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Resistance of Grape Rootstocks to Plant-parasitic Nematodes

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Abstract: Candidate grape rootstocks were selected through a rigorous screening program initiated with important sources of resistance to *Meloidogyne* pathotypes and to *Xiphinema index* in *Muscadinia rotundifolia* and *Vitis* species native to North America. Based on their rooting capability and horticultural characteristics, 200 candidates were selected from 5,000 progeny of multiple crosses between commercial grape rootstocks and wild grape species that exhibited resistance to nematodes. After a 15-year screening process, 13 selections emerged with either almost complete or complete combined resistance to *M. incognita* Race 3, *M. incognita* pathotype Harmony C, *M. arenaria* pathotype Harmony A, and *X. index*, important nematode pests of grapevines. Durability of this broad resistance was tested by challenging the selections with the target nematodes in combination and with the target nematodes in combinations with species not included in the screening process. Durability of resistance of the candidate rootstocks was also tested by exposure to the nematode communities of infested field soils from different locations. Breadth of resistance was determined on the basis of their host status to non-target nematodes, including *Mesocriconema xenoplax*, *Pratylenchus vulnus*, *Tylenchulus semipenetrans* and *Paratylenchus hamatus*. After a total of 204 separate trials, the rootstocks were released to the grape industry as UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4, and UCD GRN5. We provide a compilation of current knowledge of the host status of these five newly released rootstocks and of 27 other rootstock cultivars to plant-parasitic nematodes.

Key words: Screening, selection, host status, broad resistance, durable resistance.

Rootstocks have been used in viticulture to protect against soil pests for 150 years (Reisch et al., 2012). Besides the root aphid, grape phylloxera, plant-parasitic nematodes are the primary soil-borne pest of grapevines (Nicol et al., 1999). Rootstocks available for grapevines differ in their susceptibility to nematodes. Important characteristics in the selection of rootstocks are that they should be easily propagated, graft compatible with scion varieties and adapted to a range of soil conditions (Reisch et al., 2012). Although rootstocks derived from interspecies crosses within *Vitis* were screened for resistance to root-knot nematodes in early studies, the *V. champinii* cultivars Ramsey (of which Salt Creek is an incorrect synonym) and Dog Ridge, emerged as exhibiting durable resistance to root-knot nematodes. In summary, sources of resistance to *Meloidogyne incognita* have been reported in *V. aestivalis*, *V. champinii*, *V. cinerea*, *V. mustangensis* (syn. *V. candicans*), *V. rupestris* and *Muscadinia rotundifolia* and to *Xiphinema index* in *V. arizonica*, *V. candicans*, *V. rufotomentosa* and *M. rotundifolia* (Snyder, 1936; Lider, 1954; Lider, 1959b; Lider 1959a, 1960; Kasimatis and Lider, 1967; Nesbitt, 1974; Bloodworth et al., 1980; Harris, 1984; Walker et al., 1994; Cousins et al., 2003).

The cultivars Harmony and Freedom, derived from complex crosses among *V. champinii, V. longii, V. vinífera, V. riparia* and *V. labrusca*, were the first root-knot nematode resistant rootstocks to emerge from a formal breeding program (Brooks and Olmo, 1997; Garris et al., 2009; Weinberger and Harmon, 1966; Reisch et al., 2012). Recognition of the importance of *M. rotundifolia*, native to the southeastern US, as a source of genes conferring resistance to several pest and disease organisms (Olmo, 1986) spurred breeders to explore interspecies crosses. Some of those crosses resulted in VR O39-16 and VR O43-43, resistant to *X. index* and tolerant to fanleaf degeneration, the virus disease vectored by this nematode (Hewitt et al., 1958; Lider et al., 1988a,b; Walker et al., 1985; 1989; 1991). In general, rootstocks have not been developed or selected for resistance to more than one nematode species. More recently, resistant rootstocks USDA 10-17A, USDA 10-23B, USDA 6-19B, RS-3 and RS-9, which exhibit resistance to more than one species, have been developed and released (Anwar et al., 2002; Gu and Ramming, 2005a,b). Rootstocks differ in the vigor they confer on the grafted scions. Some have horticultural characteristics that make them valuable for specific soil and climatic situations but render them less suitable for more general usage (Lider, 1959a; Lider, 1960; Lider et al., 1965; Olmo, 1986).

A wide diversity of plant-parasitic nematodes has been documented from California vineyards. Besides several species of root-knot nematode, two species of *Xiphinema* (dagger nematodes), *Pratylenchus vulnus* (root-lesion nematode), *Mesocriconema xenoplax* (ring nematode), *Tylenchulus semipenetrans* (citrus nematode), and *Paratylenchus* spp. (pin nematodes) occur commonly (Raski and Lider, 1959; Siddiqui et al., 1973; Pinkerton et al. 2005; Pinochet et al., 1976; Ferris and McKenry, 1976). Additionally, the selection pressure resulting from wide usage of Harmony rootstock has resulted in the emergence of virulent pathotypes of *M. incognita* and *M. arenaria* (Cain et al., 1984; Anwar and McKenry, 2002a; Esmenjaud and Bouquet, 2009; McKenry, 1992). Similar virulent pathotypes have been selected by the closely-related Freedom rootstock (Anwar et al., 1999).

