Resistance in *Vitis* and *Muscadinia* Species to *Meloidogyne incognita*

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ABSTRACT

Walker, M. A., Ferris, H., and Eyre, M. 1994. Resistance in *Vitis* and *Muscadinia* species to *Meloidogyne incognita*. Plant Dis. 78:1055-1058.

Rootstocks resistant to root-knot nematodes are needed for wine, table, and raisin grape culture in California's San Joaquin Valley. As a first step in a breeding program, selections of the following species were screened for resistance to the root-knot nematode *Meloidogyne incognita*: 10 *Vitis acerifolia*, 2 *V. aestivalis*, 4 *V. berlandieri*, 4 *V. californica*, 7 *V. champinii*, 1 *V. cinerea*, 2 *V. labrusca*, 2 *V. riparia*, 1 *V. rufotomentosa*, 2 *V. rupestris*, and 11 *Muscadinia rotundifolia*. The rootstocks Freedom, Harmony, 1613 Couderc, and 1616 Couderc were used as standard resistant controls, and *V. vinifera* cvs. Cabernet Sauvignon, French Colombard, and Thompson Seedless were used as susceptible controls. Three replicates of each selection were inoculated with 1,000 second-stage juveniles; after 4 mo, numbers of second-stage juveniles hatching from egg masses and root weights were determined. Resistance was common in *M. rotundifolia*, but the difficulty in rooting this species from dormant cuttings and cytogenetic differences from *Vitis* species may limit its use in rootstock breeding. Promising sources of resistance were also found in *V. aestivalis*, *V. champinii*, *V. cinerea*, *V. rufotomentosa*, and *V. rupestris*.

Rootstocks are used to control, or limit damage caused by, root-knot nematodes (*Meloidogyne* spp.) in vineyards on the sandy soils of California's San Joaquin Valley (14,18). However, none of the available rootstocks is ideal across the range of viticultural situations encountered in the region. Most of the rootstocks induce high levels of vegetative vigor in scions grafted onto them, causing problems with berry coloration, bud fertility, and fruit quality. Grape rootstocks have been screened against a variety of aggressive root-knot nematode species and populations, both singly and in combinations, but all the rootstocks tested had problems with the breadth of their nematode resistance or with their viticultural characteristics (14; M. V. McKenry, *personal communication*). In addition, more aggressive populations of root-knot nematode have been discovered, such as the Harmony population of *M. arenaria* (Neal) Chitwood (6), that are capable of overcoming the resistance in currently used rootstocks. Nematicides also have been used to control root-knot nematodes, but the use of soil pesticides will probably be severely limited in the near future.

Given these problems, the need to breed new rootstocks with broad and durable resistance to grapevine-damaging nematode species is clear. The first step in such a breeding program is to assess the available germ plasm for resistance. *Muscadinia rotundifolia* Small has been reported to be resistant to *M. arenaria*, *M. incognita* (Kofoid & White) Chitwood, and *M. javanica* (Treub) Chitwood (3,13), but chromosomal differences from *Vitis* species and rooting difficulties make this species difficult to use in rootstock breeding. These problems prompted this screening of *Vitis* and *Muscadinia* species to identify sources of resistance to *M. incognita*.

MATERIALS AND METHODS

The *Vitis* and *Muscadinia* species and selections tested are listed in Table 1. These species are followed by University of California, Davis (UCD) Department of Viticulture and Enology identifiers: numbers 01 through 08 are UCD selection numbers, U28 numbers are UCD vineyard locations, numbers 1200 to 1900 are USDA National Germplasm Repository-Davis (NGR-D) accessions, and numbers above 7000 are introductions made by H. P. Olmo in 1970 and 1971. *V. vinifera* L. cultivars Cabernet Sauvignon, French Colombard, and Thompson Seedless were included as susceptible standards and the rootstocks 1613 Couderc (1613C), 1616 Couderc (1616C), Freedom, and Harmony were included as resistant standards.

