of the inoculum suspension per plant = 3,300 eggs per plant) using a disposable syringe. Presence of root galls in the susceptible control was checked weekly. The most adequate time to carry out the germplasm evaluation was established 45 days after inoculation (identical to that of the first assay). Three traits (gall number, number of eggs, and reproduction factor) were evaluated for each plant essentially as described in the first assay.

Statistical analyses of the first and second assays

The statistical model for the first assay was a randomized complete block design $y_{ij} = \mu+\pi_i+\beta_j+\varepsilon_{ij}$, where y_{ij} is ijth observation, μ is an overall mean, π_i is the effect of ith treatment, β_j is the block effect jth, and ε_{ij} is the usual NID $(0,\sigma^2)$ random error term. Exploratory data analysis for the two assays were carried out in order to check the assumptions underlying analysis of variance and homoscedasticity of the data set using the Shapiro-Wilk and Bartlett tests (SAS, 2009). In both assays a departure was detected from the normality for all variables observed (gall number, egg number and reproduction index). For this reason, we used an adaptation of the Box-Cox transformation family as described in Yamamura (1999). In the first assay the variables were transformed to ln(y) and in the second assay the number of galls was transformed to ln(y), number of eggs was transformed to $\sqrt{y+0.5}$, and reproduction factor was transformed to $\ln(\sqrt{y+0.5})$. The Scott-Knott test was carried out to assess significant differences among accessions. The tests for normality, homoscedasticity and the Box-Cox transformations were carried out with the software package SAS 9.2 (SAS, 2009). The Scott-Knott test was carried out using the software package SISVAR 5.3 (Ferreira, 2011).

Third assay: Evaluation of the three most promising *Solanum* (*Lycopersicum*) accessions to a distinct *M. enterolobii* population and to *M. javanica* and *M. incognita* race 1 populations

This experiment was carried out from May to September 2014 under greenhouse conditions at Embrapa Hortaliças (15º56'00"S, 48º06'00"W, 25ºC). Three tomato accessions (Yoshimatsu, CNPH 1195 and CNPH 1246) identified in previous assays as being the most promising resistance sources to *M. enterolobii* were re-evaluated for their reaction to a distinct *M. enterolobii* population (aiming to confirm their reaction) as well as to one *M. javanica* population and one *M. incognita* race 1 population. The susceptible and resistant controls were tomato cultivars Rutgers and Nemadoro, respectively. Females of *M. javanica* and *M. incognita* race 1 populations were collected from individually infected tomato roots in the experimental area of Embrapa Hortaliças. *Meloidogyne incognita* race was characterized after inoculation of a set of race-differential host species (Taylor & Sasser, 1978). *M. enterolobii* was obtained from infected guava trees in Palmas, Tocantins State, Brazil (Charchar *et al*., 2010). All populations used as inoculum sources were kept under greenhouse conditions. Analyses of the perineal pattern morphology confirmed the species identification of each population. Species-specific esterase patterns (Carneiro & Almeida, 2001) also confirmed the taxonomic status of each population.

Inoculum production

Nematode populations were multiplied in tomato cv. Rutgers. Seedlings (ten days after germination) obtained in styrofoam trays were transplanted to pots containing 3 L sterile Plantmax® substrate. The inoculation of the seedlings' roots was performed eight days after transplanting using a suspension of 4,000 eggs and second stage juveniles (J2) of each species separately. Inoculum suspension (5 mL) was distributed around the crown of each plant. Around 60 days after inoculation, J2 and eggs were extracted from the root systems following the methodology described by Hussey & Barker (1973) and modified by Boneti & Ferraz (1981).

Evaluation of the tomato accessions

Fourteen-day old seedlings of the three tomato accessions and the two standard cultivars obtained in styrofoam trays were transplanted to pots containing 3 L sterile Plantmax® substrate. The inoculation of the seedlings' roots was performed eight days after transplanting using a suspension of 4,000 eggs and J2 of each species separately. The experiment was conducted in a completely randomized factorial design 5*x*3 (five tomato genotypes *x* three nematode species), with six replicates (one plant per pot). Eighty-three days after inoculation, plants were evaluated for egg mass index, gall index, number of eggs per gram of root, and reproduction factor. For egg-mass index (IMO), the plants were collected, root systems washed under running water, and the roots colored by immersion in a solution of phloxine B (0.5 g/L water) during 15 minutes. Then, the egg mass number was counted, using a stereoscopic microscope, throughout the plant's root system/replication (Taylor & Sasser, 1978). The IMO in the roots was obtained according to Taylor & Sasser (1978) using a scale of notes (0= roots without egg mass; 1= presence of 1 to 2 egg masses; 2= presence of 3 to 10 egg masses; 3= presence of 11 to 30 egg masses; 4= presence of 31 to 100 egg masses and 5= more than 100 egg masses). The traits gall number, number of eggs, and the reproduction factor were evaluated for each plant essentially as described in the first assay.

