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P. Cousins · M. A. Walker

Genetics of resistance to *Meloidogyne incognita* in crosses of grape rootstocks

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Abstract Progeny testing was used to investigate the value of selected grape varieties as parents in breeding nematode-resistant rootstocks. Six pistillate-flowered rootstocks (Ramsey, Dog Ridge, Harmony, Freedom, 1613C, and 161-49C) and four staminate-flowered rootstocks (Riparia Gloire, 3309C, 1616C, and St. George) were used. Each male was crossed to each female. Six weeks after inoculation with 1,500 second-stage juveniles of *Meloidogyne incognita* race 3, roots were stained in an aqueous solution of eosin-Y (0.25 gm/l for 1 h). Seedling resistance was measured by counting the number of stained nematode egg masses visible per root system. Nematode reproduction on each cross was calculated as the average number of egg masses on ten seedlings per replicate. The females Harmony and Freedom produced the greatest level of resistance in their seedlings across all male parents. Seedlings of Dog Ridge, Ramsey, and 1613C had intermediate levels of resistance, while seedlings of 161-49C were the least resistant. The male 1616C contributed the greatest resistance to its progeny, while seedlings from crosses with the males Riparia Gloire, 3309C, and St. George had lower levels of resistance. Segregation ratios of resistant and susceptible seedlings are consistent with a single dominant allele model for root-knot nematode resistance.

Keywords *Vitis* species · *Meloidogyne incognita* · Inheritance · Nematode resistance

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P. Cousins
USDA-ARS, Plant Genetic Resources Unit,
New York State Agricultural Experiment Station,
Cornell University, Geneva, NY 14456, USA

M.A. Walker (✉)
Department of Viticulture and Enology, University of California,
Davis, CA, 95616, USA
e-mail: awalker@ucdavis.edu
Fax: +1-530-752-0382

Introduction

Root-knot nematodes, especially the species *Meloidogyne incognita, M. javanica, M. arenaria*, and *M. hapla* (Anwar et al. 2000; Nicol et al. 1999) are serious pests in many vineyards. Damage associated with their feeding on grape roots includes galling and cracking of the roots, reduced capacity to take up water and nutrients, and increased susceptibility to other soil-borne pests and pathogens. Resistant grape rootstocks are used to mitigate root-knot nematode damage. However, currently available nematode-resistant rootstocks have several horticultural faults. Dog Ridge, Ramsey, Freedom, and Harmony are often excessively vigorous on fertile soils, and they are prone to excess potassium uptake. Dog Ridge and Ramsey can be difficult to root and can induce zinc deficiency in scions. Finally, Dog Ridge, Ramsey, 1613C, and Harmony may not be adequately resistant to phylloxera (Hardie and Cirami 1988; Lider 1960; Winkler et al. 1974). In contrast, many rootstocks with excellent phylloxera resistance, appropriate vigor, and facile root strike, such as St. George, Riparia Gloire, and 3309C, are susceptible to root-knot nematodes.

Investigation of the genetic control of root-knot nematode resistance has been conducted in the interest of breeding new rootstocks. Lider (1954) examined the inheritance of resistance to *M. incognita* Kofoid and White (Chitwood) in crosses of wild *Vitis* L. species accessions and hybrids of the University of California, Davis collection, describing a model in which nematode resistance was due primarily to a single dominant allele found in *V. champinii* Planch., *V. mustangensis* Buckley, and 1613C. Firoozabady and Olmo (1982) screened *Vitis* × *Muscadinia* Small hybrids and their seedlings, estimating the heritability of nematode resistance in that population at 0.391 on the basis of parent-offspring regression. They concluded that selection for nematode resistance could occur in a breeding program aimed at producing varieties with both desirable fruit characteristics and resistance to root pests, including phylloxera. Intermediate stages of variety development, with nematode and phylloxera resistance but substandard fruit, were suggested for use as rootstocks.

The use of a mating design that permits estimation of components of variance in a single generation would facilitate grape rootstock improvement. Grapes have a relatively long generation time (generally over 2 years), so methods that do not require multiple generations could represent substantial acceleration. In Design II, a series of females is each mated to a series of males. This mating design takes advantage of the predominating dioecy found in grape rootstocks, a condition that would complicate the use of the diallel, which ordinarily requires selfing and reciprocal crosses. Two estimates of general combining ability as well as an estimate of specific combining ability are provided by a Design II analysis, and components of genetic variance can be estimated (Hallauer and Miranda-Folho 1988).