Because of the large number of plants and the logistics of the nematode assay, the grapevines were propagated and tested in two phases. Herbaceous cuttings taken from clonal selections of the tested *Vitis* species were rooted under intermittent mist in flats of vermiculite and perlite (1:1) mix with 25 C bottom heat. Once rooted, they were potted in 6.5 × 25.5 cm Deepots (Stuewe & Sons, Inc., Corvallis, OR) filled with coarse sand and fir mulch (1:1). After 4 mo of growth, the potted plants were inoculated with nematodes. The first set of plants was rooted during July 1991, inoculated 7-14 November 1991, and sampled for nematode reproduction 5-21 March 1992. The second set of plants was propagated during May 1992, inoculated with nematodes on 21 September 1992, and sampled for nematode reproduction 13-17 January 1993.

Plants were grown in a greenhouse with a temperature range of 20-30 C and watered with an overhead sprinkler system set to operate for 2 min every other day. Plants were fertilized with pelletized

Accepted for publication 29 July 1994.

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slow-release 17-6-10 (N-P-K) plus micronutrient fertilizer. Shoots were pruned back to about six nodes about once a month.

The *M. incognita* isolate used for inoculum was obtained from greenhouse pot cultures maintained on tomato. It originated from a field used for a variety of row crops in the San Joaquin Valley of California. Second-stage juveniles were collected by placing 3-cm-long infected roots in a mist chamber and collecting hatched juveniles at 12-hr intervals. Collected nematodes were maintained in an incubator at 10 C for no more than 3 days, with air bubbled into the suspension, until sufficient nematodes had been collected for the number of plants to be tested. Each plant was inoculated by dispensing 10-ml aliquots containing about 1,000 second-stage juveniles into three holes 2.5–5.0 cm deep around the plant base. Each hole was covered with soil mix after inoculation.

Nematode reproduction was assessed by removing shoots at the soil level and separating roots from soil with a semiautomatic elutriator (5). Each root system was blotted dry and weighed, cut into approximately 3-cm lengths, and then placed in a mist chamber for 5 days. We estimate that about 50% of the viable eggs in egg masses attached to the root

Table 1. Reproduction of *Meloidogyne incognita* on *Vitis* and *Muscadinia* species

Species selection[y]	Selection number	Resistance class[z]	Mean no. of J2 nematodes collected (SD)	Mean log (1+*x*) transformation of nematode no.	Av. root weight (g)
V. acerifolia	1295	S	7,343 (12,607)	2.577	8.7
V. acerifolia	1296	S	9,995 (6,192)	3.92	10.8
V. acerifolia	1297	PR	987 (1,396)	1.996	7.9
V. acerifolia	1298	S	1,005 (1,738)	1.393	5
V. acerifolia	1299	PR	377 (651)	1.177	3.7
V. acerifolia	1396	PR	225 (390)	0.944	10.7
V. acerifolia	1397	S	3,214 (3,340)	3.19	7.9
V. acerifolia	1398	PR	322 (291)	1.786	14.1
V. acerifolia	1399	S	6,237 (6,924)	3.457	17.1
V. acerifolia	1400	PR	37 (58)	0.992	4
V. aestivalis	7034	R	3 (6)	0.347	10.5
V. aestivalis	7127	R	1 (2)	0.233	3.8
*V. berlandieri**	1590	S	20,418 (23,543)	3.107	11.4
*V. berlandieri**	1601	PR	500 (808)	1.665	8.7
*V. berlandieri**	1602	S	3,482 (4,611)	3.161	6.6
V. berlandieri	1639	S	5,988 (8,836)	2.993	5.7
V. californica	1275	R	19 (27)	0.851	10.2
V. californica	1836	S	4,351 (4,240)	2.762	20.0
V. californica	1837	R	1 (1)	0.159	4.2
V. californica	1838	S	1,129 (1,842)	2.255	8.3
V. champinii	1279	R	1 (1)	0.161	7.3
V. champinii	1388	PR	423 (503)	2.242	7.6
V. champinii	1588	R	0	0	11.8
V. champinii	1646	R	3 (5)	0.318	7.3
V. champinii	1836	R	7 (9)	0.659	7.4
V. champinii Dog Ridge	03	R	1 (2)	0.233	8.7
V. champinii Ramsey	1A	R	3 (5)	0.318	9.6
V. cinerea	1284	R	1 (1)	0.159	14.5
V. labrusca	1391	S	15,029 (25,609)	3.124	12.2
V. labrusca	1393	S	1,326 (1,427)	2.17	10.1
V. riparia	1438	PR	148 (241)	1.303	10.4
V. riparia	1448	PR	129 (87)	2.046	13.0
V. rufotomentosa	1416	R	3 (6)	0.347	5.1
V. rupestris	1406	S	4,920 (6,036)	3.39	8.0
V. rupestris	1595	R	3 (3)	0.441	5.0
M. rotundifolia Creswell*	U28:1	R	1 (1)	0.159	6.9
M. rotundifolia Hunt*	U28:3	R	9 (10)	0.759	6.7
M. rotundifolia Irene*	U28:4	R	3 (2)	0.466	9.5
M. rotundifolia James*	U28:5	R	3 (3)	0.441	6.3
M. rotundifolia LaSalle*	U28:6	R	0	0	7.3
M. rotundifolia Magoon*	U28:8	R	1 (1)	0.159	6.6
M. rotundifolia November*	U28:10	R	0	0	10.3
M. rotundifolia Onslow*	U28:11	R	0	0	6.5
M. rotundifolia Pride*	U28:12	R	0	0	7.3
M. rotundifolia San Jacinto*	U28:14	R	2 (2)	0.392	6.1
M. rotundifolia Thomas*	U28:15	R	0	0	11.8
Susceptible controls					
V. vinifera Cabernet Sauvignon	08	S	22,192 (13,046)	4.291	12.5
V. vinifera French Colombard	04	S	21,650 (26,904)	3.717	12.0
V. vinifera Thompson Seedless	02A	S	2,417 (1,925)	3.191	30.2
Resistant controls					
1613 Couderc	02A	R	16 (20)	0.877	23.4
1616 Couderc	02	PR	66 (54)	1.603	19.0
Freedom	01	R	1 (2)	0.233	7.2
Harmony	01	R	4 (7)	0.371	13.0