Over a 15-year period, in 204 separate experiments, we have screened and tested species of *Vitis*, and progeny of crosses among *Vitis* species and between *Vitis* and *Muscadinia* species, to determine their suitability in providing grape rootstocks with broad and durable resistance to important plant-parasitic nematode pests of California vineyards. Herein we document the

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development, selection and characteristics of five new grape rootstocks with broad and durable nematode resistance and with a range of horticultural characteristics targeted at four general grape-growing regions of California: a) the North Coast with its areas of *X. index* and nematode-transmitted grapevine fanleaf virus; b) the northern San Joaquin Valley, where pressures are experienced from *Meloidogyne* spp., *X. index* and fanleaf virus, and other nematode pests, including ring, citrus and root-lesion nematodes; c) the central coast regions with *X. index,* root-knot and ring nematodes; and d) the central and southern San Joaquin Valley and the Coachella Valley with nematode pressures from the root-knot nematode complexes, ring, root lesion, citrus and other nematodes (Raski and Lider, 1959; Ferris and McKenry, 1976).

During the course of developing and testing the new rootstocks we included a large number of existing rootstocks in our studies for comparative purposes and in order to evaluate their host status to nematodes under standardized conditions. We provide a summary of their host status to nematodes. In parallel studies, the genetics and heritability of resistance have been elucidated in some rootstock candidates and their parents. It appears that resistance to the *Meloidogyne* strains can be explained by a single dominant gene (Cousins and Walker, 2002; Cousins et al., 2003; Lowe and Walker, 2006).

Materials and Methods

Sources, crosses and selection of plant genotypes: A wide range of grape species and rootstock breeding selections was available from past collecting and plant breeding activities of H.P. Olmo and L.A. Lider of the Department of Viticulture and Enology at the University of California, Davis. Some of this germplasm had been characterized as nematode resistant by Olmo, Lider and colleagues (Patel and Olmo, 1955; Lider, 1960; Kunde et al., 1968; Olmo, 1986; Walker et al., 1994; Walker 2009a). The material was available to the grape rootstock breeding program initiated by Walker in 1990 (Walker 2009a) and selections reported as resistant were crossed with *V. riparia* and *V. rupestris* to improve their rooting ability. In a strategically-designed breeding and selection program, 200 candidates were selected from the 5,000 progeny of the various crosses based on their vigor, growth habit and rooting ability. Then, a two-channel assay protocol was initiated (Fig. 1). In one channel, selections purportedly originating from *V. rupestris* x *M. rotundifolia* crosses, many of which were later found to be products of other crosses (Riaz et al., 2007), were first screened for resistance to *X. index*. Those without root-tip galling were screened for resistance to *M. incognita* Race 3 and those without galls or egg masses graduated to screening against two virulent *Meloidogyne* strains (*M. arenaria* pathotype Harmony A and *M. incognita* pathotype Harmony C). One rootstock candidate graduated from the channel. In the second channel, selections of crosses designed to provide resistance to *Meloidogyne* spp. were screened first against *M. incognita* Race 3 and then *X. index* followed by the two virulent *Meloidogyne* pathotypes. There were 12 graduates from that channel.

In the final nematode assay phase, the 13 rootstock candidates were subjected to a series of advanced screening tests. They were challenged by the *Meloidogyne* variants and *X. index* in combination; eight showed minor galling or root tip swelling and were eliminated, five were free of symptoms. The five remaining candidates were screened for durability of resistance to the *Meloidogyne* and *Xiphinema* species when in combination with nematodes not included in the selection process, including *M. xenoplax*, *P. vulnus*, and *T. semipenetrans*. Finally, tests were conducted in naturally infested field soil from different locations. In parallel experiments, the effect of soil temperature on durability of resistance was determined. Failure at any step resulted in elimination from the selection process. All five rootstock candidates emerged successfully from this series of tests (Table 1). The final selections were tested for their ability to support grape phylloxera on the young root tips. The number of phylloxera eggs, juveniles and root-tip galls over a 21-day period were compared to commercial rootstocks using an excised root assay (Granett et al., 2001).

Screening process for host status to nematodes: Our basic protocol for all nematode screening was to establish rooted cuttings in 10-cm square plastic pots and then inoculate the soil with either 500 or 1,000 individuals of the test nematode. After 3 months, the aboveground portion of the vine was removed and weighed. In the case of ectoparasites and migratory endoparasites, nematodes were extracted from the soil either by a modified decanting and Baermann technique or decanting followed by sugar centrifugation (Barker, 1985) and then counted. For *Meloidogyne* spp., roots were stained with $0.1 gL^{-1}$ erioglaucine to facilitate counting of egg masses (Omwega et al., 1988) while for *X. index*, number of root tip galls was determined. Root dry weights were determined after heating at 85°C for 24 hours. That enabled us to assess impact of the nematodes on root vigor and also to normalize across differences in root size and vigor by expressing nematode numbers or symptoms on a per g root basis. Controls in all experiments included susceptible cultivars, usually *V. vinifera* cv Colombard, *V. rupestris* cv St. George, and a cultivar designated as resistant, cv Harmony. In each case, numbers of nematodes, egg masses or root tip galls on a selection were expressed as a percentage of those on the susceptible cv Colombard control in the same trial. That allowed comparison of results across trials. Our criteria for resistance levels of the selections relative to cv Colombard were $<10\%$ = resistant, 10 to $<30\%$ = moderately resistant, 30 to 50% = moderately susceptible, $>50\%$ = susceptible.

