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Mapping a novel heat-stable resistance to *Meloidogyne* in *Lycopersicon peruvianum*

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Abstract The root-knot nematode heat-stable resistance locus from *L. peruvianum* LA2157 was mapped on chromosome 6. All wild tomato LA2157 entries and the LA2157 S_1 progeny tested were resistant to *Mi*-avirulent *Meloidogyne* spp. isolates at 32°C, indicating that the self-compatible accession is homozygous for heat-stable nematode resistance. The novel resistance locus was mapped on a RFLP linkage map; this map was based on a segregating F_2 population obtained from the interspecific F_1 between *L. esculentum* cv 'Solentos' and *L. peruvianum* LA2157. The inheritance of the heat-stable resistance was evaluated in 100 F_3 lines derived from one F_1 interspecific hybrid. The genotype of the resistance locus of the individual F_2 plants was based on the phenotypic classification of their F_3 lines, and the data were used to map the resistance locus on the arm of chromosome 6 with the closest linkage to TG178. The position of the novel heat-stable resistance of LA2157 was localized in the resistance genes' cluster close to the location of gene *Mi-1*. Cuttings of the F_3 lines expressed resistance to *Mi-1*-avirulent *M. incognita* and *M. javanica* biotypes at 25°C and at 32°C (a temperature at which *Mi-1* resistance is not expressed). There was no difference in the segregating population for expression of heat-unstable resistance and heat-stable resistance to *Mi-1*-avirulent *Meloidogyne* spp. However, LA2157 and cuttings of the above F_3 lines were susceptible to a *Mi-1*-virulent *M. incognita* isolate at 30°C and to a *M. hapla* isolate at 25°C.

Key words Heat-sensitivity · Virulence · Tomato · Root-knot nematodes · Mapping

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Introduction

Root-knot nematodes (*Meloidogyne* spp.) are important soil pests of many crops grown in warm temperate, subtropical and tropical regions (Lamberti 1979; Sasser 1977). Host-plant resistance to *Meloidogyne* spp. is utilized in many regions worldwide with respect to processing and fresh market tomato (*Lycopersicon esculentum* Mill.) varieties. All tomato cultivars with resistance to *Meloidogyne* have been developed from one resistant *L. peruvianum* L. interspecific hybrid plant (Smith 1944), and this resistance is expressed by the dominant gene *Mi-1* (Gilbert and McGuire 1956) located on chromosome 6 (Messeguer et al. 1991). The resistance conferred by *Mi-1* is effective against *M. incognita*, *M. arenaria* and *M. javanica*, but not against *M. hapla* populations (Dropkin 1969). The intensive use of a single resistance gene raises concerns over the durability of resistance due to the potential for selecting virulent nematode populations (Roberts 1995). There are reports of virulent populations of root-knot nematodes selected for several generations on plants bearing the *Mi-1* gene and of non-selected, naturally occurring virulent populations that overcome the resistance conferred by *Mi-1* (Roberts et al. 1990; Kaloshian et al. 1996).

The resistance conferred by *Mi-1* is temperature-sensitive and breaks down above 28°C (Holtzmann 1965; Dropkin 1969). The *Mi-1* gene breaks down at high temperatures to isolates of *M. javanica* in fields in Cyprus (Philis and Vakis 1977) and under greenhouse conditions (Tzortzakakis and Gowen 1996). The high

soil temperatures in the fields of Florida also reduce *Mi-1* gene expression in fresh market tomato (J. W. Noling, personal communication). Temperature sensitivity of *Meloidogyne* resistance genes has been reported in several other crops, including alfalfa (Griffin 1969), sweet potato (Jatala and Russell 1972) and cotton (Carter 1982), suggesting that it is a relatively common characteristic of plant defense expression of root-knot resistance. This phenomenon has also been reported for other disease or pest plant resistance interactions, for example the tobacco mosaic virus resistance gene *N* in tobacco (Whitham et al. 1994), in rust disease resistance in wheat (Luig and Rajaram 1972) and in flax (Islam et al. 1989) and for Hessian fly resistance in wheat (Tyler and Hatchett 1983).