[y] * = Selections from the second phase of testing.

[z] R = resistant, 0–20 juveniles detected; PR = partially resistant, >20–1,000 detected; and S = susceptible, >1,000 detected.

hatch during that time interval. Second-stage juveniles hatching from eggs were collected and counted.

The tested plants were separated into the following classes based on the number of second-stage juveniles recorded per root system: resistant = 0–20 juveniles, partially resistant = >20–1,000 juveniles, and susceptible = >1,000 juveniles. Because the treatment standard deviations were often proportional to the treatment means, a log $(1+x)$ transformation of the data was performed prior to analysis of variance.

RESULTS AND DISCUSSION

Table 1 presents the species selections and rootstocks tested in the order in which they will be discussed. Nematode reproduction was often variable among the replicates of a given species selection, as indicated by the large standard deviations reported with the means. Table 2 presents the mean rankings of the log-transformed data following a highly significant analysis of variance ($P = 0.0001$) and mean separations with Fisher's protected LSD ($\alpha = 0.05$). The results are discussed within each species tested.

V. solonis Hort. Berol. ex Planch. is presumed to be the basis of the root-knot resistant rootstocks 1613C (*V. solonis* × 'Othello' ('Clinton' (*V. riparia* Michx. × *V. labrusca* L.) × *V. vinifera* 'Muscat Hamburg')) and 1616C (*V. solonis* × *V. riparia*), although the *Meloidogyne* sp. was not specified in original reports (14,16). Lider (13) found *V. solonis* to be resistant to *M. incognita* var. *acrita* at 17 of 19 sites but susceptible at the other two. *V. solonis* is considered to be a synonym for *V. longii* Prince (1,12), which is now considered to be *V. acerifolia*. Because of earlier reports of *M. i. acrita* resistance in *V. solonis* (13) and its presence in the parentage of 1613C and 1616C, we tested 10 selections of *V. acerifolia*. However, none of the *V. acerifolia* selections tested greatly suppressed *M. incognita* reproduction, and some allowed high levels of reproduction (Table 1). *V. acerifolia* seems to be a poor choice as a parent for the production of *M. incognita*-resistant rootstocks.

