Screening *Lycopersicon* spp. for New Genes Imparting Resistance to Root-Knot Nematodes (*Meloidogyne* spp.)

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ABSTRACT

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Lycopersicon peruvianum, L. glandulosum, L. cheesmanii, L. parviflorum, and *L. pimpinellifolium* accessions were tested for root-knot nematode resistance. *L. peruvianum* accession 270435 and *L. glandulosum* accessions 126440 and 126443 were resistant to *Meloidogyne hapla.* Six *L. peruvianum* accessions tested were resistant to *M. incognita* and *M. arenaria.* Variations in the level of resistance to four *M. incognita* races were observed among *L. peruvianum* accessions. Variation also occurred within the same accession. Race 3 of *M. incognita* reproduced less than other *M. incognita* races on *L. peruvianum* and *L. glandulosum* accessions. Results from greenhouse tests were complemented by laboratory isozyme studies of the variant in locus 1 of acid phosphatase (*Aps*-1[1]). Results of our work suggested the possibility of a new resistance gene(s) to *M. hapla* and to the other *Meloidogyne* spp.

Additional key words: breeding, tomato

Lycopersicon esculentum (L.) Mill., *L. glandulosum* C. H. Mull., *L. hirsutum* H.B.K., *L. pimpinellifolium* (Jusl.) Mill., and *L. peruvianum* (L.) Mill. were tested for resistance to root-knot nematodes by Bailey (2) in 1940. Eleven of 25 *L. peruvianum* accessions tested were resistant in greenhouse and field tests (9,20). Use of *L. peruvianum* as breeding stock to develop tomato cultivars with resistance to root knot and other diseases (1) was pursued. A successful cross between *L. peruvianum* and *L. esculentum* was not possible, however, because of natural incompatibility barriers occurring between the two species.

This problem was solved by Smith (23), who used an embryo culture technique to successfully cross *L. esculentum* 'Michigan State Forcing' and *L. peruvianum* PI 128657. One F_1 plant was obtained from this cross and cuttings from this plant were backcrossed to *L. esculentum* (28). Backcross progeny were distributed for use in breeding programs. This root-knot nematode resistance is controlled by a major gene (*Mi*) located on chromosome six (10). *Mi* is tightly linked to an acid phosphatase isozyme variant at locus 35 (19). This isozyme is used as a phenotypic marker for *Mi*. Starch gel electrophoresis is used to characterize the isozyme (16).

The number and the nature of genes conferring resistance to root-knot nematodes in tomato is not yet clearly defined (4,5,22). The *Mi* gene is the only source of root-knot nematode resistance in all currently available tomato cultivars (16). At present, tomato breeders rely entirely on the germ plasm available in the cultivated stock. This gene has been reported to confer resistance to *Meloidogyne incognita* (Kofoid & White) Chitwood, *M. arenaria* (Neal) Chitwood, and *M. javanica* (Treub) Chitwood (4,26). It does not confer resistance to *M. hapla* Chitwood, however, and failure of resistance to populations of *M. javanica, M. arenaria,* and *M. incognita* has been reported (3,11,12,17,25,27). Resistance is significantly diminished at temperatures higher than 28 C (7).

Because of the economic importance of root-knot nematodes on tomato (14) and the failure of resistance in some hot areas of the world, a large number of wild forms of tomato were screened for resistance to root-knot nematodes (*Meloidogyne* spp.) in an attempt to identify new resistance genes. A preliminary examination of resistant material was made using the acid phosphatase isozyme as a marker for the original *Mi* gene.

MATERIALS AND METHODS

Accessions investigated. The accessions used in this study were *L. glandulosum*, USDA accessions 126443 and 126440; *L. peruvianum*, USDA accessions 126928, 128656, 129152, 128657, 128648, and 270435; *L. pimpinellifolium*, USDA accessions 379058 and 390691; *L. parviflorum* Rick et al, USDA accession 379033; and *L. cheesmanii* Riley, USDA accession 379039. *L. esculentum* 'Rutgers' and 'VFN8' were used as susceptible and resistant controls, respectively. USDA accessions were obtained from R. Clark, USDA Regional Plant Introduction Center, Iowa State University, Ames. All *L. esculentum* seeds were obtained from commercial sources.

