

Consequences of *Mesocriconema xenoplax* Parasitism on Pinot noir Grapevines Grafted on Rootstocks of Varying Susceptibility

R. Paul Schreiner,^{1*} Inga A. Zasada,¹ and John N. Pinkerton¹

Abstract: Pinot noir grapevines grafted to five rootstocks (*Vitis vinifera*) and a self-rooted control known to vary in resistance to ring nematode (*Mesocriconema xenoplax*) were studied over four years to evaluate durability of resistance to ring nematode and to better understand how ring nematode parasitism affects below- and aboveground vine growth and physiology. Ring nematode populations in infested microplots of all three susceptible vines (self-rooted, 3309C, 1103P) increased rapidly during the second year and remained high throughout the study, while nematodes increased in two of the previously resistant rootstocks (110R, 101-14) during the third year. Only 420A remained resistant through the entire 4-year period. The impact of ring nematode parasitism on vines was most apparent in the susceptible rootstocks and self-rooted vines with reductions in fine root growth and colonization by arbuscular mycorrhizal fungi (AMF) occurring as early as the second year. Reductions in both fine root production and AMF colonization due to ring nematode were greater in subsequent years in the susceptible vines. The frequency of fine roots containing vesicles of AMF was reduced in all five rootstocks that supported a population increase of ring nematode (only 420A was unaffected). Ring nematode did not alter aboveground vine performance until the third or fourth growing season, when shoot lengths and pruning weights were reduced in the three susceptible vines. Ring nematode did not alter shoot growth in any of the three resistant rootstocks, nor did it affect leaf gas exchange or leaf water potential in any vines in any year. However, by year four ring nematode reduced fruit yield as a main effect across all rootstock treatments.

Key words: arbuscular mycorrhizal fungi, ring nematode, root growth, soil respiration, *Vitis vinifera*

The ring nematode, *Mesocriconema xenoplax* (Raski) Loof & de Grisse, is the most commonly encountered plant-parasitic nematode in western Oregon vineyards (Pinkerton et al. 1999) and an important pest in vineyards worldwide (Pinonchet and Cisneros 1986, Güntzel et al. 1987, Walker 1995). The ring nematode is a fastidious ectoparasite that may feed for up to eight days from a single cortical cell (Hussey et al. 1992). The nematode stylet invaginates the plasma membrane of a cortical “food cell” without penetrating it and plasmodesmata are modified such that nutrient flow probably increases into the cell. Such elaborate modifications may explain why grape roots show little noticeable damage from ring nematode (Raski and Radewald 1958, Nigh 1965, Schreiner and Pinkerton 2008).

The impact of this nematode on the growth and productivity of grapevines is poorly understood, as some studies have

reported no apparent reductions in vine shoot or root growth (Raski and Radewald 1958, Nigh 1965, Pinkerton et al. 1999), while others have (Klingler and Gerber 1972, Klingler 1975, Santo and Bolander 1977, Ambrogioni et al. 1980). McKenry (1992) estimated that ring nematode populations >500 kg⁻¹ soil reduced grape yields in California by 10 to 25%. Numerous mature vineyards in western Oregon also had populations exceeding >500 kg⁻¹ soil yet no reduction in crop yield was measured (Pinkerton et al. 1999). Young plantings are more likely at risk to ring nematode parasitism causing vigor or yield declines (Pinkerton et al. 2004).

McKenry et al. (2001) reported that all 14 grapevine rootstocks tested in microplots were susceptible to ring nematode but that seven of these appeared tolerant (based on vine weights) after 21 months. In another study, ring nematode reduced fruit yield of only one of 10 grapevine cultivars in a 6-year microplot study (Ramsdell et al. 1996). Pinkerton et al. (2004) observed that ring nematode reduced growth of 3- to 4-year-old self-rooted Pinot noir and Chardonnay vines planted in microplots. These studies suggest that the impact of ring nematode on grapevines varies with the grape cultivar, plant age, and other stresses on the plant. An understanding of this variability is an important consideration when trying to manage ring nematode through rootstock selection.

The ability of ring nematode to reproduce on a variety of grape rootstocks was recently evaluated in the greenhouse and in an experiment planted on an infested site (Pinkerton et al. 2005). Several rootstocks were classified as highly or moderately resistant to a population of ring nematode from

¹USDA-ARS, Horticultural Crops Research Laboratory, 3420 NW Orchard Ave., Corvallis, OR 97330.

*Corresponding author (email: Paul.Schreiner@ars.usda.gov)

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western Oregon, while many rootstocks commonly used in the region were classified as highly susceptible. Based on these findings, five rootstocks and self-rooted vines—two classified as highly resistant (420A, 101-14), one as moderately resistant (110R), and three as susceptible (self-rooted, 3309C, 1103P)—were chosen for further evaluation in field microplots.

One objective of this study was to better understand vine growth and physiological responses to ring nematode parasitism of resistant and susceptible rootstocks as well as a self-rooted vine. A second objective was to evaluate the durability of rootstock resistance to ring nematode over a longer time frame than the prior greenhouse evaluations using a system where nematode infested and noninfested vines could be directly compared. This article focuses on vine responses to ring nematode, highlighting the main effect of ring nematode treatment and interactions between ring nematode and rootstock treatments. Less emphasis is placed on the main (or direct) effect of rootstock on measured parameters.