V. aestivalis Michx. is a wide-ranging and complex taxon found from Texas to the southern Atlantic states. The *V. aestivalis* selections tested in this study were difficult to propagate, and once rooted, they were difficult to cultivate in containers, which may hinder their use as rootstocks. Of the 11 selections attempted, only two had sufficient replications to report. Both of these greatly suppressed *M. incognita* reproduction. *V. rufotomentosa* Small also greatly suppressed *M. incognita* reproduction. The results for *V. rufotomentosa*, a species that has been described within *V. aestivalis* (7,17), are interesting because this accession is reported to suppress reproduction of *Xiphinema index* Thorne & Allen, the dagger nematode vector of grapevine fanleaf virus (11).

V. berlandieri Planch. is a species from central and southwestern Texas and northeastern Mexico. Lider (13) tested selection 1273 (his selection 3602) for resistance to *M. i. acrita* and found that it ranged from very susceptible to resistant at different test sites. Such differences may have been due to root-knot nematode populations that varied in aggressiveness. Selection 1601 suppressed *M. incognita* reproduction but was not considered resistant. *V. berlandieri* was chosen for this study because of reports of *Meloidogyne* spp. resistance in rootstocks with *V. berlandieri* × *V. riparia* parentage, including Teleki 5C, SO4, and Kober 5BB (16; M. V. McKenry, *personal communication*). However, three of the *V. berlandieri* selections supported high levels of *M. incognita* reproduction. Some of this variability within *V. berlandieri* may be due to taxonomic misidentification and inclusion of off-types or hybrids within this taxon (1).

V. californica Benth. grows near streams along many vineyards in coastal and central California. Selections 1836 and 1838 supported high levels of *M. incognita* reproduction, which suggests that they may serve as a reservoir for *M. incognita* on the border of vineyards. Selection 1837 greatly suppressed nematode reproduction and may be useful in breeding.

Six of the seven selections of *V. champinii* Planch. greatly suppressed *M. incognita* reproduction, and 1588 did not support any reproduction. Selection 1388 has been used in crosses designed to produce rootstocks resistant to a range of nematodes, but results from this screen caution against its use for *M. incognita* resistance. Dog Ridge and Ramsey have been used in California and Australia as rootstocks resistant to *Meloidogyne* spp. In our study, only one replication each of Dog Ridge and Ramsey supported any nematode reproduction. However, they are vigorous rootstocks for use in coarse-textured soils with poor fertility, and the high vegetative vigor they induce leads to problems with berry coloration and bud fertility. Selection 1279 greatly suppressed *M. incognita* reproduction in the present study. However, Lider (13) found selection 1279 (his selection 3639) to be susceptible at two of 13 sites.

The one selection of *V. cinerea* Engelm. ex Millard. tested suppressed nematode reproduction. This species also has strong resistance to grape phylloxera (*Daktulosphaira vitifoliae* (Fitch)) (2,4,19). Selection 1284 propagates well, in contrast to other *V. cinerea*, and may serve as an excellent parent for rootstock breeding.

V. labrusca was tested in this study because it was suspected to be highly susceptible. Lider (13) reported that selection 1391 (his selection 3632) was susceptible to *M. i. acrita*, and it was susceptible to *M. incognita* in our study. Selection 1393 also was a very good host.

V. riparia is in the parentage of the standard resistant rootstocks 1613C and 1616C, in addition to Teleki 5C, SO4, and Kober 5BB. The two selections tested in this study did not suppress nematode reproduction. Dormant cuttings of *V. riparia* root easily. If a source of resistance to root-knot nematode could be

Table 2. Rankings (low to high) of the species selections based on the means of the log $(1+x)$ transformed nematode reproduction data