RESULTS AND DISCUSSION

First screening assay employing 101 *Solanum* (*Lycopersicon*) accessions

For the criterion number of galls, 34 accessions displayed values significantly lower than that of the susceptible standard tomato 'Santa Cruz' (Table 1). Twelve from this group also showed significant lower gall index values in comparison to tomato 'Santa Cruz'. Two of these accessions [*S. habrochaites* 'PI-247087' (= CNPH 1288) and *S. habrochaites* 'PI-126449' (= CNPH 1290)] were classified as highly resistant. Ten accessions were classified as resistant viz. *S. peruvianum* 'PI 126408' (= CNPH 0102), *S. lycopersicum* 'Venus' (= CNPH 0181), *S. lycopersicum* Cannary Row (= CNPH 0969), *S. chmielewski* (CNPH 1022), *S. lycopersicum* 'Hawaii-7996' (= CNPH 1048), *S. lycopersicum* (CNPH 1226), *S. chilense* 'LA 1963' (= CNPH 1238), *S. lycopersicum* 'PI 126428' (= CNPH 1260), *S. pennellii* 'LA 416' (= CNPH 409) and *S. peruvianum* 'LA 1616' (= CNPH 798). The remaining accessions presented high number of galls, similar to that observed in the susceptible standard (Table 1). The gall number and gall index are practical and non-destructive methods to evaluate *Meloidogyne*-host plant interactions. In relation to gall number, the ideal phenotypic reaction from the resistance breeding standpoint is an immunity-like response characterized by the complete absence of root galls and giant cells. The presence of giant cells in the vascular cylinder induced by nematode attack is the main factor restricting water flow and proper nutrient uptake in susceptible plants (Westerich *et al*., 2011).

In the first assay, the gall index was efficient to discriminate the accessions, which allows the allocation of the genetic materials in a wide range of responses, varying from highly resistant to highly susceptible (Table 1). Twenty-three accessions displayed mean values for gall index significantly lower than that of the susceptible standard (the tomato cultivar Santa Cruz). In this assay, the accessions were classified according to the gall index into the following reaction groups: two accessions were classified as highly resistant; 21 as resistant; 39 as moderately resistant; 35 as susceptible and four as highly susceptible. Eleven accessions evaluated in our assay were also evaluated in a previous screening assay to *M. enterolobii* reaction (Pinheiro *et al.*, 2009). The accessions *S. habrochaites* 'PI 247087' (= CNPH 1288) and *S. habrochaites* 'PI 126449' (= CNPH 1290) were also classified as highly resistant displaying the lowest gall index values (Pinheiro *et al*., 2009). Likewise, the accession *S. lycopersicum* 'CNPH 0969' classified as resistant in our assay was also reported as resistant.

In our first assay, 46 accessions had

Table 1. Gall index; number of galls; number of eggs; and reproduction factor values of 101 *Solanum* (section *Lycopersicon*) accessions and the susceptible standard cultivar *S. lycopersicum* 'Santa Cruz' evaluation (45 days after inoculation) after *Meloidogyne enterolobii* inoculation. Recife, UFRPE, 2012.

