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Developmental Response of a Resistance-Breaking Population of *Meloidogyne arenaria* on *Vitis* spp.

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

Abstract: Pre- and post-infection resistance mechanisms expressed by *Vitis* rootstocks RS-9 and Teleki 5C against second-stage juveniles (J2) of resistance-breaking populations of *Meloidogyne arenaria* were observed and correlated with juvenile development and nematode reproduction. Cabernet Sauvignon grape was used as a susceptible control for comparison. Similar numbers of J2 penetrated Teleki 5C and Cabernet Sauvignon roots. Root-tip necrosis, a hypersensitive reaction, occurred in both rootstocks but was effective in reducing J2 penetration only in RS-9 roots. Juvenile development occurred in roots of all three rootstocks by 13 days after inoculation, with the highest number of swollen juveniles present in Cabernet Sauvignon roots. Cortical necroses restricted the ability of J2 to reach vascular bundles, thereby restricting access to successful feeding sites and leading to dead or underdeveloped juveniles in RS-9 roots. At 35 days after inoculation, only 5% and 25% of the initial inoculum in RS-9 and Teleki 5C roots, respectively, reached the adult stage compared to 32% in Cabernet roots. Giant cells were of sufficient size to support nematode development to maturity in Cabernet. Cell necrosis and underdeveloped giant cells were apparent in the resistant rootstocks, which delayed development of adults and limited egg production. Inadequate development of giant cells may provide long-term population reductions in woody-rooted perennial crops.

Key words: development, grape rootstock, hypersensitive reaction, *Meloidogyne arenaria* Harmony population, nematode, penetration, reproduction, resistance.

The root-knot nematode *Meloidogyne* spp. is a very common pest of grapevines, *Vitis* spp. New damaging pathotypes or biotypes of this pest are a common occurrence, especially when rootstocks with only partial resistance are used and resistance-breaking populations are preferentially selected from the normal population. Survey work by the junior author has revealed a number of resistance-breaking populations of *Meloidogyne* spp. (Cain et al., 1984). Using a 2-year field exposure screen, a population of *M. arenaria* isolated from resistant Harmony grape rootstock was found to break root-knot nematode resistance of every rootstock challenged. However, two rootstocks selected half a century earlier for resistance to phylloxera, *Daktulosphaeria vitifoliae,* reduced population buildup of this nematode pathotype and restricted root-knot nematode gall development to younger roots of Teleki 5C, a Hungarian selection, and Schwarzmann, a selection from Germany (McKenry, unpubl.) Schwarzmann was also shown to be moderately resistant to *M. javanica* and to possess resistance to *Xiphinema index*. Teleki 5C is also of interest because it possesses slight resistance to a diversity of nematode genera attacking grape (Anwar et al., 2002).

Nematode-resistant plants may express resistance mechanisms during penetration, development, or reproduction of the nematodes (Anwar and McKenry, 2000). Penetration by *Meloidogyne* spp. occurs just behind the root tip, and subsequent development is influenced by plant genotype (Ferris et al., 1982). Juveniles may enter roots of susceptible or resistant plants in about equal numbers (Moura et al., 1993; Schneider, 1991; Windham and Williams, 1994) but also in different numbers (Ferris et al., 1982; Lawrence and Clark, 1986; Powers et al., 1992). Subsequently, fate of juveniles is determined by the root resistance factors. The mechanisms to limit entry of root-knot nematodes include morphological and pre-existing factors such as nematode repelling exudates (Jatala and Russell, 1972) and induced responses such as plant hypersensitivity (Anwar and McKenry, 2000). Some mechanisms affect post-penetration development by activating physiological processes within the roots to prevent or delay juvenile development and limit reproduction (Anwar and McKenry, 2000; Creech et al., 1995; McClure et al., 1974a, 1974b; Minton, 1962).

Effects of the plant on nematode reproduction, measured by the number of juveniles or eggs produced and root-gall development, commonly define resistance to root-knot nematodes. Reports vary with regard to root-knot fecundity. Powers et al. (1992) observed more eggs per female on resistant compared to susceptible plants. No effect or few eggs per female (Person- Dedryver, 1988) or complete lack of reproduction on resistant plants (Anwar and McKenry, 2000) also have been reported. Absence of galling does not always indicate that nematodes have not reproduced, as reproduction may occur in the absence of galls (Cook and Evans, 1987).

