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Nematode and Grape Rootstock Interactions Including an Improved Understanding of Tolerance

M. V. McKenry,[1] Safdar A. Anwar[2]

Abstract: Sixteen cultivars of grape were screened over a two-year period in the presence or absence of 10 different nematode populations. Populations of *Meloidogyne* spp., *Xiphinema index*, and *Mesocriconema xenoplax* developed more rapidly and caused greater damage than populations of *X. americanum* and *Tylenchulus semipenetrans*. Populations of mixed *Meloidogyne* spp. having a history of feeding on grape were among the fastest developing populations. Tolerance to nematode parasitism appeared to be based on different mechanisms. Slow developing, less pathogenic nematode populations often stimulated vine growth, thus vines appeared to possess tolerance. Likewise, cultivars selected for nematode resistance often stimulated vine growth when fed upon by the nematode. However, tolerance sources that resulted from nematode resistance are vulnerable due to the occurrence of populations that break resistance mechanisms. Growth of cultivars with phylloxera (*Daktalospharia vitifoliae*) resistance was unchanged by the presence of nematodes, indicating that phylloxera resistance may provide a useful source of nematode relief. These and several additional sources of specific tolerance are discussed.

Key words: dagger nematodes, grape rootstocks, inhibition, ring nematode, root-knot nematode species / populations, stimulations, tolerance.

Grapes are grown on rootstocks for numerous reasons including protection from certain soil-borne pests and diseases. Grape growers in the San Joaquin Valley of California are confronted by at least 12 species of nematodes that may cause decline of established vines or poor establishment of replanted *Vitis vinifera* (McKenry, 1992). *Pratylenchus vulnus*, *Meloidogyne incognita*, *M. javanica*, *M. arenaria* and *Mesocriconema xenoplax* are commonly distributed in California vineyards and seriously affect grape yield (Lider, 1960; Raski et al., 1973). *Xiphinema index* is currently estimated to occur in about 10% of the grape-growing area of California, predominantly in the north coast and north San Joaquin Valley regions and recently has expanded in Kern County (McKenry et al., 2004). *Xiphinema americanum* is commonly found and thought to cause indirect damage to weak vineyards in both California (Ferris and McKenry, 1975) and Michigan (Ramsdell et al., 1996). *Tylenchulus semipenetrans* is less common in grape but is often found in close proximity to plantings of citrus.

The most commonly occurring situation in commercial vineyards is to have a mixture of these nematode pests plus additional species of lesser importance. Concomitant inoculations of *P. vulnus* and *X. index* (Pinochet et al., 1976) or *M. incognita* and *P. vulnus* (Anwar and Van Gundy, 1989) caused greater stunting of shoots and roots than inoculations with either nematode species alone. Our own work has demonstrated substantial differences among populations of *M. arenaria* parasitizing grape (Cain et al., 1984; Anwar and McKenry, 2000; Anwar et al., 2000; Anwar and McKenry, 2002), including a hastening of penetration, development and reproduction by the more aggressive populations.

Rootstock trials for assessing nematode resistance or tolerance generally have been conducted by using a single nematode species. However, it is difficult to extrapolate the results of such tests to the field situations where occurrence of more than one species is common. Plants resistant to one nematode species are not always resistant to another (Sasser and Kirby, 1979). A further complication is that plant genes conferring resistance to one population of a nematode species may not protect against other populations of that same species (Dropkin 1989; Cain et al., 1984).

In response to the lack of appropriate information, we set out to quantify the resistance and tolerance of 16 grape cultivars including the best known rootstocks to field populations of nematodes representing a range of pathogenic variation (Anwar et al., 2000; McKenry et al., 2001a, 2001b). Some of the nematode populations had never been in association with grape, whereas others were common to certain localities, cropping history, or soil textures.

Our definition for resistance is the ability of a plant to prevent reproduction by the nematode (Trudgill, 1991; Roberts, 1992) and was assessed by counting the final nematode population at termination of the experiment. These results have been published elsewhere (McKenry et al., 2001a, 2001b). Our definition for tolerance is the ability of the plant to grow satisfactorily in the presence of nematodes and was assessed by comparing vine growth in the presence or absence of nematodes (Anwar et al., 2003).