Accession	Gall index[1,2,3]	Accession	Number of galls[1,2]	Accession	Number of eggs[1,2]	Accession	Reproduction factor[3]
CNPH 1288	1.34 a	CNPH 1288	5.59 a	CNPH 0499	2498 a	CNPH 0499	3.52 a
CNPH 1290	1.59 a	CNPH 0409	6.67 a	CNPH 1298	2654 a	CNPH 1298	3.74 a
CNPH 0102	1.80 a	CNPH 0698	7.49 a	CNPH 1226	2991 a	CNPH 1226	4.22 a
CNPH 1185	1.82 a	CNPH 1454	7.53 a	CNPH 0409	3500 a	CNPH 0409	4.93 a
CNPH 1260	1.87 a	CNPH 0707	7.76 a	CNPH 0866	3707a	CNPH 0866	5.22 a
CNPH 1226	1.88 a	CNPH 1225	8.38 a	CNPH 1260	4250 a	CNPH 1260	5.99 a
CNPH 1249	1.93 a	CNPH 1260	8.64 a	CNPH 1120	4434 a	CNPH 1120	6.24 a
CNPH 1034	1.94 a	CNPH 0017	8.84 a	CNPH 1456	4833 a	CNPH 1456	6.81 a
CNPH 1238	2.00 a	CNPH 1607	8.90 a	CNPH 0398	5000 a	CNPH 0398	7.05 a
CNPH 1195	2.00 a	CNPH 1238	9.00 a	CNPH 0698	5350 a	CNPH 0698	7.54 a
CNPH 1092	2.04 a	CNPH 1048	9.47 a	CNPH 0663	5371 a	CNPH 0663	7.57 a
CNPH 1022	2.10 a	CNPH 1226	9.50 a	CNPH 0865	5504 a	CNPH 0865	7.75 a
CNPH 0899	2.13 a	CNPH 1092	9.53 a	CNPH 0017	5798 a	CNPH 0017	8.17 a
CNPH 0798	2.17 a	CNPH 1185	10.55 a	CNPH 0390	5807 a	CNPH 0390	8.18 a
CNPH 0409	2.17 a	CNPH 0969	10.67 a	CNPH 0955	5807 a	CNPH 0955	8.18 a
CNPH 0969	2.17 a	CNPH 1246	10.88 a	CNPH 1454	5833 a	CNPH 1454	8.22 a
CNPH 1048	2.20 a	CNPH 0798	11.25 a	CNPH 0784	5917 a	CNPH 0784	8.34 a
CNPH 0602	2.25 a	CNPH 1561	11.30 a	CNPH 0899	6208 a	CNPH 0899	8.75 a
CNPH 0417	2.25 a	CNPH 0181	11.40 a	CNPH 0182	6336 a	CNPH 0182	8.92 a
CNPH 0181	2.29 a	CNPH 0019	11.56 a	CNPH 1238	6400 a	CNPH 1238	9.02 a
CNPH 1124	2.32 a	CNPH 0102	11.72 a	CNPH 1195	6633 a	CNPH 1195	9.34 a
CNPH 0423	2.32 a	CNPH 0182	11.76 a	CNPH 0184	6694 a	CNPH 0184	9.43 a
CNPH 0780	2.34 a	CNPH 0156	12.07 a	CNPH 1246	6725 a	CNPH 1246	9.47 a
CNPH 0876	2.42 a	CNPH 0733	12.10 a	CNPH 1056	6731 a	CNPH 1056	9.49 a
CNPH 0724	2.43 a	CNPH 1039	12.50 a	CNPH 0181	6750 a	CNPH 0181	9.51 a
CNPH 1521	2.44 a	CNPH 1290	12.50 a	CNPH 0402	6857 a	CNPH 0402	9.66 a
CNPH 1224	2.48 a	CNPH 0865	12.73 a	CNPH 1048	6880 a	CNPH 1048	9.69 a
CNPH 1011	2.50 a	CNPH 1121	12.75 a	CNPH 0717	7071 a	CNPH 0717	9.96 a
CNPH 0945	2.50 a	CNPH 0117	12.79 a	CNPH 1289	7164 a	CNPH 1289	10.09 a
CNPH 1035	2.50 a	CNPH 0876	13.09 a	CNPH 0798	7167 a	CNPH 0798	10.09 a
CNPH 0045	2.55 a	CNPH 1522	13.29 a	CNPH 0790	7429 a	CNPH 0790	10.47 a
CNPH 0202	2.57 a	CNPH 1195	13.40 a	CNPH 1526	7629 a	CNPH 1526	10.75 a
CNPH 0182	2.57 a	CNPH 0945	13.50 a	CNPH 1225	8007 a	CNPH 1225	11.28 a
CNPH 0784	2.60 a	CNPH 1022	13.70 a	CNPH 1607	8500 a	CNPH 1607	11.98 a
CNPH 0698	2.65 a	CNPH 1298	14.34 b	CNPH 1521	8514 a	CNPH 1521	12.00 a
CNPH 0534	2.65 a	CNPH 0866	14.57 b	CNPH 0268	8571 a	CNPH 0268	12.08 a
CNPH 0499	2.67 a	CNPH 0378	14.60 b	CNPH 1121	8800 a	CNPH 1121	12.40 a
CNPH 1522	2.69 a	CNPH 1560	14.73 b	CNPH 0969	9198 a	CNPH 0969	12.96 a
CNPH 0419	2.69 a	CNPH 1514	14.92 b	CNPH 0117	9214 a	CNPH 0117	12.98 a
CNPH 1225	2.69 a	CNPH 0602	15.14 b	CNPH 0803	9273 a	CNPH 0803	13.09 a
CNPH 0733	2.70 a	CNPH 1056	15.29 b	CNPH 1039	9600 a	CNPH 1039	13.52 a
CNPH 0376	2.73 a	CNPH 0376	15.37 b	CNPH 0019	9765 a	CNPH 0019	13.76 a
CNPH 1246	2.73 a	CNPH 0790	15.41 b	CNPH 0113	9863 a	CNPH 0113	13.89 a
CNPH 1121	2.75 a	CNPH 0499	15.42 b	CNPH 0156	9996 a	CNPH 0156	14.08 a

Table 1. continued....