General procedures. Nematode resistance tests were carried out in the greenhouse. The tests used 1-mo-old seedlings or rooted cuttings that were in vigorous growth. Plants were grown singly in 600-cc pots (Western Pulp Products Co., Corvallis, OR) containing steamed (full steam for 1 hr at 100 C) loamy sand. Initially, the young plants were irrigated with Hoagland's solution; subsequently, they were fertilized with Osmocote (Sierra Chemical Co., 1001 Yosemite Dr., Milpitas, CA) (18:12:16, NPK). *M. incognita* races 1, 2, 3, and 4, *M. javanica, M. arenaria,* and *M. hapla* were identified morphologically and by use of the North Carolina differential host test (21).

For each species and race, the inoculum source was established from a single egg mass and was increased in the roots of Rutgers plants. Inocula for resistance tests were prepared by the method of Hussey and Barker (13). A suspension of 2,500 eggs was pipetted into three holes in the soil around the roots in each pot. During the experiment, the soil temperature in the pot was about 24 C for *M. hapla* and about 26 C for the other *Meloidogyne* spp. Two months after inoculation, roots were gently washed free of soil and assessed for root galling and egg masses and/or eggs per gram (fresh weight) of root.

The egg mass index (EI) was determined as follows: 0 = no egg masses, 1 = 1–2, 2 = 3–10, 3 = 11–30, 4 = 31–100, and 5 = more than 100 egg masses per root system. The galling index (GI) was determined as follows: 0 = no galls, 1 = 1–24% of the roots galled, 2 = 25–49%, 3 = 50–74%, and 4 = 75–100% of roots galled. Eggs per gram of root were not necessarily correlated with the EI because some egg masses may have contained very few eggs. Recovery of eggs from the total root system was done by a modification of the method of

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Hussey and Barker (13).

Seedling resistance tests. In the first experiment, 10 seedlings of each accession were tested against *M. incognita, M. javanica, M. arenaria*, and *M. hapla*. Resistance was evaluated on the basis of the EI and GI. Plants with an EI value lower than 2 and little or no galling were labeled and cloned immediately for further studies.

Clone resistance tests. Highly resistant (low EI and GI) plants selected from the first screening test were cloned further. Three-node cuttings of stem tissue were made with a sterilized razor blade and the basal ends of the cuttings were dipped in a rooting medium. Cuttings were rooted in a moist 1:1:1 mixture of fine vermiculite, peat moss, and perlite. Initially, flats of cuttings were covered with polyethylene and placed under Saran-cloth shade in the greenhouse. After 2 wk, 10 plants of each accession were potted in steamed loamy sand and grown for further tests with *M. hapla* and *M. incognita* races 1, 2, 3, and 4. *L. peruvianum* accessions 128648 and 128657 and *L. esculentum* 'Rutgers' and 'VFN8' were grown from seed. Inoculum preparation and inoculation procedures were the same as reported before. Root galling was observed and total number of eggs in the roots of each plant were determined, and data are reported as eggs per root system and eggs per gram of roots.

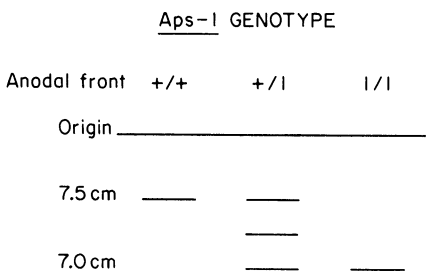

Fig. 1. Electrophoretic banding patterns of acid phosphatase in locus 1. The band located at 7.5 cm characterizes the susceptible homozygous, the one located at 7.0 cm is for the homozygous resistant (as with the *Mi* gene), and the three bands between 7.0 and 7.5 cm characterize the resistant heterozygous types.