Rootstock varieties that could be used as parents vary in nematode resistance as well as in other viticulturally important attributes such as phylloxera resistance, vigor, and rooting ability. Freedom, Harmony, Dog Ridge, Ramsey, 1613C, and 1616C are generally considered to be resistant to root-knot nematodes, while 161-49C, St. George, Riparia Gloire, and 3309C are regarded as being nematode-susceptible (Hardie and Cirami 1988; Lider 1960; Stirling and Cirami 1984; Winkler et al. 1974).

Breeding rootstocks that combine nematode resistance with improved horticultural characters and additional pest resistances requires an understanding of the genetic control of nematode resistance. The Design II mating format permits genetic analysis of both qualitative (discrete) and quantitative (continuous) traits. Determination of the components of genetic variance and Mendelian genetic aspects of nematode resistance helps breeders decide which parents will be useful in developing new rootstocks. Breeding approaches that focus on major genes may be easier to manage than quantitative methods but could be more subject to loss of rootstock efficacy due to selection for virulent nematode populations.

Materials and methods

Six pistillate-flowered (Harmony, Freedom, Dog Ridge, Ramsey, 1613C, and 161-49C) and four staminate-flowered (St. George, Riparia Gloire, 3309C, and 1616C) grape rootstocks were crossed utilizing the Design II format (Hallauer and Miranda-Folho 1988). Pistillate flower clusters were enclosed in paper bags to prevent unwanted pollination, and opened flowers were removed prior to bagging. Staminate flower clusters were bagged to harvest pollen. Pollen was applied to female clusters by placing a bag into which pollen had shed over the receptive female flower clusters, then shaking the bag to distribute pollen. Following pollination, clusters were rebagged.

Each female parent was crossed to each male parent, for a total of 24 crosses. A minimum of 40 clusters per cross was pollinated. All crosses were completed during the spring of 1997 using mature plants in the University of California, Davis vineyards. Fruits were harvested when ripe and when seeds were brown and hard. Seeds were manually extracted, and floating seeds were discarded prior to stratification. Seeds of *V. vinifera* L. cvs. Carignane and Colombard were harvested from ripe, open-pollinated clusters.

All seeds were cold-treated for 3 months at 4 °C. *Vitis vinifera* seeds were rinsed, then planted at six seeds per pot. These seedlings were thinned at the cotyledon stage to one seedling per pot. Seeds of rootstock crosses were bathed 24 h in 37 °C H_2O, then washed, rinsed, and placed on moist tissue paper in plastic culture dishes. Culture dishes were held in the dark in a greenhouse. As seeds germinated, they were transferred to individual pots. Flats of pots containing sprouted, transplanted seedlings were covered with moist newspaper until cotyledons emerged. All seedlings were grown in a steam-sterilized soil: fir bark: sand mix (10% soil: 25% fir bark: 65% sand by volume) in 6-cm-square plastic pots. Seedlings were maintained in a greenhouse with the control set for 20°–30 °C.

Ten rootstock seedlings per cross were inoculated in each of six replicates. More than ten seedlings per cross were germinated for each replicate. Ten seedlings per cross were selected to create a uniform developmental age among the seedlings from the various crosses. Plants were inoculated once they had two true leaves (approximately 1 month after plating for rootstock crosses or planting for *V. vinifera* seedlings). At this stage roots began to emerge from the drain holes of the pots. Each seedling tray held two crosses (ten seedlings each) and three *V. vinifera* seedlings. Seedlings were grown in a greenhouse from May through October 1998.

Larger samples of the crosses 1613C × Riparia Gloire and 1613C × 3309C were grown in the winter/spring of 1999 to examine qualitative segregation ratios of nematode resistance. One hundred and five seedlings of 1613C × 3309C and 38 seedlings of 1613C × Riparia Gloire were tested using the same protocol.

The nematode population used in this study was derived without selection from a *M. incognita* race 3 population used by Walker et al. (1994). This population feeds on known susceptible *V. vinifera* varieties such as Carignane and Colombard, and it reproduces at low levels or not at all on the six resistant parents. The population was maintained on tomato plants in greenhouse pot culture. Juvenile nematodes were extracted from tomato roots in a mist chamber (Barker 1985) and 1,500 juveniles pipetted into the soil near the crown of each grape seedling.

