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Differential Response to Root-Knot Nematodes in *Prunus* Species and Correlative Genetic Implications[1]

D. ESMENJAUD,[2] J. C. MINOT,[2] R. VOISIN,[2] J. PINOCHET,[3] M. H. SIMARD,[4] AND G. SALESSES[5]

Abstract: Responses of 17 *Prunus* rootstocks or accessions (11 from the subgenus *Amygdalus* and 6 from the subgenus *Prunophora*) were evaluated against 11 isolates of *Meloidogyne* spp. including one *M. arenaria,* four *M. incognita,* four *M. javanica,* one *M. hispanica,* and an unclassified population from Florida. Characterization of plant response to root-knot nematodes was based on a gall index rating. Numbers of females and juveniles plus eggs in the roots were determined for 10 of the rootstocks evaluated against one *M. arenaria,* one *M. incognita,* one *M. javanica,* and the Florida isolate. These 10 rootstocks plus Nemaguard and Nemared were retested by growing three different rootstock genotypes together in containers of soil infested individually with each of the above four isolates. Garfi and Garrigues almonds, GF.305 and Rutgers Red Leaf peaches, and the peach-almond GF.677 were susceptible to all isolates. Differences in resistance were detected among the other rootstocks of the subgenus *Amygdalus.* The peach-almond GF.557 and Summergrand peach were resistant to *M. arenaria* and *M. incognita* but susceptible to *M. javanica* and the Florida isolate. Nemaguard, Nemared, and its two hybrids G × N no. 15 and G × N no. 22 were resistant to all but the Florida isolate. In the subgenus *Prunophora,* Myrobalan plums P.1079, P.2175, P.2980, and P.2984; Marianna plum 29C; and *P. insititia* plum AD.101 were resistant to all isolates. Thus, two different genetic systems of RKN resistance were found in the subgenus *Amygdalus:* one system acting against *M. arenaria* and *M. incognita,* and another system also acting against *M. javanica. Prunophora* rootstocks bear a complete genetic system for resistance also acting against the Florida isolate. The hypotheses on the relationships between these systems and the corresponding putative genes of resistance are presented.

Key words: Amygdalus, Meloidogyne arenaria, Meloidogyne incognita, Meloidogyne javanica, Prunophora, Prunus amygdalus, Prunus cerasifera, Prunus persica, resistance.

Root-knot nematodes (RKN), *Meloidogyne* spp., reduce fruit and nut production in several economically important *Prunus* species, including peach (*P. persica*), almond (*P. amygdalus*), plum (*P. salicina, P. domestica*), and apricot (*P. armeniaca*). Currently, RKN are managed primarily by costly preplant nematicide treatments; however, many of these pesticides are being removed from the market because of their negative impacts on the environment. One of the most economical and environmentally sound methods for managing RKN in *Prunus* spp. is the use of RKN-resistant rootstock cultivars (Fernandez et al., 1994; Kester and Grasselly, 1987; Layne, 1987; Nyczepir, 1991; Nyczepir and Halbrendt, 1993; Scotto La Massèse, 1989; Sherman and Lyrene, 1983; Sherman et al., 1981).

Breeding of perennials is based on long-term programs in which the best sources of resistance must be used (Salesses et al., 1992). *Prunus* classification is based mainly on morphologic data (Rehder, 1954), crossing relationships, and chromosome counts (Salesses et al., 1992) completed by phylogenetic data at the molecular level (Badenes and Parfit, 1995). Horticulturally important sources of RKN resistance exist in the subgenera *Amygdalus* (L.) Focke (peach and almond) and *Prunophora* (L.) Batsch (plum and apricot). To efficiently breed useful RKN-resistant rootstocks, it is necessary to characterize the available sources of resistance for their reaction to several *Meloidogyne* spp. and also to determine the genetic basis for these resistances. Although several resistance sources have been identified in the genus *Prunus* (Kester and Asay, 1986;

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[2] Research Nematologist and Research Assistants, Laboratoire de Biologie des Invertébrés, Institut National de la Recherche Agronomique (INRA), B.P. 2078, 06606 Antibes Cedex, France.

[3] Research Nematologist, Departamento de Patologia Vegetal, IRTA, Ctra. de Cabrils s/n 08348, Cabrils, Barcelona, Spain.