Starch gel electrophoresis. *L. peruvianum* accession 128657 (source of *Mi* gene) and different clones established as highly resistant (low GI and low egg count per gram of roots) to *M. hapla* and *M. incognita* were assayed by starch gel electrophoresis for the variant allele in locus 1 of acid phosphatase isozyme using equipment designed by Tanksley (24). Preparation of leaf tissue and detection of acid phosphatase activity in the gel were carried out as described by Medina-Filho and Stevens (15). *L. esculentum* 'VFN8' and 'Rutgers' were used as resistant and susceptible controls, respectively. Four replicates were used for each accession or cultivar tested. Three electrophoretic banding patterns were usually observed depending on the acid phosphatase genotypes tested (Fig. 1). Homozygous resistant is represented by a single retarded band (labeled *Aps*-1^1). The susceptible homozygous is represented by a band labeled *Aps*-1^+ and the resistant heterozygous by a band labeled *Aps*-$1^{(1/+)}$.

RESULTS

Seedling resistance tests. *L. parviflorum, L. cheesmanii*, and *L. esculentum* 'Rutgers' showed significant gall development and supported good nematode reproduction (EI 4–5) by the four *Meloidogyne* spp. (Table 1). *L. pimpinellifolium* accessions showed some resistance (GI 1.6–3.2, EI <4) to *M. hapla* but were susceptible to the other root-knot species. *L. glandulosum* accessions and *L. peruvianum* accession 270435 showed a good average level of resistance to *M. hapla* (GI 1.4–2.2, EI <4), with some plants within each accession showing a high level of resistance. The other *L. peruvianum* accessions and *L. esculentum* 'VFN8' had good resistance to *M. incognita* and *M. arenaria* but they were relatively susceptible (EI 3.5–4.8) to *M. javanica* under our experimental conditions. This particular *M. javanica* isolate has also been shown to attack resistant lines of beans in other work carried on in this laboratory (I. J. Thomason, *personal communication*). In this preliminary experiment, the EI appeared to be more reliable than the GI. For example, note that *L. peruvianum* accessions showed little galling when infected by *M. javanica* but numerous egg masses were present.

Clone resistance tests. Selected clones of *L. glandulosum*, *L. peruvianum*, and the tomato cultivar VFN8 showed the same level of resistance to *M. incognita* races 2 and 3 and did not differ significantly ($P = 0.01$) from each other (Table 2). *L. peruvianum* accession 128657 (*Mi* source), and *L. glandulosum* accession 126440 were susceptible to *M. incognita* race 4 and presented intermediate resistance to race 1.

L. glandulosum accessions 126440 and 126443 and *L. peruvianum* accession 270435 showed a high level of resistance to *M. hapla* on the basis of total egg production and eggs per gram of root (Table 3). *L. peruvianum* accession 128656 and *L. pimpinellifolium* accession 390691 showed intermediate resistance and differed significantly ($P = 0.01$) from the susceptible control (Rutgers).

Starch gel electrophoresis. This

Table 1. Egg mass (EI) and galling (GI) indices observed on selected tomato (*Lycopersicon* spp.) accessions or cultivars inoculated with *Meloidogyne* spp.[x]