Heat-stable resistance to *M. incognita* has been identified in clones of several *L. peruvianum* accessions (Ammati et al. 1986; Cap et al. 1993; Veremis and Roberts 1996c). Variability in the reproduction of different biotypes of *Meloidogyne* spp. has been demonstrated on different *L. peruvianum* genotypes (Veremis and Roberts 1996b). Within the genus *Lycopersicon* variability for resistance to *Meloidogyne* spp. is limited within the *L. peruvianum* complex (Veremis and Roberts 1996a). The wild tomato *L. peruvianum* is a highly polymorphic species (Rick 1986; Taylor 1986) that has incompatibility barriers when crossed to cultivated tomato, *L. esculentum*, controlled by polygenic mechanisms. However, the unilateral incompatibility barriers between the species can be overcome with bridge line and or embryo rescue methods (Lefrancois et al. 1993; van Heusden et al. 1995; Veremis and Roberts 1996c). *L. peruvianum* is a self-incompatible species except for accession LA2157 that is self-compatible (Rick 1986). The natural self-compatibility in LA2157 is associated with a lack of style S-RNase ribonuclease activity (Kowyama et al. 1994). The sequence of the allele of the self-compatible *S*-locus reveals the loss of a histidine residue that has been proposed to be the active site of the enzyme (Royo et al. 1994). Many angiosperm species employ self-incompatibility to maintain genetic diversity in a population, and self-compatibility is believed to have evolved from self-incompatible stocks (de Nettancourt 1997). The *L. peruvianum* accession LA2157 belongs to north Peruvian stock, collected in a region that may be the ancestral center of the *L. peruvianum* complex (Rick 1986). Ammati et al. (1986) found that accession LA2157 was highly resistant to root-knot nematodes at soil temperatures of 25°C and 30°C. Introduction of additional resistance sources that are heat-stable and expressed in the areas where gene *Mi-1* breaks down are needed for tomato crop protection. Analysis of the specificity and location of the novel resistance identified in LA2157 will be used in efforts to incorporate additional nematode resistance into cultivated tomato. The objective of the work presented here was to map the locus that contains the factor controlling expression of heat-stable nematode resistance in *L. peruvianum* LA2157.

Materials and methods

Plant material

Plant genotypes used in this study were *Lycopersicon peruvianum* LA2157 collected by the Lycopersicon expedition of 1980 in Tunnel Chotano, Cajamarca, in northern Peru, field number SAL 5002 (Esquinas-Alcazar 1981), and sent to us from Dr. C. M. Rick, Department of Vegetable Crops, University of California, Davis, and F_3 lines and F_5 lines derived from an F_1 interspecific hybrid from *L. esculentum* cv 'Solentos' × *L. peruvianum* LA2157 (van Heusden et al. 1995). A single plant of LA2157 was selfed and seed was collected from a single fruit, thereby providing the S_1 progeny.

Nematode cultures

Cultures of *Meloidogyne incognita* isolates Project 77 and Muller and *M. javanica* isolate 811 were started from field populations on greenhouse-grown tomato cv 'Tropic'. The *M. incognita Mi-1*-virulent isolate Cote d'Ivoire had been laboratory-selected for virulence to gene *Mi-1* and was cultured on greenhouse-grown tomato cv 'Piersol' (Roberts et al. 1990). The *M. hapla* isolate San Bernardino was started from a field population on greenhouse-grown tomato cv 'VFN-8'. The identities of the nematode isolates were confirmed as described previously (Cap et al. 1991).

