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Spectrum of the *Ma* genes for resistance to *Meloidogyne* spp. in Myrobalan plum

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Abstract The Myrobalan plum, *Prunus cerasifera*, bears a complete-spectrum resistance to the root-knot nematodes (RKN) *Meloidogyne* spp. in comparison to the main resistance sources in *Amygdalus* rootstocks that have more restricted spectra, as evidenced by a differential resistance test based on the predominant species *M. arenaria*, *M. incognita* and *M. javanica* and the population *M.* sp. Floride. Resistance to *M. arenaria* (A) in Myrobalan plum is controlled by the *Ma* major resistance genes that are completely dominant and confer a non-host behaviour that totally prevents the multiplication of the nematode. The inheritance of resistance of this self-incompatible species to *M. incognita* (I), *M. javanica* (J) and the population *M.* sp. Floride (F), considered as belonging to a new RKN species, was studied using G_1 hybrids from a diallel cross based on five parents, the two resistant P.2175 (*Ma1* gene; heterozygous) and P.1079 (*Ma2* gene; homozygous) and three host parents, P.2032, P.2646 and P.16.5 (recessive for both genes), completed with the G_2 backcrosses P.16.5 × (P.2646 × P.1079), P.2646 × (P.16.5 × P.1079) and P.2175 × (P.2646 × P.1079). G_1 and G_2 clones obtained from softwood cuttings sampled from trees in the field experimental design, rooted in the nursery, and inoculated in containers (six replicates per clone) under greenhouse conditions, were simultaneously evaluated for their host suitability to two to four of the RKN species, based on a 0–5 gall index (GI) rating under a high and durable inoculum pressure of the nematode, and then classified into resistant (R; GI $\leqslant$ 0.2) or host (H; GI $\geqslant$ 1.3) classes. The resistance classification of each individual clone, evaluated to two (A/J: 319 clones), three (A/J/I: 249 clones) and four (A/J/I/F: 161 clones) RKN species, from segregating and non-segregating crosses involving either *Ma1* or *Ma2* or both or none, was identical whatever the species. The independence of the R/H classification from the tested RKN indicates that the *Ma1* and *Ma2* genes control resistance to all of them, and it is assumed that these genes also control resistance to other minor RKN species. The relationship of the *Ma* genes with the putative genes involved in *Amygdalus* sources is discussed with the objective of introducing them into new interspecific rootstocks expressing a complete-spectrum and high-level resistance.

Key words Diallel · *Prunus cerasifera* · Oligogenic resistance · Root-knot nematode

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Introduction

Root-knot nematodes (RKN) (*Meloidogyne* spp.) are major pests of crops all over the world (Sasser 1977; Lamberti 1979). Species with the highest economic importance are the Mediterranean and Tropical species, *M. arenaria*, *M. incognita* and *M. javanica*, that are highly polyphagous and can develop parthenogenetically (Triantaphyllou 1985) on hundreds of cultivated and wild plant species (de Guiran and Netscher 1970). *Prunus* crops are severely affected by these soil pests which are easily propagated at the national and international scale from nursery plants.

Plant resistance has been used to control the main RKN species (Minz and Cohn 1962; Kochba and Spiegel-Roy 1976; Kester and Grasselly 1987; Layne 1987; Scotto La Massese et al. 1990; Nyczepir 1991; Fernandez et al. 1994a). Nevertheless, RKN-resistant

rootstocks express different control efficiencies depending on their source of resistance (Scotto La Massese et al. 1984; Esmenjaud et al. 1997). In the subgenus *Amygdalus* (cultivated and wild species of peach and almond), three types of plant response have been identified. Common rootstock material expresses a complete host suitability to RKN. The peach Shalil and its peach-almond hybrid GF.557 are resistant to *M. arenaria* and *M. incognita* but are hosts for *M. javanica* (Esmenjaud et al. 1994) and a RKN population from Florida [considered as belonging to a new species and designated as *M.* sp. Floride (Esmenjaud et al. 1997)]. The peach Nemaguard, and related material such as Nemared and Garfi almond × Nemared (termed G × N), also resist *M. javanica* but not *M.* sp. Floride. By contrast, in the subgenus *Prunophora* (plum and apricot species) the clones P.2175 and P.1079 of the Myrobalan plum *P. cerasifera* also proved resistant to the *M.* sp. Floride population (Esmenjaud et al. 1997). Their resistance was not overcome by any of the over 30 tested RKN species and populations (Esmenjaud et al. 1994; Fernandez et al. 1994 a), and was not modified under conditions known to affect plant defense mechanisms to RKN such as high temperature and high inoculum pressure (Canals et al. 1992; Fernandez et al. 1994 b; Esmenjaud et al. 1996a). Consequently the Myrobalan plum sources appear particularly useful for RKN-resistant rootstock breeding because of their high-level and wide-spectrum RKN resistance.