The goal of our work is to provide predictability to recommendations concerning use of rootstocks. In addition, such data might be helpful in reducing the number of rootstock candidates required in regional field tests.

Materials and Methods

Soil pest populations: We have observed differential vine damage in California fields due to differing soil pest complexes, soil conditions and rootstock choices.

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[1] Nematologist and [2]Postdoctoral Researcher, University of California, Department of Nematology, Riverside, CA 92521.
E-mail: mckenry@uckac.edu

The nematode populations collected during these field observations provided the basis for the current experiments. The history and origin of the various nematode pests and their initial inoculum density per vine are listed in Table 1.

Nematode inoculum was collected from field sites and reared on suitable host plants in a greenhouse or microplot setting except for a mixed population involving phylloxera + mixed nematodes (*Meloidogyne* spp. + *X. index* + *P. vulnus).*

At the time of vine planting, each inoculum source was collected into large bins, mixed and then equally distributed to individual vines. Three aliquots of each inoculum were extracted for nematodes to determine the initial population density (Pi). The population levels extracted from soil and vine roots at 10 or 18 mon after inoculation are referred to as the final population density (Pf).

Microplot design: All studies were conducted at the University of California Kearney Agricultural Center, Parlier, CA. The site consisted of 48 individual 7 m × 7 m microplots, each lined by 12-cm thick concrete walls that span 30 cm above and 1.7 m below the field surface. The soil was an undisturbed sandy loam (65% sand, 27% silt, and 8% clay). The soil of each microplot was fumigated with 4.5 kg methyl bromide (450 kg/ha) 18 mon before experimentation. Three vines of each grape cultivar were planted together in an equilateral triangle design with 30 cm separating the three vines. Three replicates of each grape rootstock were randomly planted into each microplot. Each soil inoculum was used in individual microplots. Vine survival was adequate to supply our needs except for rootstocks O39-16 and 171-6, for which only partial data could be collected. One stake was placed in each group of three vines, and shoots of all three vines brought up on a single stake. Vines were irrigated by a dripper system with an emitter in the middle of the triangle design. Weed control was by hand-hoeing.

Grape rootstocks: The 16 vine cultivars listed in Tables 2 and 3 were collected from virus-free sources at the USDA Fresno Plant Breeding Station, University of California Kearney Agricultural Center, Parlier, California, or University of California Davis Foundation Plant Material Service. Standard 35-cm-length cuttings were cut in half to retain two nodes and placed in heated sawdust beds 3 mon before planting. The rooted cuttings were randomly planted throughout the microplots. The Thompson Seedless was clone 2A, heat treated in 1960. The 1613C selection was clone 2.

Two independent experiments were conducted to test the response of grape rootstocks against nematode populations in microplots (Tables 2,3). All the experimental conditions and procedures were identical. Ten grape cultivars were included in experiment 1 and seven in experiment 2 (Tables 2,3). Noninoculated vines served as the control for growth comparison. Thompson Seedless and Flame Seedless were included

TABLE 1. Description of soil pest sources, their relevant characteristics and inoculum levels.