Accession	Gall index[1,2,3]	Accession	Number of galls[1,2]	Accession	Number of eggs[1,2]	Accession	Reproduction factor[3]
CNPH 1148	2.77 a	CNPH 0784	15.54 b	CNPH 0378	10042 a	CNPH 0378	14.14 a
CNPH 0402	2.79 a	CNPH 1521	15.86 b	CNPH 1035	10050 a	CNPH 1035	14.16 a
CNPH 0790	2.81 a	CNPH 0398	15.90 b	CNPH 0045	10054 b	CNPH 0045	14.16 b
CNPH 0707	2.82 a	CNPH 1249	16.10 b	CNPH 1560	10071 b	CNPH 1560	14.19 b
CNPH 0006	2.82 a	CNPH 1250	16.14 b	CNPH 1250	10300 b	CNPH 1250	14.51 b
CNPH 0117	2.82 a	CNPH 1123	16.21 b	CNPH 0095	10673 b	CNPH 0095	15.04 b
CNPH 0398	2.85 a	CNPH 0899	16.34 b	CNPH 0780	11250 b	CNPH 0780	15.85 b
CNPH 1514	2.88 b	CNPH 0717	16.41 b	CNPH 1092	11273 b	CNPH 1092	15.88 b
CNPH 0378	2.89 b	**Santa Cruz**	16.86 b	CNPH 1565	11367 b	CNPH 1565	16.01 b
CNPH 1289	2.89 b	CNPH 0419	16.86 b	CNPH 0643	11667 b	CNPH 0643	16.43 b
CNPH 1056	2.90 b	CNPH 1034	17.01 b	CNPH 1522	11750 b	CNPH 1522	16.55 b
CNPH 0017	2.92 b	CNPH 1224	17.13 b	CNPH 0668	11916 b	CNPH 0668	16.79 b
CNPH 1556	2.94 b	CNPH 1124	17.32 b	CNPH 1556	11946 b	CNPH 1556	16.83 b
CNPH 0095	2.98 b	CNPH 0457	17.69 b	CNPH 1438	12067 b	CNPH 1438	17.00 b
CNPH 1561	2.98 b	CNPH 1227	17.75 b	CNPH 1011	12125 b	CNPH 1011	17.08 b
CNPH 1123	2.98 b	CNPH 0789	17.79 b	CNPH 0638	12175 b	CNPH 0638	17.15 b
CNPH 0638	2.98 b	CNPH 0871	17.84 b	CNPH 1561	12180 b	CNPH 1561	17.15 b
CNPH 1039	3.00 b	CNPH 0750	17.98 b	CNPH 1563	12251 b	CNPH 1563	17.26 b
CNPH 0866	3.01 b	CNPH 0417	18.00 b	CNPH 0707	12727 b	CNPH 0707	17.93 b
CNPH 1607	3.05 b	CNPH 1035	18.08 b	CNPH 0610	13142 b	CNPH 0610	18.51 b
CNPH 0508	3.06 b	CNPH 1526	18.19 b	CNPH 1290	13317 b	CNPH 1290	18.76 b
CNPH 1515	3.07 b	CNPH 0668	18.42 b	CNPH 1288	13750 b	CNPH 1288	19.37 b
CNPH 0803	3.09 b	CNPH 0643	18.47 b	CNPH 0945	14375 b	CNPH 0945	20.25 b
CNPH 0457	3.11 b	CNPH 1563	18.54 b	CNPH 1514	14396 b	CNPH 1514	20.28 b
CNPH 1020	3.13 b	CNPH 0390	18.69 b	CNPH 0875	14517 b	CNPH 0875	20.45 b
CNPH 0156	3.13 b	CNPH 0955	18.69 b	CNPH 0534	14529 b	CNPH 0534	20.47 b
CNPH 1298	3.13 b	CNPH 0045	18.82 b	CNPH 0724	14593 b	CNPH 0724	20.56 b
Santa Cruz	3.14 b	CNPH 0423	18.82 b	CNPH 1022	14900 b	CNPH 1022	20.99 b
CNPH 0789	3.15 b	CNPH 1011	18.92 b	CNPH 0602	15171 b	CNPH 0602	21.37 b
CNPH 1438	3.17 b	CNPH 1289	19.17 b	CNPH 1185	15353 b	CNPH 1185	21.63 b
CNPH 0871	3.17 b	CNPH 1438	19.25 b	CNPH 0313	15521 b	CNPH 0313	21.86 b
CNPH 0113	3.19 b	CNPH 0402	19.56 b	CNPH 0418	15719 b	CNPH 0418	22.14 b
CNPH 1250	3.20 b	CNPH 0534	19.57 b	CNPH 0487	15767 b	CNPH 0487	22.20 b
CNPH 0268	3.22 b	CNPH 0113	19.98 b	CNPH 0789	15871 b	CNPH 0789	22.36 b
CNPH 0418	3.25 b	CNPH 0663	20.51 b	CNPH 0417	16000 b	CNPH 0417	22.54 b
CNPH 0955	3.27 b	CNPH 0724	20.52 b	**Santa Cruz**	16080 b	**Santa Cruz**	22.65 b
CNPH 0390	3.27 b	CNPH 0638	21.07 b	CNPH 0876	16150 b	CNPH 0876	22.75 b
CNPH 1454	3.30 b	CNPH 0313	21.53 b	CNPH 1135	17944 b	CNPH 1135	25.27 b
CNPH 0313	3.31 b	CNPH 0803	21.59 b	CNPH 0457	18340 b	CNPH 0457	25.83 b
CNPH 0610	3.36 b	CNPH 1020	21.63 b	CNPH 1123	19072 b	CNPH 1123	26.87 b
CNPH 0487	3.37 b	CNPH 1148	22.00 b	CNPH 1249	19158 b	CNPH 1249	26.99 b
CNPH 0865	3.37 b	CNPH 0508	23.01 b	CNPH 1020	19221 b	CNPH 1020	27.08 b
CNPH 1456	3.38 b	CNPH 1565	23.47 b	CNPH 0419	19256 b	CNPH 0419	27.12 b
CNPH 1526	3.48 b	CNPH 0006	24.68 b	CNPH 1515	20138 b	CNPH 1515	28.37 b
CNPH 0643	3.49 b	CNPH 0487	24.87 b	CNPH 0750	20671 b	CNPH 0750	29.12 b
CNPH 0750	3.50 b	CNPH 1456	24.88 b	CNPH 0423	20884 b	CNPH 0423	29.42 b