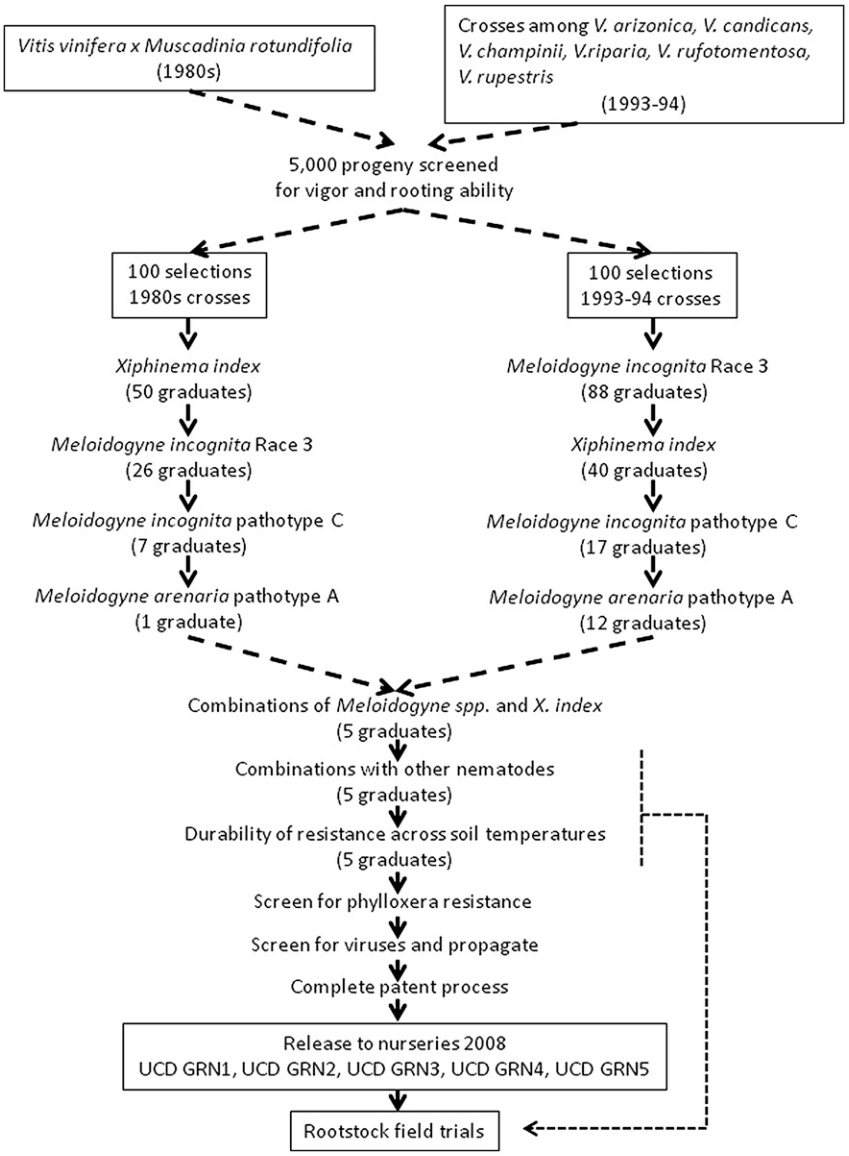


FIG. 1. The succession of events in creating hybrid progeny of interspecies crosses among *Vitis* and *Muscadinia* species, and the sequence of screening and testing that has resulted in the release of five rootstocks with broad and durable resistance to nematodes.

In the screening process we frequently faced the challenge of developing rooted cuttings at similar development states from genetically different material, originating as either dormant wood or herbaceous shoots, at a time coinciding with the availability of nematode inoculum. Sometimes one or more genotypes were not ready at the same time as the majority and were omitted from the test. Consequently, screening tests were often repeated several times with the number of available genotypes varying. The inclusion of susceptible and resistant controls in every test allowed us to rate nematode reproduction on each rootstock selection relative to that on the susceptible controls and thus to compare resistance and susceptibility across several trials. The resistant control is particularly important to ensure that the identity and virulence of *Meloidogyne* pathotypes has not been compromised.

Host status of parental genotypes: To further understand the breadth, durability and sources of the resistance to nematodes expressed in the UCD GRN rootstocks, we tested the host status of their parent species and crosses to *M. incognita* Race 3 and to the virulent *Meloidogyne* pathotypes. The parentage of the rootstocks is detailed in the footnote of Fig 2. The final crosses that resulted in the five successful rootstocks were: UCD-GRN1 = *V. rupestris* cv A.de Serres x *M. rotundifolia* cv Cowart; UCD-GRN2 = L514-30 x *V. riparia* cv Riparia Gloire; UCD-GRN3 = L514-10 x *V. champinii* cv c9038; UCD-GRN4 = L514-10 x *V. champinii* cv c9038; UCD-GRN5 = L6-1 x *V. champinii* cv c9021.