In recent years, the number of RKN resistance genes, evidenced among the diverse but short-cycle crops such as tomato (Cap et al. 1993; Veremis and Roberts 1996), pepper (Fery and Dukes 1996), potato (Janssen et al. 1997), carrot (Wang and Goldman 1996) or common bean (Omwega et al. 1990), has considerably increased. By contrast, in *Prunus* and other perennials, the genetic control of RKN resistance has been poorly investigated mainly because of the long generation intervals that are required for such crops. The differential plant response observed in *Prunus* species suggests that resistance is controlled by different genes (Esmenjaud et al. 1997). In Myrobalan plum, the genetics of resistance to *M. arenaria*, the most common species in Northern Mediterranean regions, has been established by Esmenjaud et al. (1996b). Resistance is monogenic and dominant, and the major genes *Ma1* and *Ma2* are respectively involved in the resistance of the clones P.2175 (heterozygous) and P.1079 (homozygous). Because resistance of both clones is highly efficient against the whole RKN species, it is important to determine whether the same or a different gene(s) is(are) also involved in their resistance towards other species.

In this study we will establish the genetics of resistance of Myrobalan plum to predominant RKN species. To this end the resistance of parental Myrobalan-plum clones and progenies will be evaluated in one representative population of each of the *M. arenaria*, *M. incognita* and *M. javanica* species and in the population *M.* sp. Floride. *Amygdalus* material, representing the main sources of resistance, will be simultaneously evaluated as differential hosts of the RKN species mentioned above. Because of the self-incompatibility of *P. cerasifera*, this study is based on the analysis of G_1 hybrids from a diallel cross involving the resistant clones P.2175 and P.1079 and three host clones P.16.5, P.2646 and P.2032, completed with appropriate G_2 crosses.

Materials and methods

Plant material

The five clones of *P. cerasifera* used to establish a diallel cross at INRA Villenave d'Ornon (France) were introduced in the years 1960–1970 from various geographical origins. Their host suitability is defined on a resistant/host terminology. Their identity and main characteristics are the following: P.1079 (South Western France; red leaf) and P.2175 (Bucarest, Rumania), both highly resistant to all tested RKN; P.16.5 (Northern Alps , France; red leaf), P.2646 (Balsgard, Sweden) and P.2032 (rootstock registered as 'Myrabi'; South-Eastern France), considered as hosts for all RKN (Scotto La Massese et al. 1990). The genotype of parental clones is presented in Table 1. Molecular studies at INRA (Dirlewanger et al. 1996 a) have identified RAPD markers for the *Ma1* gene and recent data using these markers (Esmenjaud, unpublished) concluded that *Ma1* and *Ma2* are at least closely linked. Consequently we will consider that *Ma1* is either the same as, or else allelic or closely linked to, *Ma2*.

Parental clones, as well as G_1 and G_2 material, were obtained as previously described (Esmenjaud et al. 1996b). In each cross, clones for further evaluation were sampled at random among the available material. Tested G_1 crosses involved all the possible hybrids (direct crosses plus reciprocal crosses when available) between the five parental clones. The tested G_2 material involved crosses of selected G_1 hybrids of P.1079 by the hosts P.2646 or P.16.5, backcrossed by these latter host clones or by P.2175. Crosses involving P.1079 (homozygous for *Ma2*) do not segregate in the G_1 progenies but segregate when backcrossed with P.2175 (heterozygous for *Ma1*) or any of the host parents (recessive for both genes), whereas crosses involving P.2175 and host parents segregate in the G_1 progenies (Esmenjaud et al. 1996b).

The plant material used as a reference for the characterization of the different resistance ranges in the subgenus *Amygdalus* was

Table 1 Putative genotypes of the diallel-cross parental clones for resistance to *M. arenaria*

Parental clone	Number of genes[a]	
	Two *Ma1* ≠ *Ma2*[b]	One *Ma1* = *Ma2*[c]
P.1079	*ma1 ma1*, *Ma2 Ma2*	*Ma1 Ma1*
P.2175	*Ma1 ma1*, *ma2 ma2*	*Ma1 ma1*
P.2032	*ma1 ma1*, *ma2 ma2*	*ma1 ma1*
P.2646	id.	id.
P.16.5	id.	id.

[a] All genes expressed in a dominant fashion
[b] *Ma1* and *Ma2* linked
[c] *Ma1* same as, or allelic to, *Ma2*

composed of one almond, one peach, and three peach-almond hybrids. The almond Garfi is a clonal selection from Spain with a good rooting capacity (Felipe 1989) and a host status to all RKN. The peach Nemared is a red-leaf selection from USA (Ramming and Taner 1983) with a near-complete RKN resistance. Peach-almond hybrids were GF.557, a cross with resistance to *M. arenaria* and *M. incognita* inherited from the peach parent Shalil (Kester and Grasselly 1987), and two brother hybrids (G × N no. 15 and no. 22) between Garfi and Nemared (Felipe 1989) that bear the same resistance range as their Nemared peach parent.