Table 1. continued....

Accession	Gall index[1,2,3]	Accession	Number of galls[1,2]	Accession	Number of eggs[1,2]	Accession	Reproduction factor[3]
CNPH 1227	3.50 b	CNPH 0095	25.00 b	CNPH 1124	21063 b	CNPH 1124	29.67 b
CNPH 1563	3.54 b	CNPH 0184	25.22 b	CNPH 1034	21115 b	CNPH 1034	29.74 b
CNPH 1135	3.57 b	CNPH 0418	25.44 b	CNPH 1224	21375 b	CNPH 1224	30.11 b
CNPH 0019	3.57 b	CNPH 1515	25.50 b	CNPH 0376	21889 b	CNPH 0376	30.83 b
CNPH 0717	3.79 b	CNPH 0875	25.72 b	CNPH 1227	22350 b	CNPH 1227	31.48 b
CNPH 0663	3.82 b	CNPH 0268	26.00 b	CNPH 0871	23243 b	CNPH 0871	32.74 b
CNPH 1565	3.91 b	CNPH 1135	26.40 b	CNPH 0102	24667 b	CNPH 0102	34.74 b
CNPH 0875	3.95 b	CNPH 0610	26.57 b	CNPH 1148	26592 b	CNPH 1148	37.46 b
CNPH 1560	4.06 b	CNPH 1556	26.88 b	CNPH 0733	26707 b	CNPH 0733	37.61 b
CNPH 0668	4.44 b	CNPH 1120	28.64 b	CNPH 0202	27117 b	CNPH 0202	38.19 b
CNPH 1120	4.53 b	CNPH 0202	29.13 b	CNPH 0508	28655 b	CNPH 0508	40.36 b
CNPH 0184	4.63 b	CNPH 0780	29.53 b	CNPH 0006	37833 b	CNPH 0006	53.29 b
Mean	2.85		16.73		12289		17.31
CV (%)	20.38		2.26		5.0		17.43

[1]Means within a column followed by same letters do not differ significantly at 5% level, Scott-Knott's cluster analysis; [2]Data transformation [*ln(y)*] using Box & Cox (1964) method; [3]Reproduction factor (RF = Final nematode population/Initial population), RF>1.0 = susceptible reaction; [3]Gall index= Values from 1.0 to 1.6 indicate high resistance; from 1.7 to 2.3 indicate resistant genotype; from 2.4 to 3.0, moderate level of resistance; from 3.1 to 4.0 indicate susceptible reaction; from 4.1 a 5.0 indicate highly susceptible.

significant lower number of eggs when compared to the standard susceptible tomato 'Santa Cruz'. Seven of them [*S. lycopersicum* 'Venus' (= CNPH 0181), *S. lycopersicum* 'Cannery Row' (= CNPH 0969), *S. lycopersicum* 'Hawaii-7996' (= CNPH 1048), *S. lycopersicum* 'CNPH 1226', *S. chilense* 'LA 1963' (= CNPH 1238), *S. lycopersicum* 'PI 126428' (= CNPH 1260), and *S. pennellii* 'LA-0416' (= CNPH 409)] also displayed significant lower values for gall index and gall number (Table 1). The trait low number of nematode eggs is very important in tomato breeding for resistance since it has an epidemiological impact by either avoiding or delaying the pathogen multiplication. The *Meloidogyne* females can lay eggs for up to three weeks with the average number of around 400 to 500 eggs; in some circumstances, the female lays up to 2,000 eggs (Taylor & Sasser, 1978). Development and life cycle completion of *M. enterolobii* were observed even in roots of tomato genotypes with the *Mi-1* gene (Yang & Eisenback, 1983; Westerich *et al*., 2011).