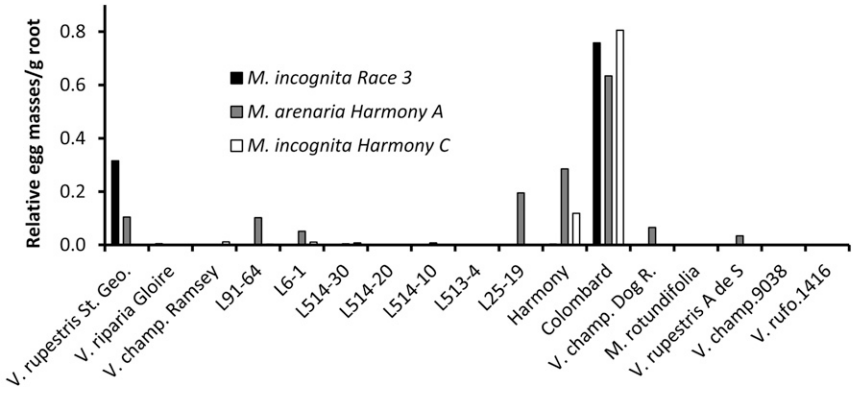
Nematode population diversity tests: Resistant rootstocks function as probes to reveal the inherent variability of nematode populations. The rootstock candidates were all selected by screening against known and characterized

TABLE 1. Resistance status of UCD GRN series rootstocks to plant-parasitic nematodes.

Rootstock	Parentage	Mi	MaA	MiC	Xi	Pv	Cx	Ts	Pah
UCD GRN1	*V. rupestris* cv A. de Serres, *M. rotundifolia* cv Cowart	R	R	R	R	MR	R	R	MR
UCD GRN2	*V. rufotomentosa, V. champinii* cv Dog Ridge, *V. riparia* cv Riparia Gloire	R	R	R	R	MR	MS	MS	MR
UCD GRN3	*V. rufotomentosa, V. champinii cv* Dog Ridge), *V. champinii* cv c9038, *V. riparia* cv Riparia Gloire	R	R	R	R	MR	MR	MR	MR
UCD GRN4	*V. rufotomentosa, V. champinii cv* Dog Ridge), *V. champinii* cv c9038, *V. riparia* cv Riparia Gloire	R	R	R	R	MR	MR	MR	MS
UCD GRN5	*V. champinii* cv Ramsey, *V. champinii* cv c9021), *V. riparia* cv Riparia Gloire	R	R	R	R	MR	R	MR	MR

Mi = root-knot nematode *Meloidogyne incognita* Race 3.
MaA = root-knot nematode *Meloidogyne arenaria* pathotype Harmony A, virulent on Harmony rootstock.
MiC = root-knot nematode *Meloidogyne incognita* pathotype Harmony C, virulent on Harmony rootstock.
Xi = dagger nematode *Xiphinema index*.
Pv = root lesion nematode *Pratylenchus vulnus*.
Cx = ring nematode *Mesocriconema xenoplax*.
Ts = citrus nematode *Tylenchulus semipenetrans*.
Pah = pin nematode *Paratylenchus hamatus*.
Resistance assessed relative to nematode reproduction on cv Colombard:
R <10% (resistant), MR 10-30% (moderately resistant), MS 30-50% (moderately susceptible), S >50% (susceptible).

populations of each nematode species maintained in greenhouse culture. The diversity of virulence and physiological characteristics among populations of nematodes of the same nominal species is becoming increasingly apparent. For example, differences in virulence in populations of *Meloidogyne*, *Mesocriconema* and other nematodes from different locations are well documented (Anwar et al., 2000; Peng and Moens, 2003; Pinkerton et al, 2005; McKenry and Anwar, 2006). To test the durability of their resistance to nematodes of



V. rupestris St. Geo = *V. rupestris* cv St. George
V. riparia Gloire = *V. riparia* cv Riparia Gloire
V. champ. Ramsey = *V. champinii* cv Ramsey
L91-64 = *V. riparia* cv Riparia Gloire x *V. candicans* cv 3642
L6-1 = (*V. riparia* cv Riparia Gloire x *V. champinii* cv Ramsey) x (*V. riparia* cv Riparia Gloire x *V. champinii* cv Ramsey)
L514-30 = *V. rufotomentosa* x (*V. riparia* cv Riparia Gloire x *V. champinii* cv Dog Ridge
L514-20 = *V. rufotomentosa* x (*V. riparia* cv Riparia Gloire x *V. champinii* cv Dog Ridge)
L514-10 = *V. rufotomentosa* x (*V. riparia* cv Riparia Gloire x *V. champinii* cv Dog Ridge)
L513-4 = *V. rufotomentosa* x *V. riparia* cv Riparia Gloire
L25-19 = *V. champinii* cv 3639) x (*V. riparia* cv Riparia Gloire x *V. champinii* cv Ramsey)
V. champ. Dog R. = *V. champinii* cv Dog Ridge
M. rotundifolia = *M. rotundifolia* cv Cowart
V. rupestris A de S = *V. rupestris* cv A. de Serres
V. champ. 9038 = *V. champinii* cv c9038
V. rufo. 1416 = *V. rufotomentosa* cv 1416

