

A Search for More Durable Grape Rootstock Resistance to Root-knot Nematode

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The resistance levels of 6-19B, 10-17A, 10-23B, RS-3, RS-2, Teleki 5C, and Ramsey rootstocks to populations of *Meloidogyne incognita* R3, *M. chitwoodi*, mixed *Meloidogyne* spp., *Meloidogyne* sp. pt. Ramsey, and two resistance-breaking populations of *M. arenaria* were compared in microplots. Freedom and Harmony rootstocks were included as commercially resistant checks and Cabernet Sauvignon was included as a susceptible check. Each replicate was inoculated by adding field soil containing each nematode population. The level of resistance was determined by comparing final population levels of J2 in soil and number of females and eggs per gram of root over a two-year period. All rootstocks suppressed reproduction of the common *Meloidogyne* spp.; however, 6-19B, 10-17A, 10-23B, RS-3, and RS-2 only suppressed reproduction by the two resistance-breaking populations of *M. arenaria*. These data suggest that these five rootstocks exhibit a more durable root-knot resistance than commercially available rootstocks. The population of *M. arenaria* pt. Freedom was unavailable for study during the original selection process of these five rootstocks.

Key words: Grape rootstocks, microplots, nematodes, *Meloidogyne* spp., reproduction, resistance, resistance-breaking populations

Root-knot nematodes are primary pathogens of grapevines that reduce growth and productivity of vines in many grape production areas of the world [10,19,25]. The root-knot nematode *Meloidogyne* spp. is a key soil pest in warm, sandy soils of California and elsewhere. In warmer regions of California, three root-knot nematode species, *M. incognita*, *M. arenaria*, and *M. javanica*, cause significant economic damage [14]. An estimated yield loss of \$190 million for a \$950 million grape crop has been attributed to root-knot nematode damage in California [19]. The use of grape rootstocks with resistance to root-knot nematodes has been a primary grape pest management tactic to reduce vine damage. However, development and selection of pathotypes of root-knot nematode that can overcome the available sources of resistance has also been a reality [16].

Historically, grape rootstocks have been screened against a variety of root-knot nematode species and populations, both singly and in combination [6,9,14,25,27]. In the field, the selected rootstocks have exhibited shortcomings with the breadth of their nematode resistance, their durability of resistance to root-knot species, and their viticultural characteristics [14,17,27]. Pertinent to this study, resistance-breaking populations of root-knot nematode such as Harmony and Freedom pathotypes of *M. arenaria* are capable of overcoming resistance of currently used rootstocks [27; M.V. McKenry, personal observations]. These selected populations are more virulent than most root-knot nematode populations associated with *Vitis vinifera* [3].

Ramsey, Freedom, and Harmony rootstocks are resistant to *M. incognita* [27] and *M. arenaria* [9]. However, resistance-breaking pathotypes of *M. arenaria* and *M. incognita* have been found in the same vineyards within 15 years of planting [5]. Each of these rootstocks is excessively vigorous and can retard berry coloration and bud fertility depending on soil and management conditions.

The emergence of new root-knot pathotypes and the existence of commercially available rootstocks that have undesirable viticultural characteristics prompted our search for rootstocks having broader nematode resistance and durable resistance to damaging root-knot nematode populations. Rigorous testing of new and promising grape rootstocks in comparison to commercially available rootstocks was required.

Plant resistance to root-knot nematode is generally determined using a pure population of a single *Meloidogyne* species in the greenhouse. However, it is difficult to correlate such results to field situations where more than one species and considerable variation in pathogenicity may occur. Resistance to one species of *Meloidogyne* does not usually imply resistance to others [23]. Also, genes that confer resistance to one particular population of nematodes may not protect against other populations of the same species [8]. Netscher and Taylor [18] questioned whether the field performance of a plant could be predicted on the basis of its reaction to a particular species and suggested that a better practical approach was to determine the reaction of plants to field populations of nematodes.

This study was designed to (1) verify the resistance possessed by five experimental and five conventional grape rootstocks against six root-knot populations containing a range of pathogenic variation and (2) determine the relative vigor of rootstocks.