Accession or cultivar	*M. incognita*		*M. javanica*		*M. arenaria*		*M. hapla*	
	EI[y]	GI	EI	GI	EI	GI	EI	GI
L. esculentum								
Rutgers	5.0 a[z]	4.0 a	5.0 a	5.0 a	5.0 a	5.0 a	5.0 a	4.0 a
VFN8	1.4 b	1.0 bc	4.5 ab	2.5 b	4.0 ab	5.0 a	5.0 a	4.0 a
L. cheesmanii								
379039	5.0 a	4.0 a	5.0 a	5.0 a	5.0 a	5.0 a	5.0 a	4.0 a
L. glandulosum								
126440	2.8 b	0.9 bc	3.0 c	2.5 b	3.1 bc	0.4 b	3.7 bc	1.8 cde
126443	2.1 b	1.0 bc	4.6 ab	0.0 c	1.3 d	0.8 b	3.7 bc	2.6 bcde
L. parviflorum								
374033	1.5 b	4.0 a	5.0 a	5.0 a	5.0 a	5.0 a	5.0 a	3.6 ab
L. peruvianum								
129152	1.7 b	1.7 b	3.5 bc	0.0 c	2.4 cd	0.7 b	4.0 ab	2.1 cde
128656	1.8 b	0.8 bc	4.3 abc	0.4 c	2.3 cd	0.2 b	3.8 bc	2.1 cde
126928	2.3 b	0.0 c	4.8 ab	0.0 c	3.0 bc	0.7 b	4.0 ab	2.9 abcd
270435	2.1 b	0.6 bc	4.1 abc	0.0 c	2.3 cd	1.2 b	2.8 c	1.4 e
L. pimpinellifolium								
379058	5.0 a	4.0 a	5.0 a	5.0 a	4.0 ab	5.0 a	3.3 bc	1.6 de
390691	5.0 a	4.0 a	5.0 a	5.0 a	4.0 ab	5.0 a	3.7 bc	3.2 abc

[x] Values are means of five to 10 replicates.

[y] EI: 0 = no egg masses, 1 = 1–2, 2 = 3–10, 3 = 11–30, 4 = 31–100, and 5 = more than 100 egg masses. GI: 0 = no galls, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, and 4 = 75–100% of roots galled.

[z] Values within a column followed by the same letter are not significantly different ($P = 0.01$) according to Duncan's multiple range test.

Table 2. Resistance of cloned tomato (*Lycopersicon* spp.) accessions to *Meloidogyne incognita* host races on the basis of nematode reproduction

Accession or cultivar[x]	Av. no. of eggs per gram of fresh root			
	Race 1	Race 2	Race 3	Race 4
L. esculentum				
Rutgers	1,360 a[y]	4,641 a	670 a	1,334 ab
VFN8	6 c	53 b	13 b	41 b
L. glandulosum				
126440	377 b	503 b	4 b	2,217 a
126443	143 c	170 b	8 b	73 b
L. peruvianum				
129152	46 c	27 b	13 b	102 b
128648	35 c	14 b	2 b	56 b
128656	42 c	204 b	19 b	244 b
128657	294 b	22 b	3 b	733 ab
270435	10 c	124 b	2 b	274 b
126928	177 b	...[z]	8 b	...[z]

[x] *L. peruvianum* (128648 and 128657) and *L. esculentum* (Rutgers and VFN8) were tested directly from seed (10 plants per experiment).
[y] Values within a column followed by the same letter are not significantly different ($P = 0.01$) according to Duncan's multiple range test.
[z] Accessions not tested (no. of clones not sufficient).

Table 3. Different degrees of resistance to *Meloidogyne hapla* observed on tomato (*Lycopersicon* spp.) accessions or cultivars on the basis of nematode reproduction

Accession or cultivar	Av. no. of eggs per gram of fresh root
L. esculentum	
Rutgers	1,118 a[z]
L. pimpinellifolium	
379058	480 b
L. peruvianum	
128656	280 bc
L. pimpinellifolium	
390691	308 bc
L. glandulosum	
126440	59 c
L. peruvianum	
270435	99 c
L. glandulosum	
126443	7 c

[z] Values followed by the same letter are not significantly different ($P = 0.01$) according to Duncan's multiple range test.

experiment was done in an attempt to obtain additional corroborative evidence of resistance genes in the clones selected from different accessions of the wild forms of *Lycopersicon*. Acid phosphatase isozyme variant (*Aps*-1^1) was used as a marker of *Mi*. The acid phosphatase genotypes observed in different *Lycopersicon* clones and cultivars tested are summarized in Table 4. *L. peruvianum* accession 128657 was either heterozygous (*Aps*-$1^{(1/+)}$) or homozygous (*Aps*-1^1) for acid phosphatase isozyme variant in locus 1, whereas accessions 128648 and 270435 were heterozygous. Only *L. peruvianum* accession 129152 did not present the acid phosphatase isozyme variant in locus 1 and showed similar genotype (*Aps*-1^+) to the susceptible control (Rutgers). *L. glandulosum* accession 126440 showed the same genotype (*Aps*-1^+) as Rutgers. *L. glandulosum* accession 126443 was heterozygous (*Aps*-$1^{(1/+)}$). *L. esculentum* 'VFN8', used as resistant control, was homozygous (*Aps*-1^1).