FIG. 2. Relative numbers of egg masses/g root (in relation to the maximum observed on cv Colombard) on parent genotypes of the UCD-GRN rootstocks after 3 months of exposure to *Xiphinema index*, *Meloidogyne incognita* race 3, *M. arenaria* pathotype Harmony A and *M. incognita* pathotype Harmony C. Data are means of two experiments for *M. incognita* race 3 and *M. arenaria* pathotype Harmony A, one for *M. incognita* pathotype Harmony C across a range of soil temperatures.

the same nominal species but with potentially different virulence characteristics, we screened advanced rootstock candidates in field soils from different locations known to be heavily infested with the target nematodes. The same three month exposure and evaluation processes were used as in our routine screening, with the exception that the nematodes were challenged at the population levels extant in the individual soils. In other experiments, we tested the reproduction and survival of ring nematode populations from five field locations on a range of rootstock genotypes.

Results

Breadth of resistance: The five successful rootstock candidates with broad and durable resistance to *Meloidogyne* spp. and *X. index* were screened in separate trials for their host status to *M. xenoplax*, *P. vulnus*, *T. semipenetrans*, and *Paratylenchus hamatus*, allowing us to document an extended host status profile for each (Table 1). The resistance expressed by the UCD-GRN series rootstocks was consistent with that of parent material (Fig. 2).

Durability of resistance – mixed inoculations: As an example of several experiments, we present data on the resistance to *X. index*, *M. incognita* pathotype Harmony C, *M. arenaria* pathotype Harmony A when rootstocks are exposed to the three nematodes in combination (Table 2). The resistance of the UCD-GRN series was not compromised by the combined exposure. The resistance to *X. index* was not compromised by simultaneous exposure to *M. xenoplax* (Table 3) or other non-target species (data not shown). In other experiments, there were no galls or egg masses on the roots of the UCD-GRN series rootstocks when they were exposed to *M. incognita* race 3, the virulent Harmony pathotypes and either *M. xenoplax* or *T. semipenetrans* (data not shown). Further, population levels of *M. xenoplax* were significantly lower on the UCD-GRN rootstocks than on either Harmony or cv Colombard after 3 months of exposure. Also, resistance to several populations of *M. incognita* and *M. arenaria* was not affected by increase in nematode density from 1,500 to 10,000 per pot (data not shown).

Durability of resistance - nematode population diversity tests: Resident root-knot nematode populations in three selected vineyard soils were virulent on the susceptible *V. vinifera* cv Colombard and *V. rupestris* cv St. George genotypes. The population from one field was also virulent on the root-knot resistant Harmony rootstock. Resistance levels of the five UCD-GRN rootstocks were high in each soil (Table 4). In a few cases we recorded a single suspected egg mass based on our root staining technique. In some of the soils exposed to our resistant rootstocks, juveniles were detected at termination of the three month experiment. We believe, although we cannot be certain, that those juveniles either survived from the initial population or hatched from egg masses present in the soil at initiation of the experiments.

Population levels of ring nematode were extremely high in soils from the three sites, especially in soil from field A (Table 4). After 3 months of exposure, population levels on *V. rupestris* cv St. George were lower

Table 2. Durability of nematode resistance in rootstocks after 3 months of exposure to *Xiphinema index*, *Meloidogyne arenaria* pathotype Harmony A and *M. incognita* pathotype Harmony C in combination.

	Xiphinema index	*Meloidogyne* spp.
Genotype	Root tip galls/g root	Egg masses/g root
101-14Mgt	108.8 a	0 c
Colombard	1.0 c	41 a
Dog Ridge	2.7 c	2 c
Freedom	0 c	17 b
Harmony	0.4 c	23 b
Ramsey	0.3 c	2 c
RS-3	6.0 c	4 c
RS-9	88.8 a	0 c
St. George	41.5 b	6 c
UCD-GRN1	0 c	0 c
UCD-GRN2	0.1 c	0 c
UCD-GRN3	0.1 c	0 c
UCD-GRN4	0 c	0 c
UCD-GRN5	0 c	0 c

In each column, numbers followed by the same letter do not differ significantly.

Table 3. Durability of resistance to *Xiphinema index* in the presence of *Criconemodes xenoplax* after 3 months of exposure.

	Xiphinema index	*Mesocriconema xenoplax*
Genotype	Root tip galls/g root	nematodes/g root
UCD-GRN4	0 a	1466 a
UCD-GRN3	0 a	1572 a
UCD-GRN5	0 a	1684 a
UCD-GRN1	0 a	3126 ab
UCD-GRN2	0 a	3505 b
Harmony	0 a	3761 b
Freedom	0 a	5468 c
Colombard	4 b	2134 ab
AxR1	8 c	6046 c
St. George	9 c	2378 ab

In each column, numbers followed by the same letter do not differ significantly.