Nematode reproduction was assessed 6 weeks after inoculation. Soil was washed from the roots using deionized water. Roots were placed in an aqueous solution of eosin-Y (0.25 g/l) (Sigma 6003) for 1 h, then rinsed to remove excess stain, following a modification of Castagnone-Sereno et al. (1994) with increased eosin-Y concentration and staining time. The roots were blotted dry, weighed, and cut into 3- to 5-cm-long pieces, and stained egg masses were counted. The numbers of egg masses were recorded for each seedling. The average number of egg masses on the ten seedlings per cross per replicate was used in the calculation of estimated components of variance. If fewer than ten seedlings reached the screening point, the average number of egg masses on the surviving seedlings was used. Egg mass numbers on individual seedlings were used in describing quantitative segregation of nematode resistance.

For qualitative segregation analysis, each seedling was classified as either resistant (≤2 egg masses observed) or susceptible (≥ 3 egg masses observed). Ratios of observed resistant to susceptible seedlings were compared to expected segregation ratios. The cut-off between resistant and susceptible was set based on Lider (1952). He observed crosses of 1613C × AXR1, a resistant × susceptible cross, to segregate in a 1:1 resistant:susceptible ratio, using the absence of galling as the definition of resistance. However, we have found that egg masses are not invariably associated with galls; egg masses frequently are present on ungalled roots (data not shown), so some of the plants that Lider considered resistant probably did have nematode reproduction. We assumed that 1613C × Riparia Gloire, also a resistant × susceptible cross, would segregate in the same ratio that Lider observed for 1613C × AXR#1. Testing 1613C × Riparia Gloire seedlings for goodness-of-fit to two resistance classes resulted in the lowest χ^2 value when seedlings with two or fewer egg masses were considered to be resistant and seedlings with three or more egg masses were considered to be susceptible. This definition was then applied to all seedling populations.

Results

Estimates of components of variance and heritability were calculated according to Hallauer and Miranda-Folho (1988) (Table 1). Based on the mean number of egg masses on their seedling progeny, female parents fell into three statistically separable groups ($P \leq 0.01$) and male parents fell into two groups ($P \leq 0.05$) (Table 2). Full-sibling populations were separable into five groups ($P \leq 0.01$) (Table 2). Fisher's protected LSD test was used to compare means. When seedling segregation was qualitatively analyzed, the segregation patterns fit four segregation ratios. A chi-square test with Yates' correction was used. When homozygous resistant parents are used in crosses (all progeny resistant, 1:0 ratio) or when both parents are homozygous susceptible (all progeny susceptible, 0:1 ratio), no segregation should be observed. Crosses of two heterozygous dominant parents are expected to segregate in a 3:1 ratio, while the cross of a heterozygous dominant and a homozygous recessive should segregate 1:1. Observed segregation ratios were consistent with expected ratios ($P < 0.05$) (Table 3).

Seedlings of crosses to Harmony and Freedom matched a pattern of 1 resistant:0 susceptible seedlings, regardless of the male parent. Seedlings from crosses with Dog Ridge or Ramsey to Riparia Gloire, 3309C, and St. George matched a 1:1 ratio. Seedlings of these females from crosses with 1616C matched a 3:1 ratio. Seedlings of 1613C segregated in a 1:1 pattern when Riparia Gloire or St. George was the male parent. When 1616C or 3309C were used as the male parents, the seedling population segregation matched 3:1. A second sample of the 1613C × 3309C seedling population, consisting of an additional 105 plants, was screened to confirm the segregation ratio. As a check, 28 additional seedlings from the cross 1613C × Riparia Gloire, which segregated 1:1 in a previous experiment, was included. No differences in segregation patterns were observed during these second tests. Seedlings of 161-49C with Riparia Gloire, St. George, or 3309C as the male parent segregated 0:1 (all seedlings susceptible). Crosses of 161-49C × 1616C segregated in a pattern that matched 1:1.

Table 1 Components of variance and heritability estimates for root-knot nematode resistance from a Design II mating design (Hallauer and Miranda 1988) of six female × four male grape rootstocks

Additive genetic variance (estimate based on females)	1,200.499
Additive genetic variance (estimate based on males)	313.738
Dominance genetic variance (estimate based on interaction)	523.865
Narrow-sense heritability (estimate based on females)	0.668
Narrow-sense heritability (estimate based on males)	0.345

Table 2 Average root-knot nematode egg masses on the seedlings of a given parent calculated from the mean of all seedling observations with that parent and on the seedlings from each cross. Seedling values constitute the average value from six, ten-seedling replicates. Fisher's LSD was used to separate means