Screening tests

One-month-old seedlings or rooted cuttings were used for tests of host reaction to nematodes. Single plants were grown in conetainers (Stuewe and Sons Inc.) or in 10-cm pots filled with steam-sterilized loamy sand and fertilized with Osmocote. Experiments that tested the heat-stability of resistance were carried out in environment growth chambers where the temperature was maintained constantly at 30°C or 32°C for 7 days before and 30 days after inoculation and then kept at $25° \pm 3°$C. The experiments requiring moderate temperatures were carried out in a glasshouse at $25° \pm 3°$C. The screening tests were prepared as described previously (Veremis and Roberts 1996a). Genotypes were tested in 5–20 replications per nematode isolate and were arranged in a completely randomized design. Nematode reproduction on roots was evaluated 60 days after inoculation. Genotypes were determined to be resistant if the mean number of egg masses per root system was less than 10% compared to the susceptible controls. The entries of the *L. peruvianum* LA2157, F_3 plants and *L. esculentum* cvs 'Pixie' and 'VFN-8' were classified as either resistant (individual plants averaged less than 25 egg masses per root system produced) or susceptible (individual plants averaged 25 or more egg masses per root system produced). Following the method of Veremis and Roberts (1996a) an F_2 plant was classified as homozygous resistant for the heat-stable resistance when all individual plants of its F_3 line were resistant, as homozygous susceptible when all plants were susceptible and as heterozygous when its F_3 line contained both susceptible and resistant individuals.

Linkage analysis

The data from the F_3 lines screened for resistance to *Mi-1*-avirulent *M. incognita* and *M. javanica* biotypes at 25°C and at 32°C were

used to determine the genotype of the F_2 plant, and the linkage analysis was done with 61 plants. These 61 plants were a subset of the 324 F_2 plants used to construct the linkage map. The map consisted of 51 restriction fragment length polymorphism (RFLP) markers dispersed over the 12 chromosomes (A. W. van Heusden et al. personal communication). In the linkage analysis, resistance was treated as a single segregating locus. Linkage analysis was done with the mapping software JOINMAP 2.0 (Stam 1993).

Results

Resistance of *L. peruvianum* LA2157 to *Mi-1*-avirulent *M. incognita* and *M. javanica* at 25°C and 32°C

Fifty entries of *L. peruvianum* LA2157 were resistant to *M. incognita* isolates at 32°C (Table 1). A few individual nematodes within the population were able to reproduce on resistant LA2157, however their egg masses contained relatively few eggs compared to those produced in a typical compatible reaction. For example, a LA2157 entry supported 20 egg masses per root system, but only 162 eggs per gram of root, compared to 'VFN-8' (possessing *Mi-1* gene, susceptible above 25°C) with 177 egg masses per root system and 5,166 eggs per gram of root (average of five root systems). The high level of reproduction of *Mi-1*-avirulent isolate 811 on 'VFN-8' at 32°C compared to the resistant response at 25°C confirmed the high-temperature induction of gene *Mi-1* susceptibility. High numbers, more than 100 egg masses per root system, were produced on cv 'Pixie' with *M. javanica* isolate 811 and with *M. incognita* isolates Project 77 and Muller at 25°C and 32°C, as expected in the absence of the gene *Mi-1* phenotype.

Cuttings of the F_3 lines and F_5 lines segregated for resistance to *M. javanica* isolate 811 at 25°C and 32°C, and to *M. incognita* isolates Project 77 and Muller at 25°C and at 32°C (Table 1). We did not observe any differential phenotypic responses with the F_3 lines and F_5 lines between the four experimental combinations of *M. javanica* and *M. incognita* isolates at 25°C and 32°C. We report only for F_3 lines that had four replications in all the above screening conditions (Table 1). These F_3 lines were entered for the linkage analysis.