Table 4. Number of egg masses of *Meloidogyne* spp. and individuals of *Mesocriconema xenoplax* after three months exposure of new rootstocks and selected controls in soils of three different vineyards (A, B, C).

	Meloidogyne egg masses/g root			*Mesocriconema xenoplax* (x100)/g root		
Genotype	A	B	C	A	B	C
Colombard	69 a	90 a	75 a	118.6 x	43.8 y	25.0 x
Harmony	31 b	0 c	3 c	375.7 v	70.1 x	36.0 w
V. rupestris St. George	10 c	26 b	16 b	26.3 z	9.6 z	12.5 y
UCD GRN4	1 d	0 c	1 c	83.5 y	66.3 xy	48.7 v
UCD GRN1	0 d	0 c	0 c	9.3 z	0.3 z	0.2 z
UCD GRN2	0 d	0 c	1 c	132.5 x	52.4 xy	47.8 v
UCD GRN3	0 d	0 c	0 c	242.6 w	49.7 xy	15.7 xy
UCD GRN5	0 d	0 c	0 c	20.4 z	0.3 z	0.7 z

In each column, numbers followed by the same letter do not differ significantly.

than on the other controls, but lowest population levels were on rootstocks UCD GRN1, with *M. rotundifolia* parentage, and UCD GRN5, which does not have *M. rotundifolia* parentage. As a caveat, UCD GRN5 has lower root mass in fine-textured soils, which may have affected reproduction of the nematode. When four genotypes, two designated as susceptible and two designated as resistant, were tested against ring nematode populations from five locations, the populations differed in virulence, as indicated by their reproduction on susceptible rootstocks. However, rootstocks UCD-GRN1 and VR O39-16 were consistently resistant to all populations of the nematode (Table 5,6).

Further evaluation of new rootstocks: In the excised root assay (Granett et al., 2001), two of the new rootstocks, UCD GRN1, UCD GRN2 were very resistant to grape phylloxera, two, UCD GRN3, UCD GRN4, were moderately resistant, and one, UCD GRN5, was susceptible at a level similar to that of *V. rupestris* cv St. George and 101-14 Mgt rootstocks. In phylloxera-resistant rootstocks, feeding may occur on young root tips but is prevented in more mature roots that have a developed periderm layer.

Prior to release to nurseries the UCD GRN series rootstocks were subjected to a complete virus and disease testing by Foundation Plant Services at UC Davis. That qualified them for registration in the California Department of Food and Agriculture Registration and Certification Program for Grapevines. In the spring of 2008, mist-propagated plants were released to UC-licensed Registration and Certification Program participant nurseries (Covert, 2008). Thus, after a 15-year sequence of intensive studies involving 204 separate trials, the five rootstocks with broad and durable resistance to root-knot and dagger nematodes, UCD-GRN1-5 (Table 1) were patented and released to nurseries for propagation and thence to the grape industry (Walker, 2009a,b,c; Walker et al., 2009; Walker and Ferris, 2009; Walker, 2010; Walker et al., 2010; Zheng et al., 2010, 2011).

Host status of common rootstocks: Over the years of these screening and selection trials, we have included a large number of existing rootstocks in our studies for comparative purposes and to evaluate their host status to nematodes under standardized conditions. We have screened a group of 22 rootstocks to avirulent and virulent strains of *Meloidogyne*, *X. index*, *M. xenoplax*, *Paratylenchus hamatus*, and *P. vulnus*. We provide a summary of available data on the host status of grape rootstocks to nematodes (Table 6). In addition, new nematode resistant rootstocks developed in other programs have been included in the list, for example rootstocks RS-3, RS-9, USDA 10-17A, USDA 10-23B, USDA 6-19B (Anwar et al., 2002; Gu and Ramming, 2005a,b). For a more complete profile, we have merged data from other programs and studies with those obtained in our own (Chitambar and Raski, 1984; Anwar et al., 1999; McKenry et al., 2001a,b; Anwar et al., 2002; McKenry and Anwar, 2006). In the case of *P. vulnus*, we have included some observations on host status based on tissue culture plantlets.

Table 6). In a relatively few cases, reports from different authors regarding host status of a rootstock were not consistent, probably reflecting differences in virulence of populations of the same nematode species and, perhaps differences in evaluation conditions. Where evaluations of host status differed, we report the more susceptible rating and we indicate by 'S?' where two assessments of the host status of a plant genotype were at opposite extremes of the resistance-susceptibility continuum.

TABLE 5. Final population levels of *Mesocriconema xenoplax* on rootstocks grown for 3 months in soil from different locations.

	Mesocriconema xenoplax /g root				
Genotype	Fresno	Livingston	Los Alamos	Mendocino	Parlier
UCD-GRN1	0 a	37 a	7 a	21 a	67 a
UCD-GRN5	86 a	719 b	1186 c	991 c	764 a
UCD-GRN2	473 a	613 b	628 b	564 b	1164 a
UCD-GRN4	203 a	519 b	432 b	214 ab	1501 a
UCD-GRN3	631 a	281 ab	287 ab	277 ab	2106 ab
RS-9	734 a	825 b	604 b	325 b	1812 a
RS-3	2133 b	665 b	619 b	479 b	2297 ab
Harmony	1827 b	1054 bc	970 bc	895 c	1639 ab
Freedom	704 a	1174 bc	1479 d	1016 c	1647 ab
Dog Ridge	659 a	1361 c	1142 c	557 b	1850 ab
Colombard	1455 b	1195 bc	1179 c	1191 c	2285 ab
101-14Mgt	1779 b	1993 c	1708 d	500 b	4429 b

In each column, numbers followed by the same letter do not differ significantly.