Soil pests	Pest source	Inoculum level per vine
Meloidogyne incognita Race-3 (Kofoid & White, 1919) Chitwood 1949	Wide host ranges but only root-knot nematode that attacks *Gossypium hirsutum* cv. Acala, which is a common crop to precede grapes	2,300
Meloidogyne javanica (Treub, 1885) Chitwood 1949	Single egg mass from roots of Thompson Seedless collected from Dinuba, CA. It is an aggressive population associated with yield reductions of Thompson Seedless, whereas mixed *Meloidogyne* spp. is not expected to be aggressive.	1,100
Meloidogyne arenaria pt. Harmony (Neal, 1889) Chitwood 1949	Single egg mass of galling root-knot nematode found to attack Harmony rootstock by Cain et al. in 1984.	800
Mixed *Meloidogyne* spp.	Mixture of *Meloidogyne incognita, M. javanica,* and *M. arenaria,* which is very common in Fresno, Kingsburg, and Madera areas of California.	9,900
Phylloxera + mixed *Meloidogyne* spp.	Mixture of phylloxera, *Meloidogyne incognita, M. javanica, M. arenaria, Xiphinema index* and *Pratylenchus vulnus.* This mixture is associated with shallow hardpan soil near Malaga and Delano, CA.	1,800
Xiphinema index Thorne & Allen, 1950	Population collected from Soledad, CA, and reared on *Ficus carica* for one year and free of grape fan leaf virus	1,300
Xiphinema americanum sensu stricto	Population collected from Kearney Agricultural Center inoculated into microplots planted to Sudan grass, *Sorghum halepense* cv. Piper, one year before trial established.	900
Pratylenchus vulnus Allen & Jensen, 1951	Population collected from roots of plum, *Prunus,* and reared on walnut, *Juglans niger.*	660
Tylenchulus semipenetrans Cobb, 1913	Population collected from *Citrus sinensis* L. cv. sour orange, Sanger, CA.	7,500
Meloidogyne chitwoodi pt. 1613	Populations collected from Dinuba and Livingston, CA.	1,900
Mesocriconema xenoplax (Raski), Luc & Raski, 1981	Population collected from peach orchard located near Parlier, CA.	1,700/250 cm^3 of soil

as susceptible standards for comparison of nematode reproduction on roots of test grape rootstocks.

Plant and nematode population measurements: Shoot weights of each vine were collected 10 mon after inoculation, and two vines of each triangle of vines were removed to quantify their root and shoot mass. The single remaining vine root was always the largest vine of the three and was allowed to grow for an additional year, when its shoots were removed and weighed. Final top weight data were gathered and added to the mean top weight data of the previous year to provide a value for total growth per vine. Root mass of two of the three vines in each triangle was removed by digging all the roots from a 45-cm-diam., 45-cm-deep hole, washing and screening to remove soil, evaluating roots for visual symptoms and then weighing their fresh biomass. After weighing the fresh roots, a 10 g sample of small feeder roots from each root system was excised, placed in a mist chamber for 5 d, and the extracted nematodes were counted under ×40 magnification. An eight-core composited soil sample was taken from the center of each triangle of three vines, and a sub-sample of 250 cm^3 for each composite was extracted for nematode assessment. All samples for *X. americanum* were extracted by a combination of Cobb sieving and 5-d mist extraction (McKenry and Roberts, 1985). *Xiphinema index* was extracted by Cobb sieving followed by filtration through cheesecloth over Baermann funnels for 5 d. All soil samples of *M. xenoplax* were extracted by Cobb Sieving followed by sugar centrifugation in a 1.3 M sugar solution (McKenry, 1992). Nematodes were viewed under a dissecting microscope, counted at ×40, and reported per volume of soil.

Host status assessment: As reported in previous papers (McKenry et al., 2001a, 2001b), the grape rootstocks were graded resistant if nematode reproduction was ≤0.2 endoparasites/g root or ≤2% of the nematode carrying capacity of Thompson Seedless for ectoparasites. They were graded moderately resistant if nematode counts were 0.21 to 0.60 endoparasites/g root or 2% to 5% of the nematode carrying capacity of Thompson Seedless for ectoparasites. Thompson Seedless is the most common root system for California vineyards. Vines were graded susceptible if there were 0.61 to 180 endoparasites/g root or >5% of the nematode carrying capacity of that on Thompson Seedless for ectoparasites. Vines were graded highly susceptible if there were 180 or more endoparasitic nematodes/g root or the carrying capacity for ectoparasitic nematodes exceeded that of Thompson Seedless by 1.8-fold.

Data analysis: A log (n + 1) transformation of the data was performed prior to analysis of variance. Data were analyzed with SAS statistical software (version 8.1; SAS Institute, Inc., Cary, NC). Significant differences in means of nematode reproduction were separated using Duncan's multiple range test ($P = 0.05$).