Table 1 Reaction of parent, S_1, F_3 and F_5 progenies of 'Solentos' × *L. peruvianum* LA2157 tested for resistance to *Mi*-avirulent *Meloidogyne* at 25°C and 32°C according to nematode egg masses

Generation	Parent or progeny	Number of plants		
		R[a]	H[b]	S[c]
Parent	*L. peruvianum* LA2157	50		
S_1	Selfed LA2157	20		
F_3 lines	F_2 selfed	24	16	21
F_5 lines	F_4 selfed	1	2	2

[a] Resistant (R), fewer than 25 egg masses per root system
[b] Heterozygous (H), segregating F_3 lines with resistant and susceptible entries
[c] Susceptible (S), 25 or more egg masses per root system

Susceptibility of *L. peruvianum* LA2157 to *Mi-1*-virulent *M. incognita* at 30°C

The *L. peruvianum* parental LA2157 and the F_3 lines were screened for resistance to the *Mi-1*-virulent *M. incognita* isolate Cote d'Ivoire at a constant temperature of 30°C. The high numbers of 50 or more egg masses per root system and large galling produced on 'VFN-8', LA2157 and the F_3 lines confirmed the susceptibility of these entries to this selected *Mi-1*-virulent *M. incognita* isolate.

Susceptibility of *L. peruvianum* LA2157 to *M. hapla* at 25°C

The *L. peruvianum* parental LA2157 and F_3 lines were tested for resistance to *M. hapla* isolate San Bernardino at 25°C. The parental entries of LA2157, the F_3 lines and 'VFN-8' supported more than 50 egg masses per root system in each case, and the egg masses were associated with significant root galling, indicating susceptibility of all the tested genotypes.

Mapping of the novel heat-stable resistance of LA2157

For mapping the heat-stable resistance locus in the genome of tomato we used an F_2 population of *L. esculentum* cv 'Solentos' × *L. peruvianum* LA2157. The segregation of the resistance locus was compared with the segregation of the 51 RFLP markers on 61 F_2 plants. Map distances and the order of markers showed that the heat-stable resistance gene is localized on chromosome 6 (Fig. 1). The data established the closest linkage of the heat-stable resistance locus with the RFLP markers TG178 and TG118 on chromosome 6 (Fig. 1). There is linkage of the heat-stable resistance locus from LA2157 with the RFLP markers TG178, TG153 and TG118 with corresponding LOD scores greater than 3.

Discussion

Interestingly, the position of the novel heat-stable resistance in LA2157 is the same region as the heat-unstable gene *Mi-1* on chromosome 6. The closest linked TG-markers were TG118 and TG178, but there was still a distance of over 20 cM between these markers and the heat-stable resistance gene. The marker TG178 is positioned at the same spot as *Mi-1* on the genetic map based on the cross

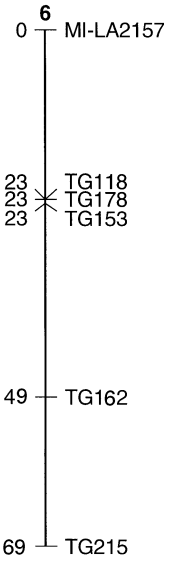

Fig. 1 Calculated map distances of the markers of chromosome 6. Recombination frequencies between the heat-stable resistance locus and its closest linked markers, TG118, TG178, and TG153 were 0.207 (LOD = 5.3), 0.212 (LOD = 4.4) and 0.236 (LOD = 3.13), respectively

L. esculentum × *L. pennellii* (Tanksley et al. 1992), but this is due to suppressed recombination in this region. Crosses between *L. esculentum* lines with *Mi-1* and *L. esculentum* lines without *Mi-1* also show a significant reduction in recombination in the region of *Mi-1* on chromosome 6 (Ganal and Tanksley 1996). Crosses within the *L. peruvianum* complex did not exhibit this suppression and showed up to 15 times more recombination (Ganal and Tanksley 1996). In general, interspecific crosses are thought to have a reduced amount of recombination compared to intraspecific crosses. Several studies have shown that this is not the case for the interspecific cross between *L. esculentum* cv 'Solentos' and *L. peruvianum* LA2157 (Bonnema et al. 1997). Although the overall map length is identical with the *L. esculentum* × *L. pennellii* map, regional differences in recombination frequencies were observed and some regions showed a significant higher level of recombination. The relative positions of *Mi-1* and the heat-stable resistance could not be determined because the two loci were not mapped in the same population or populations with equal recombination frequencies. The substantial differences in recombination frequencies preclude us from a conclusion as to whether the heat-stable resistance gene and *Mi-1* are alleles of each other or not. With respect to fine mapping of the heat-stable resistance gene, a higher recombination frequency reduces the number of plants that have to be analyzed.