[4] Research Geneticist, Station de Recherches Fruitières Méditerranéennes, INRA, B.P. 91, 84914 Avignon Cedex 9, France.

[5] Research Geneticist, Unité de Recherche sur les Espèces Fruitières et la Vigne, INRA, B.P. 81, 33883 Villenave d'Ornon Cedex, France.

E-mail: esmenjau@antibes.inra.fr.

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Kochba and Spiegel-Roy, 1976; Marull et al., 1994; Scotto La Massèse et al. 1994; Scotto La Massèse et al., 1990), resistance has been characterized only in species related to peach (Malo, 1967; Wehunt, 1972). Inheritance of resistance has been determined only in peach (Sharpe et al., 1969), almond (Kochba and Spiegel-Roy, 1975), and the Myrobalan plum *P. cerasifera* Ehr. (Esmenjaud et al., 1996b).

The objective of this study was to evaluate the host response of different *Prunus* species against a wide range of RKN isolates and to relate the results with the putative resistance genetic systems involved.

Materials and Methods

Evaluation of plant material for nematode resistance is generally performed by infesting the soil with nematode inoculum once, termed a short inoculum pressure (SIP) (Esmenjaud et al., 1996a). In our tests, evaluations were performed under severe conditions, i.e., with a method providing a high and durable inoculum pressure (DIP) of the nematode (Esmenjaud et al., 1992) combined with high-temperature regimes. Thus, only strong resistances could be evidenced, and minor variations attributed to environmental factors were not taken into account. Susceptible reference rootstocks were tested simultaneously with several RKN-resistant rootstocks that represent most sources of resistance currently used in rootstock breeding programs.

Plant material: Seventeen *Prunus* rootstocks or accessions were evaluated: 11 rootstocks from the subgenus *Amygdalus* represented by peach (*P. persica* (L.) Batsch), almond (*P. amygdalus* Batsch), and interspecific hybrids, and six from the subgenus *Prunophora* represented by Myrobalan plum (*P. cerasifera* Ehr.), Marianna plum (*P. cerasifera* × *P. munsoniana* Wight & Hedr.), and the plum *P. insititia* L. All of the rootstocks are diploid (2n = 2× = 16) except Marianna and *P. insititia* plums, which are triploid (2n = 3× = 18) and hexaploid (2n = 6× = 48), respectively. Their identity and characteristics are summarized in Table 1. Seed rootstocks of peach (GF 305, Rutgers Red Leaf, Nemaguard, and Nemared) and almond (Garfi and Garrigues) were propagated as follows: seeds were stratified in perlite trays at 4 °C for 90 to 120 days and then moved to a greenhouse at a mean temperature of 25 °C to induce germination. The rootstocks Myrobalan 29C and AD.101, previously micropropagated by Agromillora Catalana (Barcelona, Spain), were repotted in 0.2-liter containers filled with a peat substrate. Semi-hardwood cuttings from other rootstocks were collected in the field at the end of August 1994 (first-year test) and August 1995 (second-year test), treated for 10 seconds with a 50% ethanol solution containing 2,000 ppm of indolebutyric acid, and kept in the dark at 18–22 °C for 4 weeks (Hartmann and Kester, 1975). Cuttings were then planted into 0.2-liter containers filled with a sterilized sand-peat mixture.

Nematode populations: Eleven RKN isolates from various geographical origins were used (Table 2). All the RKN isolates, except *M.* sp. Floride and *M. incognita* Landes, were reared from single egg masses. The isolates were maintained on tomato (*Lycopersicon esculentum* Mill cv. St. Pierre). The isolate Floride, reared on tomato from a soil sample provided by W.B. Sherman (Univ. of Florida), originated from an orchard where resistant Nemaguard seedlings were galled by an RKN population identified as *M. incognita* race 3 (Sherman and Lyrene, 1983). However, the esterase b pattern was different from the pattern for *M. incognita* and other *M.* spp. (Janati et al., 1982); thus, we designated this population as *M.* sp. Floride.