Little has been reported on the mechanisms of nematode resistance in grape (Lider, 1954). This study involves comparison of nematode developmental rates of a single resistance-breaking population of *M. arenaria* in roots of partially resistant Teleki 5C and RS-9 compared to the susceptible Cabernet Sauvignon. Our goal was to characterize mechanisms of resistance encountered by juveniles during the infection process and the effects of each rootstock on nematode development.

Materials and Methods

Grape rootstocks: Two grape rootstocks with varying sources of resistance were selected to assess the development rate of *M. arenaria*. Teleki 5C is a hybrid of *V.*

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[1] Postdoctoral Researcher and [2] Nematologist, University of California, Department of Nematology, Riverside, CA 92521.
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E-mail: anwar@uckac.edu; mckenry@uckac.edu
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berlandieri x *V. riparia*. The RS-9 rootstock is a recent hybridization of *V. champinii* cv Ramsey with Schwarzmann (*V. riparia* × *V. rupestris*) carried out by David Ramming at the USDA Plant Breeding Station in Fresno, California. The cross was made to take advantage of the resistance in Ramsey against endoparasitic nematodes and the resistance in Schwarzmann to ectoparasitic nematodes. Rootstock RS-9 offers improvements in nematode and phylloxera resistance over commercially available lines including resistance to a resistance-breaking population of *M. arenaria*. Cabernet Sauvignon, *Vitis vinifera* was used as a susceptible control for comparison.

Generation of grape seedlings: Plants of rootstocks were grown from shoot-tip cuttings by placing them in a bed consisting of a 2.5-cm-thick layer of autoclaved sand layered over a 5-cm-thick layer of a peat-perlite mixture (50:50). Propagation beds were irrigated by a water mist of 30-second duration every 9 minutes in a greenhouse maintained at 30 °C. Plants of uniform root and shoot size were selected and transplanted into Deepots (Stewe and Sons, Corvallis, OR) of 5-cm-diam. × 25-cm-depth filled with autoclaved sand. The Deepots were watered immediately with Hoagland's solution. Plants were allowed to grow for 7 days to heal injuries before nematode inoculation. Plants were fertilized with Hoagland's solution biweekly.

Nematode inoculum: The population of *M. arenaria* was obtained from Harmony rootstock in a 25-year-old vineyard located near Livingston, CA. Hatched J2 were collected from roots using Baermann funnels placed in a mist chamber for 5 days. Suspensions of J2 in tap water were adjusted to enable the desired inoculum density to be added in 10 cm^3 of water per plant. Plants of each rootstock and the Cabernet control were inoculated with 500 J2 of *M. arenaria* by injection on two sides of the plant. All plants were placed on a greenhouse bench in a completely randomized design with five replications for each of five root harvest dates.

Development and reproduction: The roots of five inoculated plants of each rootstock were harvested 4, 13, 21, 27, and 35 days after inoculation. Roots were washed free of soil, blotted dry and weighed. The whole root system of each plant at each harvest was stained with acid fuschin (Byrd et al., 1983) and spread in a film of glycerin between two glass plates. The glycerin improves optical qualities of the system, prevents drying, and helps to hold the plates together. Nematode penetration and development within the roots were determined under a dissecting microscope. Root systems of plants harvested 21, 27, and 35 days after inoculation were stained with Phloxine B (Holbrook et al., 1983) and assessed for the presence of egg masses, before staining with acid fuschin. The root systems were rated for galling and egg mass presence on a 0-to-5 scale (Quesenberry et al., 1989), where 0 = no galls or egg masses, 1 = 1 or 2, 2 = 3 to 10, 3 = 11 to 30, 4 = 31 to 100, and 5 > 100 galls or egg masses per root system. The number of nematodes in each stained root system was recorded at each sampling date. Nematodes were classified into four developmental stages (Anwar and McKenry, 2000): vermiform, non-swollen J2; swollen, sausage-shaped J2; globose, subspherical juveniles exhibiting a spiked tail; and adult (fully developed female with or without eggs).

At each harvest the roots of all three grape rootstocks were examined under a dissecting microscope followed by a compound microscope to assess the number of hypersensitive loci developed in response to juvenile infection. Depending on location of the loci within the root region, they were designated as epidermal, cortical, or vascular. The nematode-infected roots of the three rootstocks were microscopically examined to compare the occurrence of hyperplasia and hypertrophy of the cells surrounding the feeding sites.