The accession of LA2157 was collected in northern Peru close to the collection sites of the other Maranon race accessions LA1708 and LA2172 that also possess nematode resistance (Veremis and Roberts 1996c). Rick (1986) suggested that the Maranon races are possible ancestral types and that speciation and subspeciation differentiation took place with migration to the south. The heat-unstable resistance of *Mi-1* is derived from the accession of *L. peruvianum* PI128657 that was collected in 1938 from the southern coastal region of Peru west of Tanca, the southern natural habitat distribution of the species. Recombination in testcrossing studies showed that the locus of the heat-unstable resistance in PI126443-1MH, PI270435-3MH and PI270435-2R2 segregated independently from the heat-stable resistance locus in each accession (Cap et al. 1993). The finding that accession LA2157 is resistant to *Mi-1*-avirulent *M. incognita* but susceptible to *Mi-1*-virulent *M. incognita* isolates provides evidence that the heat-stable resistance gene in LA2157 is different from genes *Mi-3*, *Mi-7* and *Mi-8* conferring resistance to the *Mi-1*-virulent *M. incognita* isolates in *L. peruvianum* PI126443-1MH, PI270435-3MH and PI270435-2R2, respectively (Veremis 1995). However, LA2157 has the same phenotype of heat-stable resistance genes *Mi-2*, *Mi-4*, *Mi-5* and *Mi-6* in *L. peruvianum* PI270435-2R2, LA1708, PI126443-1MH and PI270435-3MH, respectively. The *Mi-3*/*Mi-5* locus in PI26443-1MH has been mapped in the telomeric region of the long arm of chromosome 12 (Yaghoobi et al. 1995). The gene from LA2157 conferring heat-stable resistance is located in the short arm of chromosome 6, therefore in a different chromosomal location from genes *Mi-3* and *Mi-5* in PI126443-1MH. The Maranon race accessions LA1708 and LA2172 are resistant to *Mi-1*-avirulent *M. incognita* biotypes and susceptible to the *Mi-1*-virulent *M. incognita* biotypes, similar to LA2157. Resistance to root-knot nematodes may be derived from a single common ancestor of the Maranon races, which then spread to other regions across the geographical barriers. However, the possibility exists that there are different multiple origins of resistance selected independently through parallel co-evolution in different areas.

Plants have conserved many resistance genes that protect them from many plant pathogens, including viruses, bacteria, fungi and nematodes. Significant progress has been made recently in cloning host-plant resistance genes to pathogens from several plant species (Hammond-Kosack and Jones 1997). Like many plant genes, most cloned resistance genes are members of multigene families and seem to be clustered in the plant genome. However, little is understood of the size, organization and complexity of resistance gene clusters or the mechanisms generating them, especially host resistance genes to parasitic nematodes. Host-plant resistance genes to a particular pathogen are organized as genetically separable loci or multiallelic clusters (Pryor and Ellis 1993; Hulbert and Bennetzen 1991; Ellis et al. 1997). In addition, the clustering of resistance genes to unrelated pathogens and pests has also been reported. One such cluster is located on the short arm of chromosome 6 of tomato (Kaloshian et al. 1995). In this one small, 1-cM region are clustered genes *Cf-2* and *Cf-5* conferring resistance to the fungus *C. fulvum*, the aphid