Nematode species

The following three RKN populations, one of each of the predominant RKN species plus the *M.* sp. Floride population were employed: *M. arenaria* 'Monteux' from Monteux, Vaucluse, France [already used for studying the genetics of resistance to *M. arenaria* by Esmenjaud et al. (1996b)], *M. incognita* 'Calissanne' from Calissanne, Bouches-du-Rhone, France, and *M. javanica* 'Higuera' from Cabrils, Cataluna, Spain. The population Floride, reared from a soil sample provided by W. B. Sherman (University of Florida), originated from an orchard where resistant Nemaguard seedlings were galled by the RKN population identified as *M. incognita* race 3 (Sherman and Lyrene 1983). However, the esterase b pattern was different from that of *M. incognita* and other *Meloidogyne* spp. (Janati et al. 1982) and thus we considered it as a new species designated as *Meloidogyne* sp. Floride (Esmenjaud et al. 1997). All the populations, except *M.* sp. Floride, were isolates that were reared from a single egg mass. The populations were maintained on tomato (*Lycopersicon esculentum* Mill.) cv St. Pierre. The identity of the populations, at the species level, was verified each year before inoculation via their isoesterase phenotype (Janati et al. 1982).

Evaluation of plant material

For Myrobalan-plum clones, the assessed material was propagated at INRA Villenave d'Ornon (France) from softwood cuttings sampled on adult trees for G_1 clones and on recently obtained 3–6-year-old trees for G_2 clones. Most of these trees were the same as those sampled for the study of the genetics of resistance to *M. arenaria* (Esmenjaud et al. 1996b). Homogeneous cuttings (25 cm long, 5 mm diameter) were harvested in May or June, rooted individually in alveolated plates in the nursery up to the next late autumn to allow for the development of rooted plants, and supplied in December to the Laboratoire de Biologie des Invertébrés at INRA Antibes (France) for resistance evaluation. Cuttings of the same clone were then re-potted by pairs during winter into 5-l containers filled with a sandy substrate.

In *Amygdalus* accessions, the seeds of Nemared were stratified in perlite trays at 4°C for 90–120 days during autumn and winter, and then moved to a greenhouse at a mean temperature of 25°C to induce germination. Semi-hardwood cuttings from other clonal rootstocks were collected in the field at the end of summer, treated for 10 s with a 50% ethanol solution containing 2000 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-l containers filled with a sterilized sand-peat mixture. Germinated seeds (Nemared) and rooted cuttings (other rootstocks) were washed free of substrate and individually planted at mid-March in 5-l containers filled with the same sandy soil as the Myrobalan-plum clones.

All the containers were placed on iron benches in the greenhouse, irrigated individually every 2 days with a 5N-11.5 P_2O_5–7.5K_2O nutrient solution at 3 g/l completed with trace elements (Algoflash: Algochimie, Tours, France) and grown until harvest for rating at a mean temperature of 25°C (extremes 22–28°C). On mid-March, on the same date as the *Prunus* planting into the 5-l containers, tomato plantlets grown in the same greenhouse in 250-ml plastic containers were inoculated with 500 juveniles, 24–72-h old, of one of the different species and deposited into two holes, 2-cm deep and 2 cm from the stem. Juveniles were obtained in a mist chamber from tomato roots previously inoculated with the same RKN species.

In mid-May, 2 months after inoculation, the top parts of tomato plants were cut and removed, and one whole soil and root system content was transplanted into each *Prunus* container. Containers inoculated with the same *Meloidogyne* species were arranged in a completely randomized block design on a greenhouse bench. Groups of containers corresponding to different species were separated from each other with transparent splash screens. For each clone-species combination, there were six replicates (three containers of two cuttings) of the Myrobalan-plum material and six replicates (six individual containers) of the reference *Amygdalus* material.

Four months after inoculation with galled tomatoes, *Prunus* plants were harvested. Each plant was carefully washed individually over a bucket and given a root-gall index rating according to a 0–5 scale (Barker 1985) (0 = no gall; 1 = 1–10% of root system galled; 2 = 11–30%; 3 = 31–70%; 4 = 71–90%; 5 > 90%) completed with 0.5 steps when galling was estimated to be at the limit between two categories. No nematode extraction and counting was performed because a previous study (Esmenjaud et al. 1992) had established that the gall index was highly significantly correlated with the $\log_{10}(x + 1)$-transformed numbers of the different nematode stages in the roots. The best linear correlation was observed with the females, followed by the eggs and the juveniles. Since these later stages represent the reproductive potential of the nematode in the plant, the gall index proved to be a good criterion to evaluate host suitability in *P. cerasifera*.