DISCUSSION

Among the wild *Lycopersicon* forms investigated, *L. peruvianum* and *L. glandulosum* were the best sources of resistance to root-knot nematodes. However, five accessions of *L. peruvianum* and one of *L. glandulosum* were susceptible to our population of *M. javanica* (Table 1). A large difference, based on the EI, was observed among individual plants of the same accession exposed to the same species. This suggests genetic differences and segregation for resistance. Selected clones from *L. peruvianum* and *L. glandulosum* showed higher resistance to *M. incognita* race 3 than to *M. incognita* race 1, 2, or 4 (Table 2). *M. incognita* race 4 reproduced abundantly (3,217 eggs per gram of roots) on *L. glandulosum* accession 126440 and reproduced well (733 eggs per gram of roots) on *L. peruvianum* PI 128657 (*Mi* source). Similar variations in response among accessions and among individual plants within accessions were reported by Dropkin et al (8), using a sensitive test tube procedure for screening for resistance to *M. incognita* and *M. hapla*.

Among *L. peruvianum* accessions tested, 270435 was resistant to *M. hapla* on the basis of the average EI value. A large difference in resistance among individuals within this accession was also observed. These variations could be the result of genetic segregation of the resistance gene(s). There is only one previous report of resistance to *M. hapla* in *Lycopersicon* spp. (6). In genetic studies on the *L. peruvianum* complex, Rick (18) observed high genetic variation as expressed in morphological (eg, form of leaves and flowers) and physiological (eg, fertility of the seeds and self or compatibility with other accessions) characters among races and populations of this species. Therefore, finding a source of resistance to *M. hapla* within some but not all accessions representing this complex is possible. Screening for resistance conferred by gene *Mi* based on the variant allele in locus 1 of acid phosphatase is reliable because of the close linkage between them. The absence of the acid phosphatase variant in *L. peruvianum* accession 129152 and its high resistance to *M. incognita* and *M. arenaria* in the greenhouse suggest that a different resistance gene may be present in this genotype.

Table 4. Acid phosphatase genotypes based on electrophoretic banding patterns as observed in the starch gel

Accession or cultivar examined	*Aps*-1[a]
Lycopersicon peruvianum	
128657	1
	1/+
270435	1/+
129152	+
128648	1/+
L. glandulosum	
126440	+
126443	1/+
L. esculentum	
Rutgers	+
VFN8	1

[a] 1 = Retarded allele of *Aps*-1, resistant homozygous genotype; + = advanced allele of *Aps*-1, susceptible homozygous genotype; and 1/+ = resistant heterozygous genotype.

The *L. glandulosum* accessions 126440 and 126443 showed good resistance to *M. hapla*. *L. glandulosum* is considered a mountain race of the *L. peruvianum* complex (C. M. Rick, *personal communication*). There is a similarity between the ecological adaptation to climate of *L. glandulosum* and the nematode *M. hapla*; both are common in temperate areas and *M. hapla* can survive in areas where soils freeze in winter. The isozyme study revealed that *L. glandulosum* accession 126440 was homozygous (*Aps*-1^+). Accession 126443 was heterozygous (*Aps*-$1^{(+/1)}$). *Aps*-1^1 is strongly linked to *Mi* in many members of the *L. peruvianum* complex. The ecological origin of *L. glandulosum* lends additional support to the possibility that it could be a source of resistance to *M. hapla*.

Our preliminary results based on the greenhouse tests and acid phosphatase isozyme variant of locus 1, suggesting the possibility of a new resistance gene(s), are not conclusive. Appropriate crosses among different clones designed to confirm our preliminary results are in progress, and progeny from the crosses will be analyzed for nematode resistance to define the number of genes involved.

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