At 35 days after inoculation, five plants of each cultivar were harvested to assess the number of eggs per root system. Eggs were extracted from galled roots by sealing the roots in mason glass jars containing 800 ml 2% NaOCl (Hussey and Barker, 1973) and agitating them for 4 minutes at 200 cycles min^{-1} on a mechanical shaker (Eberbach, Ann Arbor, MI). This shaking was followed with a thorough rinse in tap water, and eggs were counted at ×40. The previously recorded root weight was used to calculate eggs per gram of root.

Statistical analysis: Analysis of variance (SAS Institute, Inc., Cary, NC, was performed; and a separate analysis was conducted for each sampling date. Means were compared with Duncan's multiple-range test.

Results

Meloidogyne arenaria recovered from Harmony rootstock developed and reproduced on roots of resistant and susceptible grape rootstocks (Table 1). The penetration and subsequent development of J2 in roots were differentially influenced by the grape rootstocks tested. Many nematodes had successfully penetrated roots by 4 days after inoculation. The roots of Teleki 5C and Cabernet contained several times more J2 than RS-9 ($P = 0.05$). In Cabernet most of the J2 were located

Table 1. Penetration and development of a resistance-breaking population of *Meloidogyne arenaria* in roots of three grape rootstocks.

	Nematodes per root system					
	Days after inoculation					
Rootstocks	4	13	21	27	35	Eggs/g root
Cabernet (check)	296 a	294 a	272 a	225 a	173 a	403 a
Teleki-5c	282 a	254 a	232 a	183 b	128 b	34 c
RS-9	52 b	88 b	49 b	38 c	25 c	81 b

Data are means of five replications. Means in a column followed by a common letter are not significantly different according to Duncan's multiple-range test ($P = 0.05$).

in galls; in the other two rootstocks, fewer J2 migrated into the developing vascular cylinder and fewer feeding sites were induced. Necrosis of root cells in the proximity of the root tip was common in Teleki 5C and RS-9 rootstocks and was not observed in the Cabernet rootstock. Hypersensitive reactions occurred in RS-9 roots, but not in Cabernet roots. Necrotic tissues surrounding the heads of 19% of the J2 in RS-9 roots were observed just behind the root cap and in adjacent cortical tissues (Fig. 1A). Fewer J2 were surrounded by necrotic tissues and were located close to the root tip in Teleki 5C.

At 13 days after inoculation, juvenile development was evident in all three grape rootstocks, although at variable rates. The total number of vermiform and swollen J2 was similar in Teleki 5C and Cabernet roots; however, the number of juveniles was one third less in RS-9 roots compared to the other two rootstocks (Table 1). Juvenile development was most rapid in Cabernet roots, with 86% swollen J2, compared to 9% and 5% in Teleki 5C and RS-9, respectively. At 13 days 91% and 64% of J2 remained vermiform in Teleki 5C and RS-9 roots, respectively, compared to only 14% in Cabernet roots (Fig. 1B). The number of necrotic J2 infection sites increased from 19% to 31% during this time in RS-9 roots (Fig. 1B). Necrosis was absent in Cabernet and Teleki 5C roots.

At 21 days, development of juveniles to swollen or globose stages or to adult females was significantly delayed in RS-9 roots only, which still contained 10% vermiform juveniles. By contrast, a greater number of nematodes was present in Teleki 5C and Cabernet roots (Table 1), which developed at similar rates and resulted in similar numbers of adult females without egg masses (Fig. 1C). Numbers of adult females without eggs masses in RS-9 were significantly ($P = 0.05$) fewer compared to those in roots of the other two rootstocks (Fig. 1C). Roots of Cabernet had more swollen J2 ($P = 0.05$) compared to the other two rootstocks (Fig. 1C).

The swollen J2 stage persisted longer in resistant RS-9 roots, with 10% of juveniles still in this stage 27 days after inoculation compared to the absence of swollen J2 stages in the other rootstocks (Fig. 1D). Cabernet roots contained twice the number of globose nematodes compared to the other rootstocks. The number of adult females with or without egg mass was similar in Cabernet and Teleki 5C roots and greater than those present in RS-9 roots ($P = 0.05$) (Fig. 1D).