Ten tomato seedlings (at the three-leaf stage) of cv. Piersol (resistant to *Meloidogyne* spp.) and cv. St. Pierre (susceptible) were inoculated with 250 second-stage juveniles (J2) of each isolate on 14 March 1995 (first-year test) and 12 March 1996 (second-year test). After 45 days the tomatoes were harvested and nematode identification was verified by esterase b phenotype (Janati et al., 1982). Virulence of the isolates to the *Mi* gene of tomato also was established as a complementary identification trait (data not shown) (Cap et al., 1993; Roberts et al., 1990).

Nematode inoculum: Second-stage juveniles

TABLE 1. Subgenus, rootstock identity, species or hybrid name, ploidy level, propagation method, and source of *Prunus* material.

Subgenus	Rootstock or accession	Species or hybrid	Ploidy level	Propagation	Source[a]
Amygdalus	Garfi	*P. amygdalus*	2n = 2x = 16	Seeds	SIA, Spain
	Garrigues	"	"	"	Unknown
	GF.677	*P. amygdalus* × *P. persica*	"	Semi-hardwood cuttings	INRA, France/ Lafond Nurseries
	GF.557	"	"	"	INRA/Lafond Nurseries
	G × N no. 15[b]	"	"	"	SIA
	G × N no. 22[b]	"	"	"	"
	GF.305	*P. persica*	"	Seeds	INRA/Lafond Nurseries
	Rutgers Red Leaf	"	"	"	Rutgers Nurseries, USA
	Summergrand	"	"	"	
	Nemaguard	"	"	"	USDA
	Nemared	"	"	"	"
		F_3 seedlings of Nemaguard × red-leaf peach			
Prunophora	P.1079	*P. cerasifera*		Semi-hardwood cuttings	INRA
	P.2175	"		"	"
	P.2980	"		"	"
	P.2984	"		"	"
	Myrobalan 29C	*P. cerasifera* × *P. munsoniana*	2n = 3x = 24	In vitro	Gregory Bros., USA
	AD.101	*P. insititia*	2n = 6x = 48	"	CSIC, Spain

[a] SIA = Servicio de Investigacion Agraria; INRA = Institut National de la Recherche Agronomique; USDA = United States Department of Agriculture; CSIC = Consejo Superior de Investigacion Cientifica.
[b] G × N = Garfi × Nemared.

(J2) of each nematode isolate were collected from infected St. Pierre tomato roots in a mist chamber over a 24- to 72-hour period. Five hundred J2 suspended in 2 ml H_2O were deposited into two holes in the soil of each 250-ml plastic container, 2 cm deep and 2 cm from the stem. Tomato plants were inoculated on 14 March 1995 (first-

TABLE 2. Species, origin, and original host of *Meloidogyne* spp. isolates used in the tests.[a]

Species	Population (abbrev.)	Origin	Original host
M. arenaria	Monteux (MT)	Provence, France	Tomato
M. incognita	Calissane (CA)	Provence, France	Tomato
	Landes (LA)	Gascogne, France	Soybean
	Villa verde (VR)	Andalucia, Spain	Peach
	Rama caida (RI)	Mendoza, Argentina	Peach
M. javanica	Oualidia (OU)	Oualidia, Morocco	Peach
	Higuera (HI)	Cataluna, Spain	Fig
	Camas (CM)	Andalucia, Spain	Peach
	Rama caida (RJ)	Mendoza, Argentina	Peach
M. hispanica	Seville (SE)	Sevilla, Spain	Peach-almond hybrid
M. sp.	Floride (FL)	Florida, USA	Peach Nemaguard

[a] Except for *M. incognita* Landes and *M.* sp. Floride, all isolates were reared from single egg masses.

year test) and 12 March 1996 (second-year test) and maintained in a greenhouse at 25 °C ± 3 °C. The level of inoculum was chosen based on a previous methodological study with *M. arenaria* Monteux (Esmenjaud et al., 1992). Tomato shoots were cut at the soil surface and removed approximately 60 days after inoculation, and one entire tomato root system with the surrounding soil was transferred into each *Prunus* container.

Evaluation of Prunus material: Plant material was evaluated in two successive tests. The first-year test was conducted in 1995 with all plant material. Nevertheless, all the rootstocks were not tested with all the populations because limited numbers of homogeneous plants were available for certain genotypes. In the second-year test (1996), 12 selected rootstocks (9 resistant rootstocks and 3 susceptible references) were retested to confirm previous results.