DISCUSSION

While the mechanisms of resistance in the UCD GRN series rootstocks are as yet undetermined, resistance and susceptibility to *Meloidogyne* spp. are often expressed phenotypically in the development and quality of the nematode feeding site. Numbers of *Meloidogyne* juveniles entering behind root tips, the time until reproductive maturity, and the rate of egg production by females differed among grape cultivars, suggesting multigene horizontal resistance to the infection and developmental processes in susceptible cultivars (Ferris, et al., 1982; Ferris, et al., 1984). The resistant reaction of Harmony and the more recent RS-3, USDA 10-17A and USDA 6-19B rootstocks is hypersensitivity along the migration path of root-knot nematodes into the differentiating vascular tissue without further development of the nematode (Anwar and McKenry, 2002b), suggestive of single gene control and consistent with the conclusion that resistance is associated with a single dominant gene (Cousins and Walker, 2002; Cousins et al., 2003). In USDA 10-23B, there was hypersensitivity but feeding sites developed although they supported undersized females that did not produce eggs while in RS 9, females of a virulent pathotype produced a few eggs (Anwar and McKenry, 2000; 2002a,b).

Since the resistance to *Meloidogyne* spp. of many of the parent species and crosses was similar to that in their

TABLE 6. Host status of grape rootstocks to nematodes. A compilation based on current studies and those published elsewhere (Anwar *et al.*, 1999; Anwar *et al.*, 2002; Chitambar and Raski, 1984; Gu and Ramming, 2005a,b; McKenry *et al.*, 2001a,b). In the case of *P. vulnus*, we have included some observations on host status based on tissue culture plantlets. Note that host status of the UCD-GRN series rootstocks is indicated in Table 1.

Genotype	Parentage	*M. incognita* Race 3	*M. javanica*	*Meloidogyne* pathotypes Harmony A&C	*M. chitwoodi*	*X. index*	*M. xenoplax*	*P. vulnu*	*T. semipenetrans*	*X. ameriacanum*	*Para. hamatus*
101-14Mgt	*V. riparia, V. rupestris*			R		S	S	MR			S
1103Paulsen	*V. solonis x V. riparia*			S		S	S	MS			S
110Richter	*V. berlandieri, V. rupestris*			MR		S	S	S			S
140Ruggeri	*V. berlandieri, V. rupestris*			MR		S	S	S			MS
1613Couderc	*V. solonis, V. othello*	R	R	S	S	MR	S	MS	S	S	
1616Couderc	*V. solonis, V. riparia*			MR		S	S	MS			S
3309Couderc	*V. riparia, V. rupestris*	S	S	S		MS	S	S	S	S	S
420A	*V. berlandieri, V. riparia*			R		S	S	MS			S
44-53Malegue	*V. riparia, V. cordifolia, V. rupestris*			S		S	MR	MS			S
AxR1	*V. vinifera, V. rupestris*			S		S	S	S			S
Borner	*V. riparia, V. cinerea*			R		R	S	MS			
Dog Ridge	*V. champinii*	R	R	S		S	S		MR	MR	MS
Freedom	*V. champinii, V. longii, V. vinífera, V. riparia, V. labrusca*	R	R	S	S?	R	MS	MS	S	MS	MR
Harmony	*V. champinii, V. longii, V. vinífera, V. riparia, V. labrusca*	R	R	S	S	MS	S	S	S	S	S
K51-32	*V. champinii, V. rupestris*	MR				MS	S	R	S		S
Kober 5BB	*V. berlandieri, V. riparia*			R		S	S	MS			MR
Ramsey	*V. champinii*	R	R	S	S?	MR	S	MS	MSS	S	S
Riparia Gloire	*V. riparia*			R		R	S	MR			S
RS-3	*V. candicans, V. riparia, V. rupestris*	R	R	MR	MR	S	S	MR			S
RS-9	*V. candicans, V. riparia, V. rupestris*	R	R	R	R	S	S	MS			S
Schwarzmann	*V. riparia, V. rupestris*	S	MR	S		MR	MS	S	S	MS	S
St. George	*V. rupestris*	S		S		S	S	MS			MS
Teleki 5C	*V. berlandieri, V. riparia*	MS	MR	S		MR	MS	S	S	S	MS
USDA 10-17A	*V. simpsoni, M. rotundifolia*	R	R	R	R	R	MS	R	R		
USDA 10-23B	*V. doanianna*	R	R	R	R	R	MR	R	R		
USDA 6-19B	*V. champinii*	R	R	MS	R	MR	MR	R	R	R	
VR O39-16	*V. vinifera, M. rotundifolia*	S	S	S		R	R	MR	S	MR	MR

Resistance assessed relative to nematode reproduction on cv Colombard (or other susceptible cultivar):
R <10% (resistant), MR 10-30% (moderately resistant), MS 30-50% (moderately susceptible), S >50% (susceptible).