At 35 days after inoculation, a high percentage of juveniles had reached the adult stage (94% in Cabernet, 98% in Teleki 5C, 81% in RS-9). However, the total number of nematodes (globose stages and adult females) was significantly ($P = 0.05$) greatest in Cabernet roots (Table 1; Fig. 1E). Roots of Teleki 5C contained five times more adult females than the RS-9 roots, but RS-9 contained twice as many globose stage nematodes (Fig. 1E).

Galls on the Cabernet root systems were visible 13 days after inoculation, with a mean index rating of 3.0. Galls on the root systems of the other two rootstocks could be seen only under the dissecting microscope. By 21 days after inoculation, the mean gall index on roots of Cabernet had increased to 5. Microscopic galls on the RS-9 root systems were visible, with a mean gall index of 1.5. The Teleki 5C root system still did not exhibit galls. The gall index remained at 5.0 on Cabernet roots but increased to 2.5 on RS-9 at 27 days after inoculation. Egg masses were visible on Cabernet and RS-9 by this time. Neither egg masses nor eggs were found in Teleki 5C roots. The gall index for Cabernet and RS-9 was similar at 27 days after inoculation, but gall size on Cabernet roots was greater than that on RS-9 roots. Root galls were absent on Teleki 5C roots. Egg masses were largest on Cabernet, intermediate on RS-9, and smallest on Teleki 5C. The number of eggs per gram of root for Cabernet was 9 and 5 times greater than that for Teleki 5C and RS-9, respectively (Table 1), and number of eggs per gram of root was greater ($P = 0.05$) for RS-9 than for Teleki 5C.

Thirty-five days after inoculation, giant cells were fully developed in Cabernet roots, intermediate in RS-9, and only slightly developed in Teleki-5C roots. Cortical cells near feeding sites were enlarged in susceptible Cabernet and of intermediate size in RS-9. Hypertrophy and hyperplasia were less in Teleki 5C, and the giant cells were small.

Discussion

Roots of RS-9 and Teleki 5C rootstocks expressed biochemical defense mechanisms by developing root-tip necrosis in response to invading J2. Roots of RS-9 also demonstrated some resistance to J2 penetration, which further reduced the number of successful J2 entering RS-9 compared to Teleki 5C and susceptible Cabernet. The most obvious resistance mechanism to *Meloidogyne* species involves a hypersensitive reaction in which necrosis occurs around nematode feeding sites (Anwar and McKenry, 2000; Huang, 1985). This type of host reaction can act as a physical or biochemical barrier to prevent nematode penetration in roots of resistant plants. The reduced number of J2 in resistant RS-9 roots appears to be due to the development of root-tip and epidermal necrosis 4 days after inoculation (Anwar and McKenry, 2000). The reduced penetration rate into RS-9 roots is comparable to that previously reported for J2 of *M. arenaria* in roots of resistant grape rootstocks (Ferris et al., 1982) and for *Meloidogyne* spp. in resistant alyceclover roots (Powers et al. 1992).

Meloidogyne J2 usually penetrate roots of resistant cultivars, as in the case of resistant grape rootstock Teleki 5C. Penetration of roots of resistant and susceptible plants by equal numbers of *Meloidogyne* spp. has been reported (Sydenham et al., 1996) in *Phaseolus vulgaris*. Similar observations have been made for *M. incognita* J2