Results

Nematode reproduction: Reproduction of root-knot nematode was assessed as number of second-stage juveniles (J2) per gram of fresh root weight. All cultivars

Table 2. Nematode population per gram of root from grape rootstocks 10 mon after planting.[1]

Grape rootstocks	*M. incognita*	*M. javanica*	*M. arenaria* *M. incognita* *M. javanica*	*M. arenaria* *M. incognita* *M. javanica* *X. index* *P. vulnus* *Phylloxera*	*M. arenaria* pt. Harmony	*P. vulnus*	*T. semipenetrans*	Nematodes/250 ml^3 *M. xenoplax*	*X. index*	*X. americanum*
Experiment 1										
Flame S.	72c	27b	544d	410c	134ab	121a	168d	131a	6a	32a
Thompson S.	28b	35b	330c	232c	264d	51a	189d	82a	4a	100a
Rubired	8a	1a	28a	50ab	146ab	26a	2a	117a	15b	51a
Dog Ridge	0.03a	0.01a	0.01a	1a	216bc	4a	4a	106a	1a	15a
1613C	0.13a	0.1a	0.4a	3a	194bc	1a	70bc	88a	0.3a	72a
Harmony	0.51a	0.1a	0.01a	0.33a	526e	3a	73c	102a	1a	52a
Freedom	0.01a	0.1a	0.1a	0.33a	216bc	1a	10ab	92a	0a	10a
Schwarzmann	7a	0.3a	52a	83ab	311d	1a	38abc	74a	0.2a	13a
VR 039-16	3a	3a	218b	113b	63a	98a	7a	—	0.1a	5a
171-6	2a	—	0.6a	—	66a	13a	5a	—	0.0a	—
Experiment 2										
Thompson S.	67ab	132b	361b	136b	216a	—	—	82a	37b	128a
Ramsey	0.1a	0.2a	0.3a	3a	109a	0.1a	0.3a	186a	3a	91a
K51-32	0.2a	1a	3a	2a	58a	0.2a	21a	131a	3a	58a
Teleki 5C	1a	0.4a	6a	0.5a	64a	10c	29a	120a	3a	92a
SO4	0.1a	0.1a	0.03a	0.01a	5a	1a	0.2a	—	4a	101a
99 Richter	160bc	7a	52a	91ab	84a	9a	1a	131a	20a	36a
3309C	291c	80ab	454c	539c	601b	1a	5a	140a	7a	57a

[1]Means in each column followed by a different letter are significantly different at $P = 0.05$ according to Duncan's Multiple Range Test.

were susceptible to the 'Harmony' population of *M. arenaria* (Table 2). Harmony supported the greatest number of J2 (526) and SO4 the least (5) per gram of root. All the root-knot nematode populations increased the most on roots of Flame Seedless and Thompson Seedless, the susceptible control cultivars. Reproduction of common *Meloidogyne* spp. was suppressed by Dog Ridge, Ramsey, 1613C, Harmony, Freedom, K 51–32, SO4 and Teleki-5C.

Reproduction of *P. vulnus* was greatest ($P = 0.05$) on roots of Flame Seedless, Thompson Seedless, Rubired, VR O39–16, and 99R, whereas on all other cultivars its reproduction was minimal. Rubired, Dog Ridge, Ramsey, SO4, and 99R cultivars were poor hosts for *T. semipenetrans* compared to all other cultivars.

Population levels of the three ectoparasitic nematode populations were influenced by cultivar in both experiments (Table 2). The final population of *X. index* was greater ($P = 0.05$) on Rubired and Thompson Seedless in experiment 2 than on all the other cultivars (Table 2). Final population levels of *X. americanum* were not different among the tested cultivars in both experiments (Table 2). After 10 months, the population of *M. xenoplax* was similar on all grape cultivars (Table 2).

Vine growth: There were growth differences between vines inoculated or not inoculated with specific nematodes, and these differences varied among grape cultivars (Table 3). Eighteen months after inoculation, there were examples of significant increases or decreases in vine growth as well as nonsignificant growth responses. The 'Harmony' population of *M. arenaria* resulted in significant ($P = 0.05$) damage to each of nine vine cultivars. By contrast, inoculation of the *X. americanum* population stimulated ($P = 0.05$) growth of 11 of 16 vine cultivars to which it was exposed.