First-year test: Germinated seeds, rooted cuttings, and micropropagated plantlets were washed free of substrate and individually planted on 15 March 1995 in 5-liter containers filled with a sandy soil (80% sand, 10% loam, 10% clay). Containers were placed on benches in a greenhouse and irrigated individually every 2 days with an N-P_2O_5-K_2O (5-11.5-7.5) nutrient solution at 3 g/liter with complete trace elements (Algoflash, Algochimie, Tours, France). Mean daily greenhouse temperatures were 25 °C (range: 22 to 28 °C) in March and April and 30 °C (range: 22 to 38 °C) in July and August.

On 15 May 1995, galled tomato roots and soil from each RKN isolate were transferred singly into *Prunus* containers when *Prunus* plantlets were approximately 30 cm tall. There were six replicates of each population-genotype combination. Pots infested with the same *Meloidogyne* isolate were arranged in a completely randomized block design in a greenhouse bench. Groups of pots corresponding to different isolates were separated from each other with transparent splash screens. *Prunus* plants were harvested 4 months after inoculation. Each plant was carefully washed and given a root gall index on a 0-to-5 scale (Barker, 1985) where 0 = no galling, 1 = 1 to 10% of root system galled, 2 = 11 to 30%, 3 = 31 to 70%, 4 = 71 to 90%, 5 = greater than 90% (0.5-step increments were assigned when galling was intermediate between two classes). After ratings, 10 selected *Prunus* rootstocks (GF.677, GF.305, Garrigues, GF.557, G × N no. 15, G × N no. 22, P.2175, P.1079, P.2980, and Myro 29C) that had been evaluated against four isolates (*M. arenaria* Monteux, *M. incognita* Landes, *M. javanica* Oualidia, and *M.* sp. Floride) chosen as representing the major RKN species and illustrating different plant responses were submitted to further analysis and their root systems were individually frozen at −20 °C until nematodes were extracted. Frozen root systems were transferred to a refrigerator (5 °C), to be thawed gradually. Fine roots (diam. ≤ 1 mm) were separated and weighed, and a random sample of 20 grams was ground with an ultra grinder at 20,000 rpm for 2 seconds. The freed nematodes were rinsed through a 250-µm-pore sieve and collected in a beaker. Roots and rootlets were recovered from the sieve, ground, and rinsed through the sieve twice. Then the contents of the beaker were centrifuged twice (Jenkins, 1964). Females, males, J2, third- to fourth-stage juveniles (J3 + J4), and eggs were counted. Tests for Nemaguard and Summergrand seedlings were performed separately (as described above) 2 months after the other plant material.

Data were analyzed separately for each isolate and separately for each genotype with a one-way analysis of variance. Nematode densities were transformed with $\log_{10}(x + 1)$ before analysis (Noe, 1985). Means were compared with the Student- Newman-Keuls multiple range test at $P \leq 0.05$.

Second-year test: Experiments were performed to confirm results of the first-year test. The reaction of 12 rootstocks (GF.677, GF.305, Garrigues, GF.557, G × N no. 15, G × N no. 22, P.2175, P.1079, P.2980, Myro 29C, Nemaguard, and Nemared) against four RKN isolates (*M. arenaria* Monteux, *M. incognita* Landes, *M. javanica* Oualidia, and *M.* sp. Floride) were determined. Three different rootstocks were grown and inoculated in a single 12-liter container. The rootstocks were combined in order to express (and confirm from the results of the first-year test) different responses to the two isolates *M. javanica* Oualidia and *M.* sp. Floride. For example, one combination was GF.557 + Nemaguard + P.2175 where GF.557 was susceptible to both isolates, Nemaguard was resistant only to Oualidia, and P.2175 was resistant to both isolates. Thus, combined rootstocks were as follows: GF.557 + Nemaguard + P.2175, GF.557 + Nemared + P.1079, GF.557 + G × N no. 15 + P.2980, GF.557 + G × N no. 22 + Myro 29C. Control containers were planted with GF.677 + GF.305 + Garrigues susceptible rootstocks. Each three-rootstock combination was replicated four times for each RKN isolate. The rootstocks were planted on 13 March 1996. On 15 May 1996, one tomato plant with galled roots was transferred into the center of each container, equidistant from each test plant. On 12 September 1996, the root systems of the *Prunus* plants were gently separated, washed, and scored for galling on the 0-to-5 scale. Data were analyzed separately for each isolate and separately for each genotype in each combination, using a one-way analysis of variance. For example, the genotype GF.557 in combination with Nemaguard + P.2175 and GF.557 in combination with Nemared + P.1079 were considered as two distinct entities for statistical analysis. Means were compared with the Newman-Keuls multiple range test at $P \leq 0.05$.