Parent	Average no. of egg masses	Cross[a]	Average no. of egg masses
Females[a]		Harmony × 3309C	0.1a
Harmony	0.3a	Freedom × 1616C	0.2a
Freedom	1.2a	Harmony × Riparia Gloire	0.3a
Dog Ridge	18.4b	Harmony × 1616C	0.3a
1613C	27.7b	Freedom × Riparia Gloire	0.4a
Ramsey	31.1b	Harmony × St. George	0.6a
161-49C	55.1c	Freedom × 3309C	0.8a
Males[b]		Dog Ridge × 1616C	1.6a
1616C	7.6a	Freedom × St. George	3.3a
3309C	23.2b	1613C × 1616C	11.2a,b
St. George	26.9b	Ramsey × 1616C	11.5a,b
Riparia Gloire	32.4b	1613C × 3309C	14.0a,b,c
		Dog Ridge × St. George	15.1a,b,c
		Ramsey × 3309C	18.4a,b,c
		161-49C × 1616C	21.2a,b,c,d
		Dog Ridge × 3309C	26.5a,b,c,d
		Dog Ridge × Riparia Gloire	29.6a,b,c,d
		1613C × Riparia Gloire	34.8b,c,d
		161-49C × St. George	42.2b,c,d
		Ramsey × St. George	43.1c,d
		1613C × St. George	50.8d,e
		Ramsey × Riparia Gloire	51.7d,e
		161-49C × Riparia Gloire	77.4e
		161-49C × 3309C	79.6e

[a] Female parents and crosses followed by the same letter do not differ at the 0.01 level

[b] Male parents followed by the same letter do not differ at the 0.05 level

Table 3 Segregation of seedlings from crosses of grape rootstock crosses tested for resistance to *Meloidogyne incognita* Race 3. Plants with two or three egg masses were considered to be resistant

Seedling population	Resistant (R)	Susceptible (S)	Proposed R:S ratio	Calculated χ^2
Ramsey				
× Riparia Gloire	30	29	1:1	0.0
× Riparia Gloire[a]	145	140	1:1	0.0561
× 3309C	31	29	1:1	0.0166
× 1616C	44	16	3:1	0.0222
× St. George	27	33	1:1	0.4166
Dog Ridge				
× Riparia Gloire	30	30	1:1	0.0166
× 3309C	27	26	1:1	0.0
× 1616C	44	12	3:1	0.2143
× St. George	26	17	1:1	1.4883
1613C				
× Riparia Gloire	35	25	1:1	1.3500
× Riparia Gloire[a]	18	20	1:1	0.0260
× 3309C	44	15	1:1/3:1	13.288[b]/ 0.0056
× 3309C[a]	76	29	1:1/3:1	20.150[b]/ 0.1785
× 1616C	47	13	3:1	0.200
× St. George	26	17	1:1	0.4629
Harmony				
× Riparia Gloire	54	1	1:0	0.0045
× 3309C	52	0	1:0	0.0048
× 1616C	47	1	1:0	0.0052
× St. George	33	3	1:0	0.1736
Freedom				
× Riparia Gloire	56	4	1:0	0.2042
× 3309C	57	2	1:0	0.0382
× 1616C	60	0	1:0	0.0042
× St. George	54	1	1:0	0.0045
161-49C				
× Riparia Gloire	9	51	0:1	1.204
× 3309C	3	57	0:1	0.1042
× 1616C	33	26	1:1	0.6102
× St. George	7	52	0:1	0.4629

[a] Additional tested populations to confirm segregation ratios and use for breeding purposes

[b] 1613C × 3309C seedling segregation does not fit a 1:1 ratio ($P < 0.001$), but does fit a 3:1 ratio consistent with a two locus model of genetic control with one locus hosting a dominant resistance allele and the other a recessive resistance allele

Table 4 Probable root-knot nematode resistance genotypes as proposed by Lider (1952). Segregation patterns in the seedlings of eight grape rootstock parents fit the model of a single gene with resistance conferred by the dominant allele, N. Two other rootstock parents require a model that includes segregation of a recessive allele for nematode resistance, m, at a proposed second locus

Rootstock parent	Proposed genotypes
Harmony	N N
Freedom	N N
Dog Ridge	N n
Ramsey	N n
1616C	N n
161-49C	n n
Riparia Gloire	n n
St. George	n n
1613C	Nn, mm
3309C	nn, Mm

Discussion

The rootstocks used here as parents in the Design II analysis are a sample of currently or historically important varieties. These rootstocks are commercially available in California, are represented in major international grape germplasm collections, and are not restricted by intellectual property protection. The sample also includes representation of major rootstock parent species, including *V. berlandieri* Planch., *V. champinii*, *V. labrusca* L., *V. riparia* Michx., *V. rupestris* Scheele, *V. solonis* Hort. Berol. ex Planch., and *V. vinifera*.