Planning of the RKN evaluations and the distribution of *Prunus* material

Trials were performed over 3 years with approximately one-third of the total G_1 and G_2 material tested in each year. A test of the reference *Amygdalus* rootstocks was performed during the first year, whereas tests of all parental clones were repeated each year. Not all the G_1 and G_2 clones were tested with all the species because limited numbers of homogeneous plants were available for some of them. Consequently, the distribution of plants was performed as follows. When, for a given clone, 24 cuttings with homogeneous top and root parts were available at planting, these cuttings were randomly separated into four groups of six replicates and planted by pairs into 5-l containers. The first group was used to evaluate to *M. arenaria*, the second one *M. javanica*, the third one *M. incognita*, and the last one *M.* sp. Floride. When only 18 to 23 homogeneous cuttings were available, 18 cuttings were used and distributed at random into three groups of six and evaluation was conducted for *M. arenaria*, *M. javanica* and *M. incognita*. Similarly when 12 to 17 homogeneous cuttings were available, 12 of them were distributed into two groups of six and evaluation was conducted for *M. arenaria* and *M. javanica*.

As six replicates of each tested clone-RKN species combination were available, data from the same-year test were analyzed separately for each RKN species using a one-way analysis of variance (Noe 1985). Mean gall index ratings were compared by a Newman-Keuls multiple range test at $P \leqslant 0.01$.

Results

In parental clones (each year) and in reference *Amygdalus* rootstocks (first-year test), GI ratings ranged from 0.0 to 4.4 (data not given). Each *Prunus*-RKN

Table 2 Resistance spectrum of *P. cerasifera* parental clones in comparison with reference *Amygdalus* material

Subgenus and rootstock material	*M. arenaria*	*M. incognita*	*M. javanica*	*M.* sp. Floride
Amygdalus				
Garfi	H[a]	H	H	H
GF.557	R[a]	R	H	H
Nemared, G × N no. 15, G × N no. 22	R	R	R	H
Prunophora (Myrobalan plum, *P. cerasifera*)				
P.1079, P.2175	R	R	R	R
P.2032, P.2646, P.16.5	H	H	H	H

[a] H = host; R = resistant

species combination could be classified into one of two statistically different ($P \leqslant 0.01$) resistant (R; GI $\leqslant 0.4$) and host (H; GI $\geqslant 1.2$) classes, with no intermediate behaviour (Table 2). For the same host rootstock, differences in host suitability within and between RKN species were observed but were not taken into account in this study. Parental clones P.1079 and P.2175 were free of galls whatever the RKN species, whereas P.16.5, P.2646 and P.2032 expressed a marked galling. Among the *Amygdalus* material, three expected differential plant responses were obtained (Esmenjaud et al. 1997). The Garfi almond showed extensive galling with any of the species. The peach-almond GF.557 was free of galls by *M. arenaria* and *M. incognita* but extensively galled by *M. javanica* and *M.* sp. Floride. Nemared, G × N no. 15 and G × N no. 22 were only galled by *M.* sp. Floride. Consequently the selected RKN species confirmed their interest for a differential resistance test between Myrobalan plum and the reference *Amygdalus* rootstocks and hence for the subsequent genetic study.

In Myrobalan plum hybrid clones, GI ratings clearly separated two statistically different classes each year ($P \leqslant 0.01$): resistant clones (R) with a GI rating $\leqslant 0.2$ and host clones (H) with a GI rating $\geqslant 1.3$, with no intermediate behaviour. Among host clones, variable levels of host suitability, with GI ranging from 1.3 to 4.8, were observed for the diverse G_1 and G_2 crosses within and between RKN species (data not given). These qualitative data have not been taken into account in this paper which considered the H class as a whole. Only incipient differences were observed in the R class for which GI ratings ranged from 0.0 to 0.2 for all confounded resistant clones. After their year-by-year statistical analysis, the data on resistance evaluations obtained during the 3 years were grouped and distributed into four types of crosses in relation to the *Ma1* and *Ma2* genes, based on the results of the genetic study for *M. arenaria* (Esmenjaud et al. 1996b), as follows: (1) G_1 crosses between P.2175 (*Ma1* gene) and host parents, segregating 1R : 1H for the *Ma1* gene (Tables 3 and 4); (2) crosses involving P.1079 (*Ma2* gene) in G_1 hybrids (P.1079 × host parents; no segregation) and G_2 backcrosses [(P.1079 × host) × host; segregation 1R : 1H] (Table 5); (3) crosses involving both P.2175 (*Ma1* gene) and P.1079 (*Ma2* gene) at the G_1 level (no segregation) or at the G_2 level [(P.1079 × host) × P.2175; segregation 3R : 1H] (Table 6); (4) crosses between host clones (none of the *Ma1* or *Ma2* genes; no segregation) (Table 7).

G_1 crosses only involving the *Ma1* gene (Table 4)

All three different possible crosses between P.2175 and P.16.5, P.2646 or P.2032 were represented. Nevertheless, the most numerous progeny that was evaluated for the four species was P.2646 × P.2175 with 72 out of the 79 total clones. As expected for crosses between P.2175, homozygous for *Ma1*, and the three recessive parents, segregation for *M. arenaria* was approximately 1R : 1H and, as observed previously (Esmenjaud et al. 1996b), the total number of resistant clones (approximately 54%) exceeded slightly that of host clones (approximately 46%). Each of these 79 tested clones expressed the same resistance behaviour (R or H) whatever the RKN species. A sample of the complete results is shown in Table 3 for 16 out of the 72 tested clones from the cross P.2646 × P.2175.