Results

First-year test gall index ratings: The reference susceptible rootstocks (almonds Garfi and Garrigues, almond-peach hybrid GF.677, and peach GF.305) and Rutgers red leaf were heavily galled by all RKNs (Table 3). The almond-peach hybrid GF.557 was heavily galled by the *M. javanica* isolates but not galled by *M. arenaria* and *M. incognita* isolates. Floride produced an intermediate level of galling on GF.557. The rootstock Nemared was highly galled by Floride but did not gall in response to Landes (*M. incognita*). Both G × N hybrids were not significantly galled by any isolate except Floride. None of the *Prunophora* rootstocks or accessions were galled. Nemaguard, tested against *M. arenaria* Monteux, *M. incognita* Calissane and Landes, *M. javanica* Higuera, Camas, and Rama caida, and the Floride isolate, was galled only by the Floride isolate (data not shown). Summergrand, tested in the same conditions with the same isolates as Nemaguard, was not galled by *M. arenaria* or *M. incognita* but was heavily galled by *M. javanica* and Floride isolates (data not shown).

Nematode numbers: Garrigues, GF.677, and GF.305 supported high numbers of females and juveniles plus eggs (Tables 4 and 5). The highest numbers of females were detected in peach GF.305, and and the highest numbers of juveniles plus eggs were observed in almond Garrigues. The almond-peach GF.557 had high numbers of females and juveniles plus eggs of *M. javanica* Oualidia and *M.* sp. Floride, but had few or no females or juveniles plus eggs of *M. arenaria* Monteux or *M. incognita* Landes. The two hybrids G × N supported only high numbers of females and juveniles plus eggs of Floride, which reproduced on all *Amygdalus* rootstocks. No nematodes were extracted from the roots of *Prunophora* clones.

Second-year test gall index ratings: The ratings clearly confirmed differences in the RKN response among *Prunus* material (Table 6). Rootstocks GF.677, GF.305, and Garrigues were severely galled by each of the four isolates. None of the other rootstocks were significantly galled by *M. arenaria* or *M. incognita.* The rootstock GF.557 was galled by all *M. javanica* and Floride isolates. Nemaguard, Nemared, G × N no. 15, and G × N no. 22 were not galled by *M. arenaria, M. incognita,* and *M. javanica* but were severely galled by *M.* sp. Floride. The *Prunophora* rootstocks, P.2175, P.1079, P.2980, and Myro 29C, were not galled by any of the four isolates.

Discussion

High and durable inoculum pressure was effective in identifying high levels of resistance in some *Prunus* genotypes. High-

TABLE 3. Gall index ratings[a] in *Prunus* rootstocks or accessions inoculated with various *Meloidogyne* species and isolates.