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In this work, resistance is defined as the ability of the plant to prevent reproduction of the nematode [7,21,22,26].

Materials and Methods

Microplot preparation. This microplot experiment was conducted from 1996 to 1998 at the University of California Kearney Agricultural Center, Parlier, CA. The soil was a Hanford sandy loam (65% sand, 27% silt, and 8% clay). In 1985, 300 microplots were established by drilling a hole of 75-cm diameter and 150-cm depth with a truck-mounted auger. A corrugated polyethylene resin tube of 61-cm diameter and 122-cm length was installed into each hole. The disturbed soil was returned around and within the tube. These open-bottomed microplots each had a 10-cm lip aboveground after the soil settling. From center to center, each microplot was 145 cm apart within the row and 175 cm between rows. A drip irrigation system was installed for uniform water delivery. Weeds were controlled by hand.

Grape rootstocks. Ten grape rootstocks (Table 1) with variable nematode resistance were exposed to six populations of *Meloidogyne* spp. The three grape rootstocks 10-17A, 6-19B, and 10-23B exhibit the broadest nematode resistance of which we are aware [1,2,3]. This finding is a result of a 1988 to 1992 intensive screening of 520 *Vitis* selections and 800 progeny of hybridized Ramsey x Schwarzmann rootstocks at the USDA Plant Breeding Station in Fresno, CA (McKenry and Ramming, unpublished data). Two new rootstocks, RS-3 and RS-2, were products of that screening. These five rootstocks were multiplied further at the Kearney Agricultural Center. Standard two-node cuttings of these selections were placed in heated sawdust beds in winter 1996 for rooting. Duarte Nursery (Ceres, CA) supplied one-year-old rootings of commercially acceptable rootstocks and cultivars, including Ramsey, Teleki 5C, Harmony, Freedom, and Cabernet Sauvignon. Cabernet Sauvignon was included as the highly susceptible control to all nematodes screened. Freedom and Harmony served as susceptible control to two populations of *M. arenaria* and Ramsey as the susceptible control to *Meloidogyne* spp. pt. Ramsey. In spring 1997,

the randomized rooted cuttings were planted in rows throughout the microplots, with one vine per microplot and three replicates for each rootstock. Harmony cuttings were not planted until February 1998.

Nematode inoculum. Microplots were individually inoculated with soil containing six different populations of *Meloidogyne* spp., which were collected from specific vineyard locations in California and inoculated into the microplots in July 1997. The Harmony pathotype of *M. arenaria* was obtained from a 25-year-old vineyard planted on Harmony rootstock, located near Livingston, CA; 1-kg soil (560 J2 per 250 cm³) was added to the appropriate microplots. The pathotype *M. arenaria* pt. Freedom was collected from an 8-year-old vineyard located near Livingston, CA; 1-kg soil (852 J2 per 250 cm³) was added to the appropriate microplots. The mixed *Meloidogyne* spp. population was comprised of *M. incognita*, *M. javanica*, *M. arenaria*, and *M. hapla*, obtained from an 8-year-old kiwifruit planting located near Clovis, CA; 1-kg soil (420 J2 per 250 cm³) was added to each appropriate microplot. *Meloidogyne* spp. pt. Ramsey was collected from King City, CA; 1-kg soil (211 J2 per 250 cm³) was added into each appropriate microplot. *Meloidogyne chitwoodi* complex was collected from Dinuba, CA; 1-kg soil (756 J2 per 250 cm³) was used as inoculum per microplot. *Meloidogyne incognita* R3 originated from a cotton field near Shafter, CA; 1500 juveniles were added per microplot.

Soil and root sampling. Soil and root samples were collected in April 1998 for assessment of nematode population build-up in soil and roots. Vines were again sampled in July 1998 to collect roots to assess the egg density of each root-knot species. The Harmony vines and vines inoculated with *M. incognita* were only assessed for egg build-up.