When the three predominant species *M. arenaria*, *M. javanica* and *M. incognita* were compared, the 23 additional tested clones also expressed the same R or H behaviour for each species. Similarly the 32 additional clones, compared only for the behaviour of *M. arenaria* and *M. javanica*, reacted identically (R or H) to both species. By accumulating the data, a total of 79 (four species), 102 (three species) and 134 (two species) clones were evaluated and showed the same behaviour whatever the species involved. In other words, all the clones that were classified as resistant to *M. arenaria* were also classified as resistant to any of the other species for which they have been evaluated; and all the clones that were classified as a host to *M. arenaria* were also classified as a host to the other species for which they have been evaluated. Thus a complete matching between the resistance classification of the four RKN is observed.

Table 3 Gall index ratings and resistance classification of a sample (16 out of the 72 total clones) of the G1 cross P.2646 × P.2175 evaluated to *M. arenaria*, *M. javanica*, *M. incognita* and *M.* sp. Floride. Data are based on six replicates

Nematode	Parents		Hybrid clones															
	P.2646	P.2175	4	5	6	8	9	10	11	13	17	18	21	28	30	34	36	39
M. arenaria	2.1a[a]	0.0d	1.4c	0.0d	0.0d	2.3a	0.0d	1.9ab	0.0d	2.1a	0.0d	0.0d	1.4c	0.0d	0.0d	0.0d	1.4c	1.6bc
	H[b]	R[b]	H	R	R	H	R	H	R	H	R	R	H	R	R	R	H	H
M. javanica	2.0abc	0.0d	2.6a	0.0d	0.0d	2.3abc	0.0d	1.7c	0.0d	1.8bc	0.0d	0.0d	2.0abc	0.0d	0.0d	0.0d	2.5ab	1.8bc
	H	R	H	R	R	H	R	H	R	H	R	R	H	R	R	R	H	H
M. incognita	2.8a	0.0c	2.4ab	0.0c	0.0c	2.1b	0.0c	2.4ab	0.0c	2.2b	0.0c	0.0c	2.3ab	0.0c	0.0c	0.0c	3.1a	2.6ab
	H	R	H	R	R	H	R	H	R	H	R	R	H	R	R	R	H	H
M. sp. Floride	3.0a	0.0c	1.9b	0.0c	0.0c	2.4ab	0.0c	2.1b	0.0c	2.2b	0.0c	0.0c	1.9b	0.0c	0.0c	0.0c	2.5ab	3.0a
	H	R	H	R	R	H	R	H	R	H	R	R	H	R	R	R	H	H

[a] Values within the same row (same RKN species) followed by the same lowercase letter do not differ according to the Newman-Keuls multiple range test at $P \leqslant 0.01$
[b] H = host; R = resistant

Table 4 Distribution of G_1 clones segregating for the *Ma1* gene and tested simultaneously to *Meloidogyne arenaria* (A), *M. javanica* (J), *M. incognita* (I) and *M.* sp. Floride (F)

Cross		Numbers and repartition of clones evaluated to									Total comparisons		
		A	J	I	F	A	J	I	A	J	A/J[a]	A/J/I	A/J/I/F
P.2175 × P.2646		0				4			13		17	4	0
P.2646 × P.2175		72				7			0		79	79	72
	Total	72				11			13		96	83	72
	R[b]	40	id.	id.	id.	7	id.	id.	5	id.	52	47	40
	H[b]	32	id.	id.	id.	4	id.	id.	8	id.	44	36	32
P.2175 × P.16.5		1				4			16		21	5	1
P.16.5 × P.2175		5				2			2		9	7	5
	Total	6				6			18		30	12	6
	R	3	id.	id.	id.	3	id.	id.	12	id.	18	6	3
	H	3	id.	id.	id.	3	id.	id.	6	id.	12	6	3
P.2175 × P.2032		0				4			0		4	4	0
P.2032 × P.2175		1				2			1		4	3	1
	Total	1				6			1		8	7	1
	R	1	id.	id.	id.	1	id.	id.	0	id.	2	2	1
	H	0	id.	id.	id.	5	id.	id.	1	id.	6	5	0
Total *Ma1* clones		**79**				**23**			**32**		**134**	**102**	**79**
	R	**44**	**id.**	**id.**	**id.**	**11**	**id.**	**id.**	**17**	**id.**	**72**	**55**	**44**
	H	**35**	**id.**	**id.**	**id.**	**12**	**id.**	**id.**	**15**	**id.**	**62**	**47**	**35**