	M. arenaria	*M. incognita*				*M. javanica*				*M. hispanica*	*M. sp.*
Plant material	Monteux	Calissane	Landes	Villa verde	Rama caida	Oualidia	Higuera	Camas	Rama caida	Seville	Floride
Amygdalus											
Garfi	4.4 a[b] A[c]	–	2.9 b C	3.9 a B	–	4.1 a AB	3.9 a B	3.9 ab B	4.1 a AB	–	–
Garrigues	3.6 b A	–	2.6 b B	–	–	3.8 a A	–	–	3.8 a A	3.2 b AB	3.6 ab A
GF.677	3.8 b A	2.9 a BC	3.1 b B	3.2 a B	3.5 a AB	3.2 a B	2.8 b BC	3.0 bc B	3.2 a B	3.3 b B	2.5 c C
Rutgers Red Leaf	–	–	3.0 b B	–	–	–	–	–	–	–	3.9 a A
GF.305	3.5 b B	3.2 a B	4.5 a A	3.9 a AB	4.0 a AB	3.5 a B	3.1 ab B	4.4 a A	3.5 a B	4.3 a A	3.5 ab B
Nemared	–	–	0.0 c B	–	–	–	–	–	–	–	3.9 a A
GF.557	0.4 c C	0.0 b C	0.0 c C	0.0 b C	–	3.1 a A	2.9 b A	3.0 bc A	3.1 a A	–	1.8 d B
G × N no 15	0.2 c C	–	0.0 c C	0.0 b C	–	0.9 b B	–	0.3 d BC	0.9 b B	–	3.1 abc A
G × N no 22	0.2 c C	–	0.0 c C	0.0 b C	–	1.0 b B	–	–	–	–	2.9 bc A
Prunophora											
P.1079	0.0 c A	0.0 b A	0.0 c A	0.0 b A	0.0 b A	0.0 c A	0.0 c A	0.0 d A	0.0 c A	0.0 c A	0.0 e A
P.2175	0.0 c A	0.0 b A	0.0 c A	0.0 b A	0.0 b A	0.0 c A	0.0 c A	0.0 d A	0.0 c A	0.0 c A	0.0 e A
P.2980	0.0 c A	0.0 b A	0.0 c A	0.0 b A	0.0 b	0.0 c A	0.0 c A	0.0 d A	0.0 c A	0.0 c A	0.0 e A
P.2984	0.0 c A	0.0 b A	0.0 c A	0.0 b A	0.0 b A	0.0 c A	0.0 c A	0.0 d A	0.0 c A	0.0 c A	–
Myro 29C	0.0 c A	–	0.0 c A	0.0 b A	–	0.0 c A	–	–	0.0 c A	–	0.0 e A
AD.101	0.0 c A	–	0.0 c A	0.0 b A	–	0.0 c A	0.0 c A	0.0 d A	0.0 c A	–	0.0 e A

Numbers are means of six replications.

[a] Gall index ratings: 0 = no galling; 5 = greater than 90% of root system galled.

[b] Data within the same column followed by the same lowercase letter are not significantly different ($P \leq 0.05$) according to the Student-Newman-Keuls multiple range test.

[c] Data within the same row followed by the same uppercase letter are not significantly different ($P \leq 0.05$) according to the Student-Newman-Keuls multiple range test.

TABLE 4. Numbers of females per g of root in *Prunus* rootstocks and accessions inoculated with four *Meloidogyne* species and isolates.

Plant material	*M. arenaria* Monteux	*M. incognita* Landes	*M. javanica* Oualidia	*M.* sp. Floride
Amygdalus				
Garrigues	111 ab[a] A[b]	80 b AB	62 ab BC	34 abc C
GF.677	61 b A	72 b A	38 b A	21 c B
GF.305	138 a A	121 a A	81 a AB	59 a B
GF.557	1 c C	0 c C	103 a A	48 a B
G × N no. 15	1 c B	0 c B	0 c B	26 bc A
G × N no. 22	0 c B	0 c B	0 c B	35 abc A
Prunophora				
P.1079	0 c A	0 c A	0 c A	0 d A
P.2175	0 c A	0 c A	0 c A	0 d A
P.2980	0 c A	0 c A	0 c A	0 d A
Myro 29C	0 c A	0 c A	0 c A	0 d A

Data are means of six replications. Actual data are presented, but data were transformed to $\log_{10}(x + 1)$ for analysis.
[a] Data within the same column followed by the same lowercase letter are not significantly different ($P \leq 0.05$) according to the Newman-Keuls multiple range test.
[b] Data within the same row followed by the same uppercase letter are not significantly different ($P \leq 0.05$) according to the Newman-Keuls multiple range test.