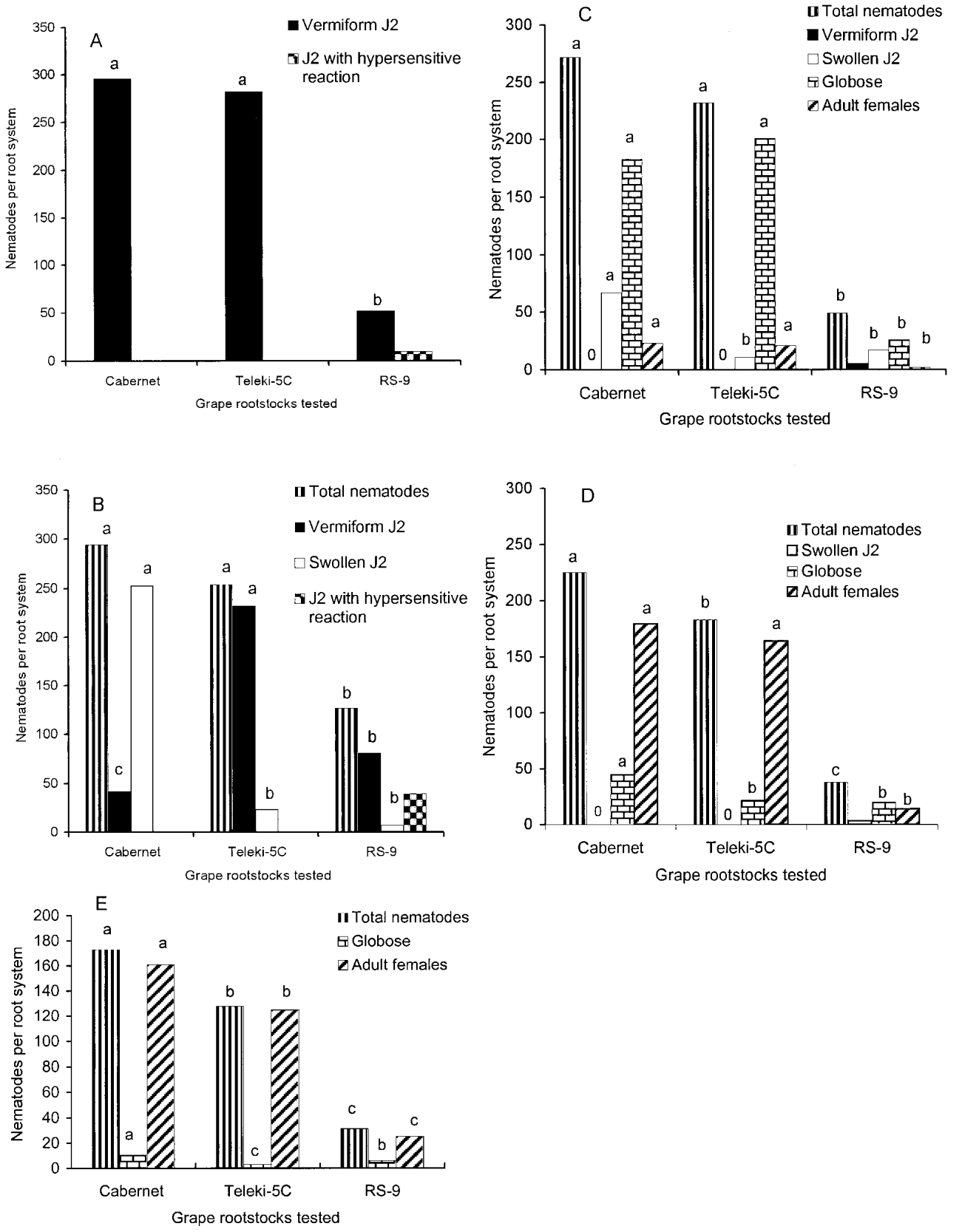

FIG. 1. Penetration and developmental life stages of a resistance-breaking population of *Meloidogyne arenaria* in roots of Cabernet, RS-9, and Teleki 5C grape rootstocks, 4 to 35 days after inoculation. A) 4 days. B) 13 days. C) 21 days. D) 27 days. E) 35 days after inoculation. Data are means of five replications. Bars with a common letter are not significantly different within a developmental stage among rootstocks, according to Duncan's multiple-range test ($P = 0.05$).

penetration into resistant and susceptible alfalfa cultivars (Potenza et al., 1996), corn (Windham and Williams, 1994), and cotton (Creech et al., 1995) and *M. javanica* penetration in tobacco (Schneider, 1991). *Meloidogyne* J2 may initially penetrate the roots of resistant cultivars, but in a few days they often leave roots of resistant cultivars, presumably due to the inability to initiate a successful feeding site (Hussey, 1985). Niblack et al. (1986) found a 27% reduction in the J2 population in roots of resistant cultivars compared to susceptible cultivars of soybean 14 days after inoculation. Similar observations have been reported for cotton (Minton, 1962), alfalfa (Griffin and Elgin, 1977; Potenza et al., 1996; Reynolds et al., 1970) and tomato (Hadisoeganda and Sasser, 1982). We observed 14% fewer J2 in Teleki 5C roots 13 days after inoculation. The limited number of J2 in Teleki 5C might be related to emigration of nematodes from roots (Reynolds et al., 1970). However, lower J2 numbers (82% less) in resistant RS-9 roots were constant at all five harvests throughout this experiment, suggesting that emigration was not a factor. This consistency in reduction in J2 population is comparable to that of *M. incognita* in resistant cotton roots (McClure et al., 1974a).