Three soil cores from each replicate were collected and composited into one sample. Each sample was thoroughly mixed and a 250-cm³ composite sample was processed through a 325-mesh sieve (pore size = 17 micrometer) followed by Baermann funnel extraction to collect second-stage juveniles. Samples of roots were removed from each replicate and divided into two equal samples, one for egg extraction and the other for determining female population within roots. Roots were washed free of soil, blotted onto paper, damp-dried, weighed, stained with acid fuchsin [4], and then spread in a film of glycerin between two glass plates (7.5 x 15 cm). (Glycerin improves optical qualities of the system, prevents drying, and adheres the plates together.) The number of females within the roots was determined under a dissecting microscope. The number of females per gram of root, with or without eggs, was estimated. Eggs were removed from all the galled roots, placed in an 800-mL sealed Mason glass jar with 2% NaOCl [12], and shaken for 4 min at 200 cycles/min on a mechanical shaker (Eberbach Corporation, Ann Arbor, MI). This treatment was followed by a thorough rinse in tap water and eggs were counted at 40x magnification. Eggs per gram of root were calculated to determine the reproductive ability of each nematode population on each rootstock.

Table 1 Parentage and origin of various grape rootstocks.

Rootstock	Parentage	Origin
Cabernet Sauvignon	<i>Vitis vinifera</i>	
Ramsey	<i>V. candicans</i> × <i>V. rupestris</i>	Texas
Harmony	1613C × <i>V. champinii</i>	USDA, Fresno, CA
Freedom	1613C × <i>V. champinii</i>	USDA, Fresno, CA
Teleki 5C	<i>V. berlandieri</i> × <i>V. riparia</i>	Hungary
USDA 10-17A	<i>V. simpsoni</i> × <i>V. muscadinia</i>	USDA, Fresno, CA
USDA 6-19B	<i>V. champinii</i> × GA-3,4,5	USDA, Fresno, CA
USDA 10-23B	<i>V. doanianna</i>	USDA, Fresno, CA
RS-3	(<i>V. candicans</i> × <i>V. rupestris</i>) × (<i>V. riparia</i> × <i>V. rupestris</i>)	Kearney Ag. Center, Parlier, CA
RS-2	(<i>V. candicans</i> × <i>V. rupestris</i>) × (<i>V. riparia</i> × <i>V. rupestris</i>)	Kearney Ag. Center, Parlier, CA

Data analysis. A log (n + 1) transformation of the data was performed prior to analysis of variance. The data were subjected to analysis of variance using SAS [24]. Significant differences in means of nematode reproduction were separated using Duncan's multiple range test ($p = 0.05$).

Results

Cabernet Sauvignon was confirmed to be an excellent host regardless of the nematode population (Tables 2, 3, 4). Although the *M. chitwoodi* population produced a large number of eggs per gram of fresh root weight (Table 2), females were present (Table 4) and J2 abundant in soil. Greatest egg production occurred with *M. arenaria* pt. Freedom.

Each of the nine rootstocks known to possess some level of resistance did express that resistance in this test. The *M. chitwoodi* population provided the most variable results with unclear separation, particularly among commercial rootstocks. The commercial rootstocks Teleki 5C, Ramsey, Freedom, and Harmony exhibited resistance to common *Meloidogyne* populations, including *M. incognita* and the mixed *Meloidogyne* spp. They were also significantly poorer hosts than Cabernet Sauvignon to *Meloidogyne* sp. pt. Ramsey. Egg production, J2 soil population, and female development of two *M. arenaria* pathotypes on the commercial rootstocks were typically similar to values obtained for Cabernet Sauvignon.

Levels of eggs, females, and J2s on the new *Vitis* selections, including 6-19B, 10-17A, 10-23B, and RS-3, were distinctly different from those on Cabernet Sauvignon (Table 2). In situations where there was not a clear reduction in one stage, there was a reduction in the other two stages.

Nematode population levels on the RS-2 selection were numerically different from Cabernet Sauvignon, but the differences were never significant in the presence of the two *M. arenaria* pathotypes. RS-2 also provided numerically reduced population levels compared to commercially available rootstocks.