Root-knot nematode resistance is defined by the effects of plant genes that either restrict or prevent multiplication in a given host species (Trudgill, 1991). In the first assay, the reproduction factor (RF) values ranged from 3.52 to 53.28. In the literature, the susceptible reaction is characterized when a given accession had a mean RF≥1.0 and a resistant reaction when RF<1.0. Therefore, under our experimental conditions, no accession could be classified as resistant according to this criterion. However, a group of 47 accessions (Table 1) presented RF values significantly lower than that of the tomato cultivar Santa Cruz (RF= 22.65), a value close to that previously reported to another susceptible tomato cultivar Rutgers (RF=17.72) (Cantu *et al*., 2009). In another study, the *M. enterolobii* - *S. lycopersicum* interaction indicated RF values ranging from 4.80 to 8.40 for cultivars Santa Clara and Santa Cruz, respectively (Melo *et al*., 2011). Variation of the *M. enterolobii* RF, ranging from 11.34 to 18.21, was previously observed in a collection of commercial tomato rootstocks carrying the *Mi-1* gene (Cantu *et al*., 2009). The reproduction of *M. enterolobii* and *M. javanica* in a set of rootstocks with the *Mi-1* gene ('Magnet' and 'Helper M') was evaluated in another set of experiments using artificial soil infestation with an inoculum pressure of 500 J2 per plant. In these two rootstocks, carrying the *Mi-1* locus, *M. javanica* was unable to complete its life cycle whereas *M. enterolobii* development was not affected with females laying a profuse amount of eggs, 24 days after inoculation.

Second assay with 20 selected *Solanum* (*Lycopersicon*) accessions

Significant differences were observed for the number of galls among accessions (Table 2). The cultivar Yoshimatsu and the accessions *S. peruvianum* 'PI 126408-6' (= CNPH 0102), *S. lycopersicum* 'Cannery Row' (= CNPH 0969), *S. lycopersicum* 'Ohio 8245' (= CNPH 1246), *S. lycopersicum* 'PI 126428' (= CNPH 1260), *S. habrochaites* 'PI 126449' (= CNPH 1290), and *S. peruvianum* 'LA 1616' (= CNPH 798) showed significantly lower number of gall differences when compared to the susceptible control 'Santa Cruz'. Cultivar Yoshimatsu showed lowest value (around 3.65 galls per root system). No significant differences were observed among accessions for the trait number of eggs (Table 2). However, in relation to the reproduction factor, the accessions *S. lycopersicum* 'Ohio 8245' (= 'CNPH

1246') (0.17), 'Yoshimatsu' (0.62), and *S. pimpinelifolium* 'CGO 7650' (= 'CNPH 1195') (1.69) had a significantly superior performance when compared to the susceptible standard 'Santa Cruz' (5.58). According to the classical definition of resistance based upon analysis of the reproduction factor, only the accessions *S. lycopersicum* 'Ohio 8245' and 'Yoshimatsu' can be classified as resistant since their values were lower than 1. The Brazilian cultivar Yoshimatsu is derived from multiple crosses involving breeding lines from Hawaii (USA) and French Guiana. This genetic material was released in 1988 after selection to adaptation to the Amazonas Basin region, tolerance to high temperatures, and bacterial wilt (*Ralstonia solanacearum*) resistance (Souza & Gentil, 2013).

Plants were conducted in 0.4 L pots in the second assay, which provided more suitable conditions for development and nutrient uptake. In fact, the overall plant development was visibly more vigorous when compared to the first assay conducted in trays. In this assay *S. pennellii* LA-416 (= CNPH 409) was found to be susceptible, confirming the reaction previously observed by Melo *et al*. (2011). The accessions *S. lycopersicum* 'PI-126428' (= CNPH 1260) as well as *S. peruvianum* 'PI 126408' (= CNPH 0102), *S. peruvianum* 'CNPH 0602', *S. lycopersicum* 'Ohio 8245' (= CNPH 1246), *S. habrochaites* 'PI 247087' (= CNPH 1288), *S. habrochaites* 'PI 126449' (= CNPH 1290), *S. lycopersicum* 'LA-3043' (= CNPH 1521), *S. peruvianum* 'LA-1616' (= CNPH 0798) and *S. pimpinellifolium* 'CGO 7650' (= CNPH 1195) displayed superior levels of resistance to *M. enterolobii* in both assays. Therefore, these results indicated that some *Solanum* (sect. *Lycopersicon*) accessions may have a stable phenotypic expression of resistance to *M. enterolobii*. All these genotypes might be considered useful genetic sources for tomato breeding

Table 2. Number of galls; number of eggs; and reproduction factor values of 20 *Solanum* (section *Lycopersicon*) accessions and the susceptible and resistant standard cultivars *S. lycopersicum* 'Santa Cruz' and 'Yoshimatsu'; respectively evaluation under *Meloidogyne enterolobii* inoculation. Evaluation was carried out 45 days after inoculation. Recife, UFRPE, 2013.