[a] Total numbers of clones evaluated to *M. arenaria* and *M. javanica* (A/J), to *M. arenaria*, *M. javanica* and *M. incognita* (A/J/I), to *M. arenaria*, *M. javanica*, *M. incognita* and *M.* sp. FL (A/J/I/F)
[b] R = resistant; H = host

Crosses involving only the *Ma2* gene (Table 5)

Limited numbers of the three G_1 crosses between P.1079 and P.16.5, P.2646 or P.2032, and higher numbers of the three G_2 backcrosses involving P.1079, P.2646 and P.16.5, were tested. As expected for *M. arenaria*, G_1 did not segregate whereas G_2 segregated approximately 1R : 1H. As previously illustrated for the G_1 cross P.2646 × P.2175 (Table 3), the eight G_1 crosses tested to four species, the 16 additional crosses tested to three species, and the five more clones tested to two species all expressed the same behaviour in response to any RKN species (data not shown). The 37 G_2 backcrosses tested to four species, the 28 additional ones tested to three species, and the 33 additional clones tested to only two species also expressed a similar behaviour whatever the RKN species employed. By summing the data, a total of 127 (29 G_1 + 98 G_2), 89

Table 5 Distribution of G_1 and G_2 clones involving the *Ma2* gene and evaluated simultaneously to *Meloidogyne arenaria* (A), *M. javanica* (J), *M. incognita* (I) and *M.* sp. Floride (F)

Cross		Numbers and repartition of clones evaluated to									Total comparisons[a]		
		A	J	I	F	A	J	I	A	J	A/J	A/J/I	A/J/I/F
P.1079 × P.2646		1				3			0		4	4	1
P.2646 × P.1079		0				7			5		12	7	0
	Total	1				10			5		16	11	1
	R[b]	1	id.	id.	id.	10	id.	id.	5	id.	16	11	1
	H[b]	0	id.	id.	id.	0	id.	id.	0	id.	0	0	0
P.16.5 × P.1079		4				4					8	8	4
	R	4	id.	id.	id.	4	id.	id.			8	8	4
	H	0	id.	id.	id.	0	id.	id.			0	0	0
P.2032 × P.1079		3				2					5	5	3
	R	3	id.	id.	id.	2	id.	id.			5	5	5
	H	0	id.	id.	id.	0	id.	id.			0	0	0
Total G_1 clones		**8**				**16**			**5**		**29**	**24**	**8**
	R	**8**	**id.**	**id.**	**id.**	**16**	**id.**	**id.**	**5**	**id.**	**29**	**24**	**8**
	H	**0**	**id.**	**id.**	**id.**	**0**	**id.**	**id.**	**0**	**id.**	**0**	**0**	**0**
P.16.5 × (P.2646 × P.1079)9		13				11			18		42	24	13
	R	4	id.	id.	id.	5	id.	id.	9	id.	18	9	4
	H	9	id.	id.	id.	6	id.	id.	9	id.	24	15	9
P.2646 × (P.16.5 × P.1079)29		13				12			8		33	25	13
	R	7	id.	id.	id.	3	id.	id.	6	id.	16	10	7
	H	6	id.	id.	id.	9	id.	id.	2	id.	17	15	6
P.2646 × (P.16.5 × P.1079)33		11				5			7		23	16	11
	R	3	id.	id.	id.	3	id.	id.	4	id.	10	6	3
	H	8	id.	id.	id.	2	id.	id.	3	id.	13	10	8
Total G_2 clones		**37**				**28**			**33**		**98**	**65**	**37**
	R	**14**	**id.**	**id.**	**id.**	**11**	**id.**	**id.**	**19**	**id.**	**44**	**25**	**14**
	H	**23**	**id.**	**id.**	**id.**	**17**	**id.**	**id.**	**14**	**id.**	**54**	**40**	**23**

[a] Total numbers of clones evaluated to *M. arenaria* and *M. javanica* (A/J), to *M. arenaria*, *M. javanica* and *M. incognita* (A/J/I), to *M. arenaria*, *M. javanica*, *M. incognita* and *M.* sp. FL (A/J/I/F)
[b] R = resistant; H = host

(24 G_1 + 65 G_2) and 45 (8 G_1 and 37 G_2) clones behaved in an identical way when evaluated with respect to two, three and four species, respectively. Thus, resistance behaviour to the material involving the *Ma2* gene was independent of the RKN species tested.

Crosses involving both *Ma1* and *Ma2* genes (Table 6)

The material tested was the G_1 cross P.2175 × P.1079 and the G_2 cross between P.2175 (heterozygous for *Ma1*), and the hybrid (P.2646 × P.1079)9 (heterozygous for *Ma2*). All tested clones segregated as resistant or host, independently of the RKN species employed. As expected for P.1079, homozygous for *Ma2*, all G_1 hybrids were resistant to *M. arenaria* and the backcross segregated in a 12R : 8H ratio in this species, which fits to the 3 : 1 segregation ratio ($0.1 < P < 0.2$) expected for a cross between parents that are each heterozygous for one of the *Ma* genes and homozygous recessive for the other.