Discussion

Measurement of host resistance and nematode virulence is generally based on an assessment of nematode reproduction and

induction of root galls by nematodes. Gall index has been frequently used to evaluate resistance of grape rootstocks [25] and other perennial crops [15]. Root galling might be a good indicator of plant response to nematode infection but not to nematode reproduction. For example, we did not observe galls on roots of Teleki 5C infected by *M. arenaria* pt. Harmony, although it supported high nematode reproduction [2]. Similarly, tobacco plants supported high reproduction of *M. incognita* without producing galls [20]. (Rootstock resistance was assessed by counting the number of females inside the roots and number of eggs per gram of root.) These two parameters are more closely related to nematode reproduction than galling [11,13].

The susceptible response of Harmony and Freedom to both *M. arenaria* populations confirms findings from vineyards. Both rootstocks are a product of nematode-resistant Dog Ridge and 1613C grape rootstocks and have proved resistant to root-knot nematodes [25,27,28]. High levels of resistance of both rootstocks against *M. incognita* were confirmed [27]. Harmony rootstock was reported immune, as J2 of the *M. arenaria* population tested was unable to penetrate and establish feeding sites inside the roots [9]. Harmony was also reported resistant to *M. incognita* and *Pratylenchus vulnus* singly and in various combinations [6]. Our study graded both Harmony and Freedom as susceptible to both *M. arenaria* populations but resistant to the other four *Meloidogyne* spp. or populations. We have also established that *Meloidogyne* spp. vary in virulence and that both *M. arenaria* populations are more virulent than the other *Meloidogyne* populations [3]. This study does not indicate the tolerance level of different rootstocks against the two virulent populations.

Resistant plants suppress nematode populations by successfully expressing their defense mechanisms against nematode penetration, development, and reproduction. The extent of suppression of each nematode population depends upon the resistance level of the rootstock. The differential reproduction of various *Meloidogyne* spp. on different grape rootstocks and selections suggests that level of resistance varies. Two broad groupings of virulence in *Meloidogyne* spp. emerged based on reproduction pattern. The first group comprises two populations of

Table 2 Reproduction (eggs/g root) of six root-knot nematode populations on roots of 10 grape rootstocks.

Rootstock	<i>M. arenaria</i> ^a pt. Freedom	<i>M. arenaria</i> pt. Harmony	<i>Meloidogyne</i> spp. pt. Ramsey	<i>M. incognita</i>	Mixed <i>Meloidogyne</i> spp. ^b	<i>M. chitwoodi</i>
Cabernet Sauvignon	2431a ^c	479a	2239a	288a	239a	7abc
Ramsey	522a	486a	10bc	4b	6b	148ab
Teleki 5C	1135a	98a	43b	14b	25ab	322a
Freedom	1176a	748a	1c	8b	1b	119ab
Harmony	247a	35ab	3bc	1b	2b	38abc
USDA 6-19B	7bc	16b	2bc	3b	1b	1c
USDA 10-23B	1b	1b	1bc	1b	1b	3bc
USDA 10-17A	6bc	1b	5bc	1b	1b	4bc
RS-2	213a	45ab	1bc	1b	4b	6abc
RS-3	92ab	1b	2bc	1b	4b	15abc

^aStatistical analysis based on Log (n + 1) transformed data. Back transformed means are shown.

^bMixed *Meloidogyne* spp. includes *M. incognita*, *M. arenaria*, and *M. javanica*.

^cMeans of three replications. Means within a column followed by the same letter are not significantly different at $p = 0.05$.

Table 3 Reproduction (J2/250 cm³ soil) of five root-knot nematode populations on roots of nine grape rootstocks.

Rootstock	<i>M. arenaria</i> pt. Freedom ^a	<i>M. arenaria</i> pt. Harmony	<i>Meloidogyne</i> spp. pt. Ramsey	Mixed <i>Meloidogyne</i> spp. ^b	<i>M. chitwoodi</i>
Cabernet Sauvignon	298a ^c	78a	650a	1035a	596a
Ramsey	180a	10abc	6b	3bc	3bc
Freedom	87ab	42ab	6b	2bc	5bc
Teleki 5C	52ab	15abc	11b	2bc	9b
USDA 6-19B	3c	32ab	9b	17b	9b
USDA 10-23B	2c	1c	30b	4bc	1c
USDA 10-17A	1c	1c	5b	1c	1c
RS-2	39ab	30ab	5b	2bc	2bc
RS-3	10bc	3bc	5b	5bc	43b

^aStatistical analysis based on Log (n + 1) transformed data. Back transformed means are shown.