Accession	Number of galls[1,2]	Accession	Number of eggs[1,3]	Accession	Reproduction factor[1,4,5]	RF[6]
Yoshimatsu	3.67 a	CNPH 1246	550 a	CNPH 1246	0.17 a	R
CNPH 0102	6.39 a	**Yoshimatsu**	2056 a	**Yoshimatsu**	0.62 a	R
CNPH 1290	10.61 a	CNPH 1195	5584 a	CNPH 1195	1.69 a	S
CNPH 0969	11.17 a	CNPH 0602	9798 a	CNPH 0602	2.97 b	S
CNPH 1260	12.67 a	CNPH 1521	13083 a	CNPH 1521	3.97 b	S
CNPH 1246	13.33 a	CNPH 1288	13631 a	CNPH 1288	4.13 b	S
CNPH 0798	16.56 a	CNPH 1260	13850 a	CNPH 1260	4.20 b	S
CNPH 1288	19.58 b	CNPH 0698	14650 a	CNPH 0698	4.44 b	S
Santa Cruz	20.67 b	CNPH 0102	15278 a	CNPH 0102	4.63 b	S
CNPH 0707	21.61 b	CNPH 0707	15333 a	CNPH 0707	4.65 b	S
CNPH 0698	21.67 b	CNPH 0876	15478 a	CNPH 0876	4.69 b	S
CNPH 1092	24.11 b	CNPH 0969	16183 a	CNPH 0969	4.90 b	S
CNPH 1048	24.67 b	**Santa Cruz**	18417 a	**Santa Cruz**	5.58 b	S
CNPH 1521	24.72 b	CNPH 1185	18550 a	CNPH 1185	5.62 b	S
CNPH 0899	28.00 b	CNPH 1225	19458 a	CNPH 1225	5.90 b	S
CNPH 0602	30.67 b	CNPH 1290	21690 a	CNPH 1290	6.57 b	S
CNPH 0409	31.00 b	CNPH 0409	24539 a	CNPH 0409	7.44 b	S
CNPH 0876	31.72 b	CNPH 1048	24608 a	CNPH 1048	7.46 b	S
CNPH 1225	32.89 b	CNPH 0499	25989 a	CNPH 0499	7.87 b	S
CNPH 1185	35.00 b	CNPH 0899	26378 a	CNPH 0899	7.99 b	S
CNPH 1195	43.44 b	CNPH 1092	26769 a	CNPH 1092	8.11 b	S
CNPH 0499	50.83 b	CNPH 0798	27779 a	CNPH 0798	8.41 b	S
$\overline{X}$[7]	22.90		16802		53.40	
CV (%)	29.46		41.16		5.09	

[1]Means within a column followed by same letters do not differ significantly at 5% level, Scott-Knott's cluster analysis; [2]Data transformation [*ln(y)*] using Box & Cox (1964) method; [3]Data transformation [*(y+0.5)^0.5*] using the Box & Cox (1964) method; [4]Data transformation [*ln(y+0.5)*] using the Yamamura (1999) method; [5] Reproduction factor (RF = Final nematode population/Initial population); [6]RF >1.0 = susceptible reaction; [7] $\overline{X}$ = overall mean.

Table 3. Reaction of tomato accessions to *Meloidogyne incognita* race 1, *M. javanica*, and *M. enterolobii*. Brasília, Embrapa Hortaliças, 2014.