Crosses between material recessive for both resistance genes (Table 7)

The material tested comprised the three possible crosses between the recessive clones P.16.5, P.2646 and P.2032. As expected, all the 30 G_1 clones evaluated for resistance to *M. arenaria* were hosts. These 30 clones, evaluated for *M. arenaria*, *M. javanica* and *M. incognita*, and the 14 additional clones evaluated for all four species, were also hosts whatever the RKN species employed.

Discussion

The RKN differential test based on *Amygdalus* material and Myrobalan-plum parents confirmed the different ranges of resistance evidenced in *Prunus* spp. (Esmenjaud et al. 1994, 1997). Our data confirm interest in the Myrobalan plum as a source bearing a complete spectrum of resistance.

Table 6 Distribution of G_1 and G_2 clones involving both *Ma1* and *Ma2* genes and evaluated simultaneously to *Meloidogyne arenaria* (A), *M. javanica* (J), *M. incognita* (I) and *M.* sp. Floride (F)

Cross		Numbers and repartition of clones evaluated to							Total comparisons[a]	
		A	J	I	F	A	J	I	A/J/I	A/J/I/F
P.2175 × P.1079		4					4		8	4
	R[b]	4	id.	id.	id.	4	id.	id.	8	4
	H[b]	0	id.	id.	id.	0	id.	id.	0	0
P.2175 × (P.2646 × P.1079)9		19					1		20	19
	R	12	id.	id.	id.	0	id.	id.	12	12
	H	7	id.	id.	id.	1	id.	id.	8	7
Total		**23**					**5**		**28**	**23**

[a] Total numbers of clones evaluated to *M. arenaria* and *M. javanica* (A/J), to *M. arenaria*, *M. javanica* and *M. incognita* (A/J/I), to *M. arenaria*, *M. javanica*, *M. incognita* and *M.* sp. FL (A/J/I/F)
[b] R = resistant; H = host

Table 7 Distribution of clones corresponding to G_1 crosses between recessive parents for both *Ma1* and *Ma2* genes and evaluated simultaneously to *Meloidogyne arenaria* (A), *M. javanica* (J), *M. incognita* (I) and *M.* sp. Floride (F)

Cross		Numbers and repartition of clones evaluated to							Total comparisons[a]	
		A	J	I	F	A	J	I	A/J/I	A/J/I/F
P.2032 × P.2646		2				3			5	2
P.2646 × P.2032		0				3			3	0
	Total	2				6			8	2
	R[b]	0	id.	id.	id.	0	id.	id.	0	0
	H[b]	2	id.	id.	id.	6	id.	id.	8	2
P.16.5 × P.2646		4				2			6	4
	R	0	id.	id.	id.	0	id.	id.	0	0
	H	4	id.	id.	id.	2	id.	id.	6	4
P.2032 × P.16.5		4				4			8	4
P.16.5 × P.2032		4				4			8	4
	Total	8				8			16	8
	R	0	id.	id.	id.	0	id.	id.	0	0
	H	8	id.	id.	id.	8	id.	id.	16	8
Total		**14**				**16**			**30**	**14**
	R	**0**	**id.**	**id.**	**id.**	**0**	**id.**	**id.**	**0**	**0**
	H	**14**	**id.**	**id.**	**id.**	**16**	**id.**	**id.**	**30**	**14**

[a] Total numbers of clones evaluated to *M. arenaria* and *M. javanica* (A/J), to *M. arenaria*, *M. javanica* and *M. incognita* (A/J/I), to *M. arenaria*, *M. javanica*, *M. incognita* and *M.* sp. FL (A/J/I/F)
[b] R = resistant; H = host

The genetics of resistance to the four species of RKN has been studied by direct comparison of the behaviour of G_1 and G_2 material. High total numbers of clones were evaluated for 2-species (319 clones), 3-species (249 clones) and 4-species (161 clones) comparisons (Table 8). Among these comparisons, segregating crosses are the most informative. Total numbers of clones from crosses segregating for confounded *Ma1*- and *Ma2*-genes were 252 (2 species), 187 (3 species) and 135 (4 species). Considering the *Ma1* gene alone, these numbers are 134, 102 and 79, respectively, and no recombination between *Ma1* (*M. arenaria*) and the putative genes controlling the other tested RKN is observed. These data indicate that the *Ma1* gene and these putative latter genes are at least very closely linked: theoretically, recombination is lower than 0.75% (*M. javanica*), 0.99% (*M. incognita*) and 1.27% (*M.* sp. Floride). Corresponding recombination between *Ma2* (*M. arenaria*) and the putative genes controlling the other tested RKN, based on the 98 (2 species), 65 (3 species) and 37 (4 species) segregating clones, should be respectively less than 1.03% (*M. javanica*), 1.54% (*M. incognita*) and 2.71% (*M.* sp. Floride). When adding the information on the 19 (4 species) and 20 (3 species) clones of the G_2 cross segregating for both genes (Table 6), these maximal recombination values can again be reduced. Furthermore, the fact that no difference in resistance behaviour is observed among non-segregating material adds to the hypothesis that the *Ma* genes (*M. arenaria*) and the putative genes that control RKN