resistance gene *Meu1* and the nematode resistance gene *Mi-1* (Kaloshian et al. 1995). A resistance to powdery mildew (*Ol-1*) is also located close to this region (van der Beek et al. 1994). Various related functions can arise from an ancestral gene pool during accidental or evolution interactions. Several evolutionary events, including duplication, mutation, transposition and recombination, seem to have played a role in generating the *Xa21* family members, although it is not yet clear what specificities have been generated (Song et al. 1997). This is true for other resistance loci including *M*, *Cf-9*, *TMV* and *Pto*, where an array of related genes are present with only one member recorded as conferring disease resistance (Anderson et al. 1997; Jones et al. 1994; Whitham et al. 1994; Martin et al. 1993). The characterization of the *Cf-4*/*Cf-9* locus demonstrates how these genes are organized at the molecular level, suggesting a common progenitor sequence (Thomas et al. 1997). Organisms are constantly evolving: in each co-evolution interaction, many variants are generated, and a few are selected and retained within the genomes. Natural selection for the original function would maintain one copy of the duplicate gene pair unchanged, while the other copy could evolve to encode a product with altered biochemical, structural, regulatory or recognition functions. Gene duplication may have been the mechanism of origin for almost all genes including the *Mi* loci. The divergence of duplicate genes presents the organism with a chance to acquire novel gene functions and variability like heat-stability. We mapped the heat-stable resistance locus from *L. peruvianum* LA2157 on the short arm of chromosome 6, but it is not yet known if it is an allele of *Mi-1* or a different locus. Duplication, mutation, transposition and recombination may have played a role in generating new specificity to nematode resistance on the *Mi* loci in tomato.

Unlike the majority of *L. peruvianum* accessions that segregated for resistance to root-knot nematodes, including LA1708, LA2172, PI126443 and PI270435, accession LA2157 does not segregate for heat-stable nematode resistance. This is in agreement with the results obtained by Ammati et al. (1986), in which three entries of LA2157 were resistant at both temperatures. The self-compatible LA2157 is in the homozygous state because all the entries and the S_1 progeny tested were all resistant. The results obtained with the F_3 lines and F_5 lines at 25°C (*Mi-1* expressed) and at 32°C (*Mi-1* not expressed) indicated that the heat-stable resistance to the *Mi*-avirulent *M. incognita* is inherited as a single dominant gene. However, disturbed segregation from expected 1:2:1 with the F_3 lines was observed, a possible explanation being that the F_2 plants heterozygous for the short arm of chromosome 6 produce fewer viable seeds resulting in not enough plants to do all four replications. If we assume that this is so, then we have a normal 1:2:1 segregation (Table 1). It is also possible that this part of chromosome 6 has a distorted segregation, resulting in a low level of heterozygotes. The occurrence of distorted segregation has been reported within the species *L. peruvianum* including accession LA 2157 (Sandbrink et al. 1995; van Ooijen et al. 1994).

The finding that the only *L. peruvianum* self-compatible accession LA2157 is also inbred for heat-stable resistance is interesting from an evolutionary perspective. Self-compatibility in *L. peruvianum* is believed to have evolved from self-incompatible stocks, as in *L. hirsutum* where the self-compatible accessions tend to be genetically uniform compared to self-incompatible ones (Rick et al. 1979). Thus, self-compatible LA2157 may be derived from a self-incompatible stock that was selected and conserved its resistance to root-knot nematodes due to fitness benefits or chance. Lines of moderate self-compatibility were developed by inbreeding and intense selection of *L. peruvianum* self-incompatible stocks (Hogenboom 1972). High temperatures in a Southern California field experiment allowed selfing of a self-incompatible interspecific *L. peruvianum* × *L. esculentum* hybrid toward the end of the season (Veremis and Roberts 1996c). Genetic factors and temperature influence self-incompatibility and durability in *L. peruvianum*. Incorporation of the evaluated heat-stable factor for resistance to root-knot nematodes from the LA2157 accession into cultivated tomato is desirable to protect the crops in high-temperature conditions. A molecular marker tagged to the heat-stable factor for resistance to *Mi-1*-avirulent isolates from LA2157 will speed the incorporation into tomato cultivars through classical and/or molecular methods and clarify further its relationship with the *Mi-1* gene locus.

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