Tomato accessions	Gall Index	Egg mass index	Number of galls/ gram of root	Reproduction factor[4]	Reaction[1]
			Meloidogyne enterolobii		
CNPH 522	3.8a[4]	3.0a	1090.1a	5.5a	S
CNPH 1195	4.2a	3.5a	1870.4a	7.7a	S
CNPH 1246	4.5a	2.8a	1672.1a	7.6a	S
Nemadoro[2]	4.2a	2.8a	1287.7a	5.8a	S
Rutgers[3]	4.7a	3.3a	1026.1a	8.5a	S
Overall Mean	4.27	3.10	1389.27	7.04	
CV (%)	13.53	19.08	54.46	34.26	
			Meloidogyne javanica		
CNPH 522	1.0d	1.0c	118.2c	0.4d	R
CNPH 1195	3.3c	4.0b	4569.3b	19.4b	S
CNPH 1246	4.0b	3.7b	12466.8a	11.8c	S
Nemadoro[2]	1.0d	1.0c	28.1c	0.1d	R
Rutgers[3]	5.0a	4.7a	10893.7a	83.9a	S
Overall Mean	2.87	2.86	5616.01	23.13	
CV (%)	8.06	17.79	65.82	24.99	
			***Meloidogyne incognita* race 1**		
CNPH 522	1.0c	1.0c	37.2c	0.1b	R
CNPH 1195	4.7b	4.0b	6546.5a	26.5a	S
CNPH 1246	5.0a	3.7b	5676.1a	24.9a	S
Nemadoro[2]	1.0c	1.0c	119.8c	0.4b	R
Rutgers[3]	5.0a	4.7a	3280.4b	29.7a	S
Overall Mean	3.33	2.87	3133.11	16.34	
CV (%)	6.93	15.60	59.11	51.21	

[1]I= Immune (RF= 0); R= resistant (RF<1) and, S= suscetível (RF>1); [2]Resistant control; [3]Susceptible control; [4]Means within a column followed by same letters do not differ significantly at 5% level, Scott-Knott's cluster analysis.

programs since they are not suitable hosts for *M. enterolobii.*

Third assay: Evaluation of the three most promising *Solanum* accessions against a distinct *M. enterolobii* population as well as one to one *M. javanica* and *M. incognita* race 1 population

The three most promising accessions (*S. lycopersicum* 'Yoshimatsu', *S. lycopersicum* 'Ohio 8245', and *S. pimpinellifolium* 'CGO 7650') were re-evaluated with a distinct *M. enterolobii* population as well as one *M. javanica* and one *M. incognita* race 1 population under higher inoculum levels (Table 3). 'Yoshimatsu' was found to be resistant to *M. javanica* and *M. incognita* race 1, but highly susceptible to a distinct *M. enterolobii* population. The other two sources displayed susceptibility to all three nematode species.

Resistant germplasm is the most tolerant and economic management strategy to control plant-parasitic nematodes. However, the presence of variants within species of the genus *Meloidogyne* that are able to overcome resistance genes and difficulties in identifying resistance genes in plants hamper progress in this area. Additionally, the well-studied *Mi-1* resistance gene from tomato proved ineffective against *M. enterolobii* (Elling, 2013). However, the results obtained here clearly indicated promising genetic solution to control damages caused by *M. enterolobii.* A subgroup of accessions with superior levels of tolerance to *M. enterolobii* were found in distinct species of the genus *Solanum* (section *Lycopersicon*) with special mention to the Brazilian cultivar *S. lycopersicum* 'Yoshimatsu' and the lines *S. lycopersicum* 'Ohio 8245' and *S. pimpinellifolium* 'CGO 7650'.

The accessions *S. lycopersicum* PI-126428, *S. peruvianum* 'PI 126408', *S. peruvianum* 'CNPH 602', *S. habrochaites* 'PI-247087', *S. habrochaites* 'PI-126449', *S. pimpinelifolium* 'LA-3043', and *S. peruvianum* 'LA-1616' displayed intermediate phenotypic responses and could be considered good sources of moderate tolerance to *M. enterolobii*. These accessions might be useful for breeding programs aiming to develop cultivars with genetic tolerance to this

emerging tomato pathogen. The *Mi-1* gene mediated tolerance is characterized by a localized necrosis of host cells near the invading nematode (Brito *et al*., 2007; Dropkin, 1969). It will be interesting to investigate which mechanism is associated with the resistance/tolerance sources reported here. *Solanum peruvianum* is an interesting genetic source since it presented one of the best performances against *M. enterolobii* and also displayed simultaneous resistance to *Meloidogyne* species in previous assays (Carvalho *et al*., 2010). The important limitation of the natural genetic factors coming from *S. peruvianum* accessions is that it will demand the employment of embryo-rescue technique after interspecific crossings, as was done to introgress the *Mi-1* gene from *S. peruvianum* 'PI 128657' into *S. lycopersicum*. However, due to this broad resistance spectrum, this accession is considered a potential multi-resistance source for breeding programs and effort to introgression of this resistance will be worthwhile.

From the preemptive breeding standpoint, the identification of superior levels of tolerance to *M. enterolobii* in the cultivated tomato *S. lycopersicum* 'Yoshimatsu' would allow a more efficient incorporation of the genetic factor(s) into elite tomato inbred lines and hybrids. In this case, the natural crossing barriers between accessions are not present. This pure inbred line would be suitable for inheritance, allelism, and linkage studies. Molecular markers could be used to help to map the resistance factors of the sources reported here and accelerate incorporation/ introgression of these genetic factors. This work might be facilitated by current available complete genome sequence of tomato (The Tomato Genome Consortium, 2012).

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