Table 8 Distribution of tested material in segregating and non segregating crosses for the *Ma1* and *Ma2* genes

Cross type		Numbers of clones evaluated to		
		A/J[a]	A/J/I[a]	A/J/I/F[a]
Segregating	*Ma1*	134	102	79
	Ma2	98	65	37
	Both	20	20	19
	Total	252	187	135
Non-segregating	*Ma2* alone	29	24	8
	Ma2 (+*Ma1*[b])	8	8	4
	None	30	30	14
	Total	67	62	26
Total material		319	249	161

[a] Total numbers of clones evaluated to *M. arenaria* and *M. javanica* (A/J), to *M. arenaria*, *M. javanica* and *M. incognita* (A/J/I), to *M. arenaria*, *M. javanica*, *M. incognita* and *M.* sp. FL (A/J/I/F)
[b] Cross P.2175 × P.1079 (see Table 6) that segregates for *Ma1*

resistance to the other tested species are either the same or else very closely linked. Thus, this complete correspondance between the responses of clones evaluated to one population of each of the predominant species, *M. arenaria*, *M. incognita* and *M. javanica*, and to *M.* sp. Floride indicates that resistance is independent of the RKN species and that the *Ma1* and *Ma2* genes for resistance to *M. arenaria* also control resistance to the other tested species. The spectrum of resistance of the clones P.2175 (*Ma1*) and P.1079 (*Ma2*) extends to all populations of the three predominant RKN species (at least the 6 *M. arenaria*, 15 *M. incognita*, and 10 *M. javanica* that have so far been tested). Considering that it also extends to the minor species *M. hapla* and to the *M.* sp. 'VSS' populations (Esmenjaud et al. 1994, 1997; Esmenjaud, unpublished) known for breaking resistance conferred by the *Mi* gene in tomato (Roberts et al. 1990), it is highly probable that the *Ma* resistance genes also control these two latter RKN species.

Another question is whether *Ma1* and *Ma2* are or are not allelic. Our data do not provide information on this issue. The test for allelism is hampered by the impossibility of performing a selfing step because of the self-incompatibility of Myrobalan plum. A molecular approach is therefore in progress to overcome this problem and to develop the marker-assisted selection that is particularly needed for perennials such as *Prunus* crops. Recent studies, based on bulked segregant analysis (BSA) (Michelmore et al. 1991) using RAPD markers, have indicated that both genes are either allelic or at least closely linked (Dirlewanger et al. 1996 b; Esmenjaud, unpublished).

Our data confirm that a minimum of two different genetic systems control resistance to RKN in *Prunus* species belonging to the subgenus *Amygdalus* (Esmenjaud et al. 1997). One can hypothesize that at least one system 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* (Table 2). In this rootstock, resistance is inherited from the parent *P. persica* 'Shalil' (Kester and Grasselly 1987; Weinberger et al. 1943). A second system also involves resistance to *M. javanica* in the rootstock 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. One can add to this the bitter almond rootstocks from the Alnem series for which a third genetic system is monogenic (dominant) and controls at least resistance *M. javanica* (Kochba and Spiegel-Roy 1975) but does not act against *M. incognita* (Scotto La Massese et al. 1984). Establishing the relationships between RKN resistance genes in *Prunus* will be facilitated by the data from the molecular mapping currently in progress for diverse *Prunus* species (Arus et al. 1994) and particularly peach (Chaparro et al. 1994; Dirlewanger et al. 1996b; Warburton et al. 1996), almond (Viruel et al. 1995) and peach-almond (Foolad et al. 1996).

Our data stress the value of introducing *Ma* genes into rootstock breeding programs (Salesses et al. 1994). Various interspecific hybrids between Myrobalan plum sources and *Amygdalus* material are being created and appear particularly promising in Mediterranean environments by accumulating numerous favourable agronomic features (Renaud et al. 1988; Salesses et al. 1992). Among these, the three-way interspecific hybrids between Myrobalan plum and the peach-almond G × N should have the widest agronomical adaptation. Obtaining information on the relationships between the RKN resistance genes of the Myrobalan-plum and Nemared sources will be very useful in the objective of keeping all the genes, particularly if they appear as non-allelic, in new rootstock material. The presence of pyramided genes will limit the risk of resistance breaking, which is theoretically higher for perennials (Roberts 1995) in which a durable resistance is particularly needed (Johnson 1983; Cook and Evans 1987). Actually, RKN are highly polyphagous and can reproduce on many weeds that are associated in the field with *Prunus* crops. These weeds are responsible for the maintenance of a high inoculum pressure for the entire crop duration and may facilitate the development of resistance breaking-populations.

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