UCD GRN series progeny, we conclude that either the same resistance genes occur frequently among *Vitis* spp. of different geographic origin or that we have compounded several sources of resistance into the UCD GRN rootstocks. The former case would suggest that resistance to root-knot nematodes in *Vitis* is conferred by a single, possibly dominant, gene that occurs frequently in the genus, in apparent concurrence with studies of the genetics of some of the material (Cousins and Walker, 2002; Cousins et al., 2003; Lowe and Walker, 2006). On the other hand, if the nature of resistance differs among parent species the resulting potential pyramiding of resistance genes should enhance durability of the resistance.

Of the new resistant rootstocks, UCD GRN1 has broadest nematode resistance. However, it has rooted and grafted inconsistently and success in these attributes appears to be related to the age of the mother vine and the quality of the cuttings; it is compromised at winter temperatures below -5°C. UCD GRN2 is resistant to *Meloidogyne* spp. and *X. index* but susceptible to *M. xenoplax* and *T. semipenetrans*. It roots and grafts easily because of the *V. riparia* parentage. In addition to its resistance to *Meloidogyne* spp. and *X. index*, UCD GRN3 and its sibling, UCD GRN4, are moderately resistant to *P. vulnus* but moderately susceptible to *M. xenoplax*. Besides its resistance to *Meloidogyne* and *X. index*, UCD GRN5 is resistant to *T. semipenetrans* (Walker and Ferris, 2009; Walker, 2009a,b,c; Walker et al., 2009; Walker, 2010; Zheng et al., 2010, 2011). Rooting and grafting success with UCD-GRN5 are somewhat lower those of UCD-GRN2-4, probably conferred by its different male parent. *V. champinii* cv c9021. Since *Vitis* and *Muscadinia* have different numbers of chromosomes, UCD-GRN1 is sterile. However, the other four GRN rootstocks are being used in crosses to complex with additional nematode resistance sources with the intent of enhancing the breadth and durability of resistance. They are also being used as parents in breeding programs for rootstocks with drought and salt tolerance.

There are many examples of plant resistance to root pathogens being broken in the presence of plant-parasitic nematodes and even of resistance to one nematode species being overcome in the presence of

another. The effect of nematode feeding and root damage on the resistance may be in providing avenues of ingress into root tissues, increasing leakage of sugars and amino acids from injured sites and hence enhancing the inoculum potential of the pest or pathogen, or by inducing physiological changes in the host tissues (Khan and Husain, 1989; Mai and Abawi, 1987; Hewezi, et al., 2010). In the UCD-GRN rootstocks, resistance to the target species is not compromised by the presence of other nematode species, whether the rootstock selection is resistant or susceptible to the other nematodes.

With strong resistance available to dagger and root-knot nematodes in grape rootstocks, it is likely that pressures from other nematodes will increase. We have identified several potential sources of resistance to these existing and emergent nematode problems in grape and we are continuing our intensive search for resistance to ring, root lesion and citrus nematodes. Further, now that the resistant rootstocks have been released, they function as probes for detecting variability in the virulence of these nematodes. If the rootstocks select for variants able to overcome their resistance, we need to have alternative sources of resistance available. In essence, we embark on an evolutionary tug-of-war with the nematodes. It is important that we monitor field trials of the new rootstocks that have been established in different areas of the state to determine whether resistance-breaking pathotypes of the nematodes occur.

The ring nematode is widely distributed in vineyards and in many other perennial crop plantings throughout the state. Recent adoption of sugar-centrifugation extraction techniques (Jenkins, 1964) by some diagnostic laboratories in California has greatly increased their detection of ring nematodes in vineyards. Although there is little doubt that *M. xenoplax* causes damage to young vines, it is difficult to test the impact of these nematodes on older vines. However, damage and crop loss are highly probable given the population levels that can be encountered (McKenry et al., 2001a; Pinkerton et al., 2005). The ring nematode has a wide host range, so it is unlikely to be eliminated by rotation to other crops before planting a vineyard. Consequently, it will be important to continue to screen candidate rootstock material against several populations of these nematodes to ensure the broadest possible resistance. *Muscadinia rotundifolia* cv Cowart, and its recently-released offspring UCD GRN1, are important sources of resistance to ring nematode. The root lesion nematode, *P. vulnus* is also widely distributed and the citrus nematode, *T. semipenetrans* is regionally distributed in vineyards. We have little information on potential sources of resistance to the root lesion nematode but UCD GRN1 and VR O39-16, both with *M. rotundifolia* parentage, are poor hosts while UCD-GRN1, UCD GRN5 and RS-3 are poor hosts of citrus nematode (Table 1,6). We continue to seek alternative sources of resistance to these and other nematodes.

With deployment of the resistant rootstocks, it will take several years to determine the optimum climatic and edaphic conditions for each. Additionally, field trials are now established in a series of locations. At all locations we intend to monitor the productivity and vigor of grapevines grafted on the UCD-GRN rootstocks and to document nematode occurrence and abundance on an annual basis. Thus far, resistance appears durable at each field location.

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