Meloidogyne incognita significantly ($P = 0.05$) reduced growth of only one selection, Flame Seedless, but stimulated growth ($P = 0.05$) of three others including Schwarzmann, Ramsey, and K51–32 (Table 3).

Inoculations with *M. javanica* stimulated growth ($P = 0.05$) of five of 16 cultivars tested, including Harmony, Freedom, Ramsey, K 51–32, and SO4.

Mixtures of *Meloidogyne* species were present in two different inoculum sources. A mixture of *M. incognita*, *M. javanica*, and *M. arenaria* resulted in damage ($P = 0.05$) to seven selections while stimulating growth of three resistant rootstocks, Harmony, Freedom and Dog Ridge. Inoculation with a broader mixture of soil pests, including *Meloidogyne* spp. plus *X. index*, *P. vulnus* and phylloxera, resulted in damage ($P = 0.05$) to four selections and stimulation of one cultivar, Freedom (Table 3).

Inoculations of *P. vulnus* suppressed growth ($P = 0.05$) of two selections, Flame Seedless and Rubired, and stimulated growth of Dog Ridge, Freedom, Ramsey and 3309C.

Inoculations with *T. semipenetrans* did not suppress growth ($P = 0.05$) of any selection but significantly stimulated growth of three, Freedom, Ramsey, and 3309C. Although SO4 also exhibited resistance to this nematode, its growth was not affected by inoculation with the nematode.

TABLE 3. Fresh vegetative vine growth (g) of grape rootstocks 18 mon after planting in the presence of various nematodes.

Experiment 1											
Grape rootstocks	Noninoc check	*M. incognita*	*M. javanica*	*M. arenaria* *M. incognita* *M. javanica*	*M. arenaria* *M. incognita* *M. javanica* *X. index* *P. vulnus* *Phylloxera*	*M. arenaria* pt. Harmony	*P. vulnus*	*T. semipenetrans*	*M. xenoplax*	*X. index*	*X. americanum*
Flame S.	1186b	569ef	1062bc	417fg	252g	431fg	754de	1164bc	980cd	944cd	1606a
Thompson S.	956bcd	1087bc	1136bc	727d	264e	424e	933cd	1230b	760d	1071bc	1512a
Rubired	1018bc	903cd	934cd	807d	779d	404e	834d	1115b	900cd	1054bc	1294a
Dog Ridge	1782c	1889c	2019bc	2709a	1997bc	823d	2686a	1846c	1470cd	1912bc	2206b
1613C	2377ab	2533ab	1886b	2264ab	2123ab	1071c	2570a	2215ab	1260c	2638a	2778a
Harmony	1694cd	1798bc	2156a	2082ab	1359d	365e	1469de	1506cd	1150d	1688cd	2124ab
Freedom	2190e	2934bc	2723cd	3536a	2397de	427f	3723a	2606cd	1290e	3438a	3285ab
Schwarzmann	1580c	2071a	1589c	980e	1115de	986e	1567c	1428cd	1120d	1649bc	1936ab
VR 039-16	584b	620b	583b	413cd	363d	277d	539bc	557bc	—	553bc	1041a
171-6	—	984b	—	790ab	—	464c	906ab	1089a	—	985b	—
Experiment 2											
Thompson S.	875a	891a	722ab	475c	708ab	605bc	945a	946a	760b	1181a	945a
Ramsey	670d	1180abc	1450ab	910cd	980cd	860cd	1230abc	1040bcd	1080a	960cd	1590a
K 51-32	1050cd	1950ab	2210a	1300bcd	1820abc	860d	1550abcd	1450abcd	1630a	1240bcd	1830abc
SO4	1380bc	1750abc	2250a	1540bc	1670abc	1140c	1590bc	1260bc	—	1340bc	1880ab
Teleki-5C	1740bcd	2200ab	2570a	1790bcd	1890bcd	1370d	1880bcd	1520cd	1180de	1340d	1330d
99 Richter	930ab	710b	1230a	750b	740b	780b	1250a	1050ab	610bc	1030ab	1240a
3309C	1060bc	1160ab	1350ab	720c	720c	740c	1452ab	1430ab	1250a	1240ab	1510a

[1]Means in each column followed by a different letter are different at $P = 0.05$ according to Duncan's Multiple Range Test.