^bMixed *Meloidogyne* spp. includes *M. incognita*, *M. arenaria*, and *M. javanica*.

^cMeans of three replications. Means within a column followed by the same letter are not significantly different at $p = 0.05$.

Table 4 Reproduction (females/g root) of five root-knot nematode populations on roots of nine grape rootstocks.

Rootstock	<i>M. arenaria</i> pt. Freedom ^a	<i>M. arenaria</i> pt. Harmony	<i>Meloidogyne</i> spp. pt. Ramsey	Mixed <i>Meloidogyne</i> spp. ^b	<i>M. chitwoodi</i>
Cabernet Sauvignon	75a ^c	23ab	86a	103a	11a
Ramsey	3b	13ab	3b	16b	3ab
Freedom	53a	66a	1b	1c	1b
Teleki 5C	3b	5bc	1b	1c	8ab
USDA 6-19B	1b	1c	1b	1c	2ab
USDA 10-23B	1b	1c	2b	1c	1b
USDA 10-17A	1b	1c	1b	1c	3ab
RS-3	3b	2c	1b	1c	1b
RS-2	21a	5bc	3b	1c	2ab

^aStatistical analysis based on Log (n + 1) transformed data. Back transformed means are shown.

^bMixed *Meloidogyne* spp. includes *M. incognita*, *M. arenaria*, and *M. javanica*.

^cMeans of three replications. Means within a column followed by the same letter are not significantly different at $p = 0.05$.

M. arenaria, which reproduced very well on susceptible Cabernet Sauvignon and Ramsey, Freedom, Harmony, and Teleki 5C rootstocks but poorly on 6-19B, 10-23B, 10-17A, RS-2, and RS-3. The second group includes all other *Meloidogyne* spp., which reproduced very well on susceptible Cabernet Sauvignon but poorly on all other rootstocks and selections.

The poor reproduction levels by all *Meloidogyne* spp. on selections 6-19B, 10-23B, 10-17A, RS-2, and RS-3 results from unknown resistance mechanisms located in these selections. Resistance mechanisms may reduce J2 penetration, delay or stop development to adult females, and suppress female reproduction [1,2,3]. Penetration into roots of 10-17A, 10-23B, 6-19B, and RS-3 by J2 of *M. arenaria* pt. Harmony is greatly reduced [1,2]. Additionally, J2 root penetration into 10-17A and RS-3 was delayed while many J2 exited the roots of RS-3 [1]. Development to adult female stage by *M. arenaria* pt. Harmony was reduced and delayed about one week in roots of RS-3 and 10-23B [1]. Reproduction by this population was suppressed greatly

in roots of 10-17A, 6-19B, and 10-23B; however, no reproduction occurred in roots of 10-23B [1].

Reproduction levels differed across these rootstocks, most likely due to differences in virulence of *Meloidogyne* species/populations. The two resistance-breaking populations of *M. arenaria* had high reproduction potential on commercial rootstocks compared to the 6-19B, 10-23B, 10-17A, RS-2, and RS-3 selections. That suggests *M. arenaria* populations are more virulent than other *Meloidogyne* spp., which agrees with the results of Cain et al. [5] and Anwar et al. [3]. Differences in reproduction between the two *M. arenaria* populations further demonstrate these results [3]. This research verifies earlier observations that *M. arenaria* pt. Freedom is more virulent on grape rootstocks than *M. arenaria* pt. Harmony [3]. Differences in reproduction among *Meloidogyne* spp. and within *M. arenaria* will affect nematode management strategies and should be considered during rootstock breeding programs and when designing cultural practices for nematode control.

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