Root-knot nematode resistance has both qualitative and quantitative aspects. Estimates of components of genetic variance show a disparity in estimates of additive genetic variance based on males (313.738) and females (1200.499) (Table 1). There is a concomitant difference in estimates of narrow-sense heritability (estimate based on males = 0.345; estimate based on females = 0.668). Sampling error might account for this difference. While there are hundreds of rootstocks available, the ten varieties tested represent only a small fraction of the potential genetic diversity. This small sample might distort estimates of population parameters. Linkage between sex expression and nematode resistance could also account for this disparity.

However, in the context of the rootstocks available in California it is more likely that the available female and male rootstock populations differ in their genetic variance for root-knot nematode resistance. While the majority of rootstock accessions are staminate flowered, only a small fraction of male rootstocks are generally considered nematode resistant. In contrast, while there are relatively fewer pistillate flowered rootstocks, most of the nematode resistant rootstocks are in this group. Since most grape rootstocks are imperfect flowered, male and female parents by necessity reflect samples of different populations. The consequence is that a sample of female rootstocks is more likely to be enriched for nematode resistant parents than a sample of male rootstocks. The disparity in estimates of additive genetic variance were probably due to the different frequencies of resistance genes in the populations of potential male and female parents.

Most of the results obtained from treating root-knot nematode resistance as a discrete trait are consistent with Lider's proposed dominant resistant allele (1954, 1952). A single gene model can assign genotypes to five female and three male rootstock parents used in this study (Table 4). Harmony and Freedom are homozygous resistant. Dog Ridge, Ramsey, and 1616C are heterozygous resistant. 161-49C, Riparia Gloire, and St. George are homo-

Table 5 Demonstration of role of recessive resistance alleles in creation of 3:1 resistant:susceptible ratio in seedlings of 1613C × 3309C

	3309C gametes	
	n M	n m
1613C gametes:		
N m	Nn Mm Resistant	Nn mm Resistant
n m	nn Mm susceptible	nn mm Resistant

zygous susceptible. 1613C and 3309C represent special cases. In crosses to three of the male parents, 1613C behaved as heterozygous resistant. The seedlings of 1613C crosses to Riparia Gloire, St. George, and 1616C segregated in patterns that match those of Dog Ridge and Ramsey crosses to those same male parents (1:1, 1:1, and 3:1, respectively). In this respect, it appeared as if 1613C was heterozygous resistant for the dominant resistance allele segregating in this population. 3309C appeared to be homozygous susceptible in crosses to all female parents except 1613C. The overabundance (relative to the single dominant gene model) of resistant seedlings observed in the cross 1613C × 3309C may reflect the action of another nematode resistance gene. Lider (1952) invoked a second gene, which he described as an inhibitor, and proposed that the dominant inhibitor was epistatic, suppressing the expression of resistance. This model accounted for apparently resistant seedlings appearing in crosses of two susceptible parents in his experiment. In the present investigation however, all resistant seedlings had at least one parent considered to be resistant.

In contrast to Lider's dominant inhibitor, a recessive allele for root-knot nematode resistance may be segregating in this population. If 1613C were heterozygous for the dominant nematode resistance and homozygous recessive for the recessive nematode resistance, and 3309C were homozygous recessive for the dominant nematode resistance and heterozygous for the recessive nematode resistance, the parent plants would be resistant (1613C) and susceptible (3309C), but would exhibit a 3:1 ratio in seedlings from their cross (Table 5). For simplicity, other parents in this population may be considered to be homozygous dominant at the second locus. However, segregation at a second locus is not required to explain the observed segregation patterns in their crosses. An evaluation of resistance in seedlings of 3309C following chemically induced hermaphrodism (Moore 1970) and self-pollination would provide a test of this model.