Inoculations with *X. index* stimulated ($P = 0.05$) growth of Thompson Seedless in experiment 2 but not in experiment 1. *Xiphinema index* suppressed growth ($P = 0.05$) of only one cultivar, Flame Seedless. The population levels of this nematode were low.

Inoculations with *M. xenoplax* suppressed growth of six of 14 cultivars, but stimulated growth ($P = 0.05$) of Schwarzmann.

Three cultivars that exhibited significant ($P = 0.05$) growth suppression on the greatest number of occasions included Flame Seedless, Thompson Seedless, and Rubired. These selections all belong to *Vitis vinifera*, though the parentage of Rubired is complex.

Three cultivars (Ramsey, K51–32, and Freedom) exhibited the highest incidence of growth stimulation ($P = 0.05$) across all 10 nematode inoculations.

Discussion

One goal of our studies was to identify vine cultivars tolerant or intolerant of nematode feeding. In previous work, we characterized these same cultivars for their nematode resistance or susceptibility using a scale based on nematodes per gram of root or per volume of soil (McKenry et al., 2001a, 2001b). Here, we were able to show that a number of factors influenced vine growth by coupling vine growth responses with nematode population development.

The vine cultivars tested were products of three distinct evaluation programs. Cultivars Flame Seedless, Thompson Seedless and Rubired were selected for the flavor, color, size, and quality of their fruit. Cultivars 3309C, SO4, Teleki 5C, 99R and Schwarzmann were selected for their tolerance or resistance to phylloxera, an insect that can gall roots or leaves of grape. As part of those screenings for resistance, phylloxera galls were acceptable at root tips but not further back on suberized roots. The remaining seven cultivars were selected originally for their avoidance of all galls produced by *Meloidogyne* spp. or *X. index*.

Screening activities that focus on fruit traits have provided the impetus to search for rootstocks with resistance or tolerance to the presence of soil borne pests. This study indicates that screening activities in search of phylloxera "resistance" provided the best opportunity for finding tolerance to soil-borne pests including these nematode populations. It appears that 99R, Teleki 5C, and SO4 provided the best examples of tolerance because they continued to grow well in the presence of high nematode population levels (Table 4).

Cultivars originally selected for nematode resistance frequently received growth stimulation in the presence of nematode probing and penetration. Growth of rootstocks selected for greatest nematode resistance (Freedom, Ramsey, and K51–32) was stimulated more often than suppressed, but development of more virulent nematode populations resulted in loss of resistance and tolerance (Cain et al., 1984). Growth stimulation associated with many of these rootstocks in the presence of a less-pathogenic nematode, *X. americanum*, should not be considered tolerance.

The nematode populations studied here included some having quite different reproduction rates. Those nematodes completing their life cycle within 30 days include *Meloidogyne* spp., *M. xenoplax* and *X. index* (Seshadri, 1964; De Guiran and Ritter, 1979; Raski, 1988). Those with slower reproduction rates include *X. americanum*, which has a four-year life cycle (Halbrendt and

Table 4. Profile of significant vine-nematode interactions and likelihood of favorable or unfavorable vine growth in the first two yr.