Cell necrosis in the feeding sites immediately around the head of root-knot nematode juveniles can limit further development and eventually reproduction (Dropkin and Nelson, 1960). Delayed development of juveniles, fewer juveniles, and fewer eggs per gram of root in resistant RS-9 roots might be related to discoloration and collapsed tissues surrounding the juveniles that blocked the flow of food (Anwar and McKenry, 2000). Cell necrosis in RS-9 may occur pre- and post-infection but does not occur once the globose stage has been attained. The limited development and reproduction of juveniles in roots of resistant RS-9 grape rootstock compared to the susceptible Cabernet roots suggest that RS-9 may use additional resistance pathways. However, some J2 were able to develop to a globose stage irrespective of the resistance mechanisms. Juveniles that successfully reached the globose stage eventually reached maturity. Some resistance mechanisms may be effective only at J2 penetration and at the transition of J2 to swollen and globose stages. These are comparable to earlier observations of development of *M. arenaria* in resistant 10–23B and RS-3 roots (Anwar and McKenry, 2000). Similar observations have been reported with *M. incognita* in resistant cotton (Jenkins et al., 1995) and *Phaseolus vulgaris* genotypes (Sydenham et al., 1996).

Three measurements, including (i) delay in ability of juveniles to develop to swollen J2 (Fig. 1B), (ii) limited numbers of juveniles progressing to adult females (Fig. 1E), and (iii) fewer eggs per gram of root in Teleki 5C, may indicate the involvement of post-infection mechanisms. This response might be due to the inability of juveniles to stimulate extensive cell hypertrophy. Cells lacking in hypertrophy have been associated with poorly developed juveniles with few eggs (Dropkin and Nelson, 1960). We also observed very small giant cells and no galls on the roots of Teleki 5C. The small giant cells are more likely related to resistance in Teleki 5C than the lack of hypertrophy.

The development of root-knot nematode galls is a response to stimulation by a secretory protein from esophageal glands that is injected by the infective juveniles (Hussey et al., 1994). Susceptible plants respond with the formation of giant cells and galls. The nematode responds with rapid juvenile growth and abundant egg production upon maturity. By contrast, the responses in resistant plants include poorly developed galls, undersized juveniles, and fewer eggs (Dropkin and Nelson, 1960). Underdeveloped giant cells, few eggs, smaller galls in RS-9, or no galls in Teleki 5C indicate the involvement of a genetic defense mechanism. The absence of galls on Teleki 5C roots suggests its defense system is stronger than that of RS-9.

Although this study was focused on the first 35 days of nematode-plant interaction, we believe that the mechanisms for resistance present in older roots might now be clearer. Root-knot nematodes can commonly be found on older roots of vines up to 10 years old. However, adult females live only for months so one hypothesis to explain root-knot habitation of older roots is that the nematode offspring of each gall replace the prior females at feeding sites. The mechanism of resistance in older roots of Schwarzmann and Teleki 5C may involve the inability of the initial female to develop adequate giant cells for subsequent offspring. Roots of Teleki 5C that are older than 6 months contain few root-knot nematode females or galls. In this study we did not examine RS-9 for egg production beyond 35 days, but this selection has remained resistant following a 2-year exposure to this same nematode population. In field settings these two rootstocks possess galls—but only on the periphery of the root system.

This research has contributed detailed information about the relationship between two grape rootstocks and a resistance-breaking field population of *M. arenaria*. Both RS-9 and Teleki 5C rootstocks developed root-tip necrosis but in different zones, which was found effective in reducing J2 population in RS-9 roots but not in Teleki 5C roots. Another mechanism we observed was cortical necrosis surrounding the nematode and necrosis of feeding sites at the vascular level only in RS-9 roots. The delay in development might be associated with vascular necrosis in RS-9 roots. The delay in development of juveniles in Teleki 5C roots might be related to the inability of juveniles to develop normal giant cells (Dropkin and Nelson, 1960). The production of egg masses on ungalled Teleki 5C roots suggests that gall formation is not essential for nematode reproduction in grape. This is also a common phenomenon of monocots.

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