Species selection[z]	
M. rotundifolia LaSalle	a
V. champinii 1588	a
M. rotundifolia November	a
M. rotundifolia Onslow	a
M. rotundifolia Pride	a
M. rotundifolia Thomas	a
M. rotundifolia Creswell	ab
V. cinerea 1284	ab
V. californica 1837	ab
M. rotundifolia Magoon	ab
V. champinii 1279	ab
Freedom	abc
Dog Ridge	abc
V. aestivalis 7127	abc
V. champinii 1646	abc
Ramsey	abc
V. aestivalis 7034	abc
V. rufotomentosa	abc
Harmony	abc
M. rotundifolia San Jacinto	abc
V. rupestris 1595	abcd
M. rotundifolia James	abcd
M. rotundifolia Irene	abcd
V. champinii 1836	abcde
M. rotundifolia Hunt	abcdef
V. californica 1275	abcdef
1613 Couderc	abcdef
V. acerifolia 1396	abcdef
V. acerifolia 1400	abcdef
V. acerifolia 1299	abcdefg
V. riparia 1438	abcdefgh
V. acerifolia 1298	abcdefgh
1616 Couderc	bcdefghi
V. berlandieri 1601	bcdefghi
V. acerifolia 1398	cdefghij
V. acerifolia 1297	defghijk
V. riparia 1448	efghijk
V. labrusca 1393	efghijkl
V. champinii 1388	fghijkl
V. californica 1838	fghijkl
V. acerifolia 1295	ghijklm
V. californica 1836	hijklmn
V. berlandieri 1639	ijklmn
V. berlandieri 1590	ijklmn
V. labrusca 1391	ijklmn
V. berlandieri 1602	jklmn
V. acerifolia 1397	jklmn
Thompson Seedless	jklmn
V. rupestris 1406	klmn
V. acerifolia 1399	klmn
French Colombard	lmn
V. acerifolia 1296	mn
Cabernet Sauvignon	n

[z] Analysis of variance among the species selections was highly significant ($P < 0.0001$). Selections followed by the same letter are not significantly different according to Fisher's protected LSD ($\alpha = 0.05$).

found within *V. riparia* it would find immediate use as a parent in crosses with species that are resistant to *M. incognita* but root poorly.

Susceptibility of *V. rupestris* Scheele selection 1406 (Rupestris St. George) to *M. incognita* (13) was confirmed in the present study. Selection 1595 (Rupestris A. de Serres), which was highly resistant in our study, has been used in a number of crosses in the UCD rootstock breeding program because it is one of the few *V. rupestris* females in the collection. The high level of resistance to *M. incognita* and the ability to root easily from dormant cuttings make selection 1595 a useful parent in the rootstock breeding program.

All of the *M. rotundifolia* selections greatly suppressed *M. incognita* reproduction (Table 1), confirming earlier reports of resistance (3,13). However, *M. rotundifolia* is very difficult to use in a rootstock breeding program; it has clusters with few flowers, blooms much later than most *Vitis* species, and does not produce many viable seeds in crosses. In addition, *Muscadinia* and *Vitis* do not share complete chromosome homology, which may account for the poor success of intergeneric crosses (15).

Thompson Seedless has been reported to be tolerant of parasitism by *M. arenaria*, compared with other *V. vinifera* cultivars (8–10). In the present study, Thompson Seedless suppressed *M. incognita* reproduction to about 10% of the levels detected on Cabernet Sauvignon and French Colombard.

Freedom, Harmony, 1613C, and 1616C all suppressed *M. incognita* reproduction (Table 1). However, there are problems, or potential problems, with all of these rootstocks. For example, 1613C induces excessive vigor in scions and its one-fourth *V. vinifera* parentage weakens its resistance to phylloxera, and 1616C lacks the level of vigor induction needed for the typically coarse-textured soils *M. incognita* inhabits. Freedom and Harmony both induce vigor in scions but have at least one-eighth *V. vinifera* in their parentage, which weakens their *M. incognita* resistance and casts doubt on their long-term resistance to phylloxera. In addition, the long-term use of Freedom and Harmony is questionable in light of the discovery of the damaging Harmony population of *M. arenaria.*

M. incognita resistance sources have been identified, particularly in *V. champinii* and also in *V. aestivalis, V. cinerea, V. rufotomentosa*, and *V. rupestris*. Tolerance to *M. incognita* feeding may also exist, but this resistance screen was not designed to measure the effects of root-knot nematode parasitism on plant vigor. Sources of tolerance to *M. incognita* parasitism would also be valuable for rootstock breeding.

ACKNOWLEDGMENTS

We thank the American Vineyard Foundation, the California Raisin Advisory Board, and the California Table Grape Commission for funding for this project.

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