temperature regimes in *Prunus* are known to be associated with a partial loss of resistance (Canals et al., 1992; Wehunt, 1972). Our tests were conducted under high temperatures, increasing the severity of reaction of susceptible rootstocks to RKN. Under these conditions, a clear separation of susceptible and resistant rootstock reactions in response to each nematode population was observed (Table 7). As expected, reference rootstocks Garrigues, Garfi, GF.677, GF.305, and Rutgers Red Leaf were confirmed as susceptible. Three types of resistance spectra were found among the other rootstocks: 1- *M. arenaria* + *M. incognita;* 2- *M. arenaria* + *M. incognita* + *M. javanica;* 3- *M. arenaria* + *M. incognita* + *M. javanica* + *M.* sp. Floride. The species-specificity of resistance to *M. arenaria* and *M. incognita* in GF.557 (Esmenjaud et al., 1994) was confirmed with the four previously untested isolates, *M. incognita* Villa verde and *M. javanica* Higuera, Camas, and Rama caida; the peach cultivar Summergrand shared the same resistance specificity.

TABLE 5. Numbers of root-knot nematode juveniles and eggs per g of roots in *Prunus* rootstocks or accessions inoculated with four *Meloidygne* species and isolates.

Prunus subgenus and rootstock	*M. arenaria* Monteux	*M. incognita* Landes	*M. javanica* Oualidia	*M.* sp. Floride
Amygdalus				
Garrigues	4392 a[a] A[b]	1564 a B	1573 a B	2010 a AB
GF.677	682 b A	355 a A	795 ab A	532 b A
GF.305	325 b A	465 a A	310 b A	1127 ab A
GF.557	9 cd B	0 b C	593 ab A	1408 ab A
G × N no. 15	5 de B	0 b C	4 c B	1441 ab A
G × N no. 22	0 e C	0 b C	4 c B	1167 ab A
Prunophora				
P.1079	0 e A	0 b A	0 d A	0 c A
P.2175	0 e A	0 b A	0 d A	0 c A
P.2980	0 e A	0 b A	0 d A	0 c A
Myro 29C	0 e A	0 b A	0 d A	0 c A

Data are means of six replications. Actual data are presented, but data were transformed to $\log_{10}(x + 1)$ for analysis.
[a] Data within the same column followed by the same lowercase letter are not significantly different ($P \leq 0.05$) according to the Newman-Keuls multiple range test.
[b] Data within the same row followed by the same uppercase letter are not significantly different ($P \leq 0.05$) according to the Newman-Keuls multiple range test.

TABLE 6. Gall index ratings[a] for sets of three different rootstocks or accessions per container inoculated with four *Meloidgyne* species and isolates.

Associated rootstocks	*M. arenaria* Monteux	*M. incognita* Landes	*M. javanica* Oualidia	*M.* sp. Floride
Garrigues	4.6 a[b] A[c]	4.2 a A	4.1 a A	4.5 a A
+ GF.305	4.1 a A	3.6 a A	3.4 a A	3.7 a A
+ GF.677	3.9 a A	3.5 a A	3.2 a A	3.6 a A
GF.557	0.1 b B	0.0 b B	4.0 a A	3.8 a A
+ Nemaguard	0.1 b B	0.1 b B	0.3 b B	3.5 a A
+ P.2175	0.0 b A	0.0 b A	0.0 b A	0.0 b A
GF.557	0.2 b B	0.1 b B	4.2 a A	4.0 a A
+ Nemared	0.1 b B	0.1 b B	0.2 b B	3.2 a A
+ P.1079	0.0 b A	0.0 b A	0.0 b A	0.0 b A
GF.557	0.1 b B	0.1 b B	3.9 a A	4.1 a A
+ G × N no 15	0.1 b B	0.1 b B	0.3 b B	3.9 a A
+ P.2980	0.0 b A	0.0 b A	0.0 b A	0.0 b A
GF.557	0.2 b B	0.1 b B	4.2 a A	4.0 a A
+ G × N no 22	0.1 b B	0.1 b B	0.3 b B	3.8 a A
+ Myro 29C	0.0 b A	0.0 b A	0.0 b A	0.0 b A

Data are means of four replications.
[a] Gall index ratings: 0 = no galling; 5 = greater than 90% of root system galled.
[b] Data within the same column followed by the same lowercase letter are not significantly different ($P \leq 0.05$) according to the Newman-Keuls multiple range test.
[c] Data within the same row followed by the same uppercase letter are not significantly different ($P \leq 0.05$) according to the Newman-Keuls multiple range test.