The number of segregating loci and alleles cannot be conclusively determined from the results of this experiment. For example, while both Dog Ridge and Ramsey behave as if they are heterozygous for a dominant root-knot nematode resistance allele, it is not known if they are both heterozygous for the same dominant allele, or even at the same locus. A cross of two parents, each heterozygous for a completely dominant resistance allele, will segregate 3:1 whether the parents are heterozygous at the same or different, unlinked loci. Lu et al. (2000) found that resistance in *Prunus* to *M. incognita* is controlled by two genes, with one of the genes also controlling resistance to *M. javanica*; further investigation is needed to determine the number of genes and alleles controlling root-knot nematode resistance in grape. Allelism has implications in rootstock development and nematode management and should be investigated to better understand the relationship between nematode and grape. Grape rootstocks with multiple nematode resistance genes might maintain their resistance longer when challenged by diverse root-knot nematode populations.

Seedlings of specific crosses were significantly more resistant than those of other crosses (Tables 4, 5). The average number of egg masses per seedling in each cross generally reflected the number of qualitative dominant resistance alleles segregating in that population. For example, the cross with the highest average number of egg masses on its seedlings, 161-49C × 3309C, has no dominant resistance alleles segregating according to our model. In contrast, the crosses with the lowest number of egg masses on their seedlings were the Harmony and Freedom crosses, in which we expected two copies of the resistance allele from the female parent. Segregation for resistance within most populations obscures analysis of other sources of variability. The individual seedlings in each population are not replicates of one another, but samples from different subpopulations (the segregating resistance classes).

Preliminary recommendations with respect to parental selection for the development of nematode-resistant rootstocks can be made based on the observed levels of resistance in seedlings of particular parents and crosses and taking into consideration to other horticultural characteristics of the parents. 1616C, Dog Ridge, and Ramsey stand out as potential parents.

1616C is notable for its relatively low vigor, ease of rooting, and good phylloxera resistance in contrast with the other sources of nematode resistance identified here (Lider 1960; Pongrácz 1983). The confirmation that 1616C is a good source of root-knot nematode resistance suggests that it has promise as a parent in breeding new rootstocks with desirable horticultural characteristics. 1616C is not thought to be closely related to *V. champinii*-based nematode-resistant rootstocks, which include Harmony, Freedom, Dog Ridge, and Ramsey. 1616C may thus possess a different allele for nematode resistance than these varieties – a possible tool for use against nematode populations that can reproduce on those four rootstocks (Cain et al. 1984).

Dog Ridge and Ramsey could serve as sources of root-knot nematode resistance. However, these rootstocks have horticultural faults, such as moderate phylloxera resistance, excessive vigor, and poor root strike. Half of the seedlings from crosses of Dog Ridge or Ramsey with Riparia Gloire, St. George, and other phylloxera-resistant rootstocks with superior horticultural characteristics are expected be resistant to nematodes. Successive crossing should result in horticulturally acceptable root-knot nematode-resistant rootstocks. Two root-knot nematode resistant rootstocks, K51-32 and K51-40, were derived from a cross of *V. champinii* × *V. riparia* made by H.P. Olmo. These rootstocks have been used only in Australia and are of minor importance (Hardie and Cirami 1988; May 1994). However, they demonstrate that easy rooting and resistance to phylloxera and nematodes can be combined in a single variety.

Although Harmony, Freedom, Dog Ridge, Ramsey, and 1613C all exhibit high levels of resistance to root-knot nematode when used directly as rootstocks (Hardie and Cirami 1988; Lider 1960; Loubser and Meyer 1987; Stirling and Cirami 1984), Harmony and Freedom are demonstrably superior to Dog Ridge, Ramsey, and 1613C with respect to the level of nematode resistance in their seedlings. Despite high levels of root-knot nematode resistance in their seedlings, Harmony and Freedom are not recommended for use as parents in rootstock due to the uncertainty about the phylloxera resistance of their seedlings. Harmony has insufficient resistance for use in phylloxera prone vineyards (Hardie and Cirami 1988) and would be a poor choice of parent. The same precautions apply to 1613C. While Freedom has not been observed to fail due to phylloxera, it is closely related to the non-resistant Harmony and 1613C and should be used with caution.

At least one root-knot nematode population has been isolated which induces galls on the otherwise resistant Dog Ridge, Ramsey, Freedom, Harmony, and 1613C (Cain et al. 1984). Other populations that damage Harmony and Freedom have been reported (M.V. McKenry, personal communication). The identification and characterization of such nematode populations is a critical step in the selection of rootstocks with resistance to them. Continued genetic study of nematode resistance, with attention to allelism and interaction with specific nematode isolates may lead to the identification and application of durable and broad resistance to root-knot nematodes.

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