Grape rootstocks	*Meoidogyne* spp./populations		*P. vulnus*	*T. semipenetrans*	*M. xenoplax*	*X. index*	*X. americanum*	Likelihood of favorable growth (%)
	Common	Aggressive						
Freedom	4R, 3st	HS, inhib	S, st	S	S	R, st	S, st	50
Ramsey	4R, 1S, 2st	SD	R, st	R	S, st	S	S, st	50
K51-32	1R, 2st	S	R	S	S, st	S	S	30
Dog Ridge	3R, 1st	HS, inhib	S, st	S	S	S	S, st	20
Harmony	4R, 2st	HS, inhib	S	S	S	R	S, st	20
3309C	S	HS	S	S	S, st	S	S, st	20
SO4	4R, 1st	S	S	R		S	S	10
Teleki 5C	2R, 1st	S	S	S	S	S	S	10 unfavorable growth
99R	S	S	S	ss	S, inhib	S	S	10
Thompson S.	S, 1 inhib	HS, inhib	S	HS	S	S	S, st	10
1613C	2R, 1S	HS, inhib	S	S	S, inhib	S	S, st	10
Schwarzmann	2R 1st, 2 inhib	HS, inhib	S	S	S, inhib	R	S, st	30
O39-16	1HS, 3S, 2 inhib	S, inhib	S	S		R	S, st	20
Rubired	S, 2 inhib	S, inhib	S, inhib	ss	S	S	S, st	30
Flame S.	S, 3 inhib	S, inhib	S, inhib	S	S, inhib	S, inhib	S, st	60

[1]Nematode reproduction: R = resistant ≤ 0.60 nematodes/g root or for ectoparasitic nematodes a nematode carrying capacity 50-fold lower than Thompson Seedless; S = susceptible 0.61 to 180 nematodes/g root; HS = highly susceptible 181 or + nematode/g root; st = stimulation, vine growth is significantly greater than check vines, inhib = inhibition, vine growth is significantly rediced over check vines.

Likelihood of favorable or unfavorable growth in first two years is based on percent incidence of stimulatory or inhibitory plant growth, e.g., Freedom growth was significantly improved 50% of the time it was planted into nematodes but Flame Seedless growth was significantly inhibited 60% of occasions when planted into nematodes.

Brown, 1992), and citrus nematode, with a life cycle of about 60 days (Van Gundy, 1958). An important result of this two-year trial was that the fastest developing populations were associated with greatest nematode damage.

Seinhorst (1965) reported that nematode infection might lead to growth stimulation or growth reduction, depending upon nematode density. The difference in plant growth might be a result of interactions between inhibitory and stimulatory processes (Wallace, 1971). The work presented in this paper compliments the hypotheses of Seinhorst (1965) and the measurements from annual crops conducted by Wallace (1971). Wherever the stimulatory processes exceed the inhibitory processes, the plant will express a level of tolerance. Conversely, where inhibitory growth processes predominate, it is recognized as intolerance. In this study, there were associations between resistant vines and vines that are stimulated to grow in the presence of the nematode.

Based on these results, we could distinguish four observable mechanisms that could lead to the designation of tolerance: 1) The aggressive 'Harmony' population of *M. arenaria* does not feed and reproduce on suberized roots of Teleki 5C or Schwarzmann. The result is feeding and reproduction restricted to younger roots, not enough to refer to the rootstock as resistant but relative to these other rootstocks the term tolerant could be used instead. 2) Tolerance is evident in 3309C and 99R. The nematode population develops to high levels but vine growth is unimpaired. The neck of female *Meloidogyne* spp. is not deeply sunken into cortical cells, and apparently the nematode is less disruptive of vascular bundles deeper within the root. This can be observed by removing soil from root surfaces and examining for the distended bodies of globose adult females along the surface of older and younger roots. In addition, it is probably not a coincidence that these same rootstocks exhibit a slight degree of resistance to the cortical feeder, *T. semipenetrans*. 3) Ramsey exhibits a far-reaching root system. This root architecture serves to separate root tips from one another. Stretching the distances between nematode feeding sites could serve to reduce the success of *Meloidogyne* spp., thus lowering nematode population levels and eventual plant damage. 4) The growth stimulating response of Freedom, Ramsey, K 51-32, and SO4 to nematode feeding is a form of tolerance associated with resistance. However, development of aggressive populations such as *M. arenaria* pt. Harmony can produce intolerance. From the grower's perspective, in the presence of nematode feeding, what is the anticipated damage level when compared to no nematodes? The summary column in Table 4 indicates the chances that growth will be significantly inhibited or stimulated depending on cultivar planted. Accuracy of any such estimates is improved by knowing which nematodes are present in the field.

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