Nemaguard, Nemared, and the hybrids Garfi (susceptible) × Nemared (resistant) have a common spectrum of resistance to *M. arenaria, M. incognita,* and *M. javanica,* suggesting that they may share the same resistance gene(s). The *Prunophora* plant material expressed resistance to all nematode isolates. In particular, the documented broad resistance of the Myrobalan genotypes P.1079 and P.2175 to RKN (Esmenjaud et al., 1994) was extended with resistance expressed to *M. javanica* isolates Higuera, Camas, and Rama caida, and the isolate Floride.

Our data indicate that a minimum of two different genetic systems control resistance to RKN in the subgenus *Amyqdalus* (Table 7). One can hypothesize that at least one system (S1) is involved in the resistance to *M. arenaria* and *M. incognita* as shown by the GF.557 species-specific differential response to these two species and to *M. javanica.* In this rootstock, resistance is inherited from the parent *P. persica* 'Shalil' (Kester and Grasselly, 1987; Weinberger et al., 1943). A second system (S2) also involves resistance to *M. javanica* in rootstocks Nemaguard and in the related genotypes Nemared, G × N no. 15, and G × N no. 22. Sharpe et al. (1969) suggested that resistance to *M. incognita* in Nemaguard and Okinawa is conditioned by one major dominant gene, whereas resistance to *M. javanica* is conditioned by at least two other dominant and independent genes. Moreover, a third system (S3) has been evidenced in almond for rootstocks of the Alnem series (Kochba and Spiegel-Roy, 1975, 1976) and is based on a single gene for resistance to *M. javanica.* In *Prunophora* material, a fourth genetic system (S4) acts against all tested nematode species and isolates. A single dominant gene controlling resistance to *M. arenaria* (Esmenjaud et al., 1996b) and also to *M. incognita, M. javanica,* and *M.* sp. Floride (Lecouls et al., in press) underlies this S4 system in each of the highly resistant *P. cerasifera* clones, P.2175 (*Ma1* gene) and P.1079 (*Ma2* gene). Inheritance studies in progress for RKN resistance in Nemared peach (Jauregui et al., 1996) should allow us to relate the respective genetic systems involved in Myrobalan plum and the subgenus *Amygdalus.* Molecular markers already have been obtained for the *Ma1* gene (Dirlewanger et al., 1996), and studies are in prog-

TABLE 7. Synthesis of the resistance range of tested *Prunus* rootstocks or accessions to *Meloidogyne* spp. and correlative genetic hypotheses for RKN resistance in *Prunus* species.

Prunus subgenera and rootstocks	Resistance range: *M. arenaraia*	*M. incognita*	*M. javanica*	*M.* sp. Floride	Putative genetic system of resistance	Resistant plant material	Number of major genes (references)
Amygdalus							
Guarrigues, Garfi GF.677, GF.305, Rutgers red leaf	S[a]	S	S	S			
GF.557 (= Shalil peach × almond), Summergrand	R[a]	R	S	S	S1	Shalil	Undefined RKN species: homozygous dominant resistance (Weinberger et al., 1943)
Nemaguard, Nemared,	R	R	R	S	S2	Nemaguard and Okinawa	*M. incognita:* monogenic dominant resistance (Sharpe et al., 1969)
G × N no. 15, G × N no. 22						Okinawa	*M. javanica:* ≥2 independent and dominant genes (Sharpe et al., 1969)
					S3	Alnem seedlings[b] (bitter almond)	*M. javanica:* monogenic dominant resistance (Kochba and Spiegel-Roy, 1975, 1976)
Prunophora							
P.1079, P.2175, P.2980, P.2984,	R	R	R	R	S4	Myrobalan plum P.2175	*M. arenaria*[c]: monogenic dominant resistance (Esmenjaud et al., 1996)
Myro 29C, AD.101						P.1079	*M. incognita, M. javanica, M.* sp. Floride: monogenic dominant resistance (Lecouls et al., in press)

[a] S = susceptible; R = resistant.
[b] Resistant to *M. arenaria* and *M. javanica* but susceptible to *M. incognita* according to Scotto La Massèse et al. (1984).
[c] *Ma1* gene for P.2175 resistance; *Ma2* gene for P.1079 resistance.

ress formarker detection in Nemared peach (Arus, pers. comm.).

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