Materials and Methods

Experimental design, soil, and vine management. A 6 x 2 factorial experiment with six different rootstocks (420A, 101-14, 110R, 1103P, 3309C, and self-rooted) and two levels of ring nematode (0 and 1.0 nematode g⁻¹ dry soil initial density) was applied to Pinot noir grapevines (*Vitis vinifera*, Wadenswil clone, FPS 02A) grown in large (100 L) pot-in-pot (Parkerson 1990) microplots (Grip Lip 10000; Nursery Supplies Inc., McMinnville, OR). Each treatment combination was replicated six times in a randomized complete block design for a total of 72 experimental units (microplots). The experiment was conducted at the Oregon State University, Woodhall Research Vineyard (OSU–WRV) located near Alpine, OR (44.568°N, 123.289°W).

The soil was a Jory series, silty-clay loam (fine, mixed, active, mesic Xeric Palehumult; containing 12% sand, 58% silt, 30% clay, and 5.5% OM) collected from the OSU–WRV. The experimental soil was mixed 2:1 (vol/vol) with coarse sand (Prestress sand mix, Knife River Inc., Corvallis, OR), and dolomite lime (50% CaCO₃, 40% MgCO₃) was added at a rate of 35 g kg⁻¹ dry soil to raise soil pH to ~6.0. The resulting soil mix and surrounding vineyard soil was fumigated with methyl bromide at a rate equivalent to 448 kg ha⁻¹ (Trident Inc., Vancouver, WA) under a plastic tarp in the summer of 2005. Microplots were arranged on a 1.8 x 2.7 m spacing and placed in augured holes. Soil was placed into pots in which the bottom of the inner pot was lined with copper screen to prevent root escape. Available soil nutrients were determined from a composite soil sample collected from the microplots on 1 May 2006 using standard methods for western Oregon soils (OSU, Central Analytical Laboratory, Corvallis, OR). Available soil nutrients (mg kg⁻¹) and pH were NO₃-N, 5.3; P (Bray 1), 14; K, 157; Ca, 1158; Mg, 285; SO₄-S, 77; Fe, 62; Mn, 70; B, 0.20; Zn, 1.2; Cu, 1.0; pH, 5.9.

Prior to grapevine planting, inoculum of arbuscular mycorrhizal fungi (AMF) comprised of four fungal species was incorporated into the upper half of soil in all microplots. A mixture of AMF was used, as grapevines are commonly

colonized by numerous species in natural vineyard systems (Schreiner and Mihara 2009). An equal mixture of pot-culture soil (30 g) containing spores, colonized roots, and hyphae of *Scutellospora calospora* (Nicol. & Gerd.) Walker & Sanders INVAM# OR219, *Funneliformis* (formerly *Glomus*) *mosseae* (Nicol. & Gerd.) Schüßler & Walker INVAM# OR218, *Rhizophagus* (formerly *Glomus*) *intraradices* (Schenck & Smith) Schüßler & Walker INVAM# OR216, and an unidentified *Rhizophagus* (formerly *Glomus*) sp. (small clear spores, isolated from the OSU–WRV) was added to each microplot. Each fungus was propagated on *Sorghum bicolor* L. and *Trifolium incarnatum* L. grown together in a sterilized low P, sandy loam soil in a greenhouse. Also prior to planting, a population of ring nematode (*Mesocriconema xenoplax*) originally isolated from the OSU–WRV (Pinkerton et al. 2005) and propagated on *Prunus* rootstock (GI 148/2) in the greenhouse was added to half of the microplots, taking care to avoid contamination of the surrounding soil and equipment. Nematodes were extracted from pot cultures using a wet-sieving sucrose flotation method and centrifugation (Jenkins 1964) and mixed together with moist vermiculite and sand to achieve a concentration of 1,000 nematodes g⁻¹. The vermiculite mixture (100 g) was added to each infested microplot and gently mixed into the soil in the upper half of the pots, so that each infested microplot received ~100,000 ring nematodes. A 20-cm long buriable, time domain reflectometry (TDR) waveguide (6005TU-L20; Soil Moisture Equipment, Santa Barbara, CA) was then installed vertically in half of the microplots (36 experimental units) at a depth of 10 cm below the soil surface halfway between the middle and side of the pots.

Green growing vines with a single shoot received from the nursery in soilless media were planted on 3 May 2006 into the microplots (1993 vines ha⁻¹). The single shoot was staked and grown without manipulation throughout 2006. In 2007, vines were two-budded, and after the threat of frost had passed, a single shoot was retained on all vines. Once all shoots attained a length of ~1.75 m, the main shoots were then cut at the fruiting wire (to establish the head) on 30 July 2007, and two laterals below the head (next year's fruiting canes) were retained for the rest of the 2007 season. In 2008, four buds on each fruiting cane plus two renewal buds (10 shoots total) were retained on each vine. Fruit clusters were thinned to one per shoot after fruit set in 2008 and carried to maturity. In 2009, eight buds were retained on each renewal spur from 2007 for a total of 16 shoots per vine. Fruit clusters were thinned also to one cluster per shoot in 2009. Vines were hedged at a height of 1.75 m aboveground in 2008 and 2009 in mid-July. Sulfur and other fungicides to control powdery mildew and bunch rot were applied as per normal practices in the region.

Vines were drip-irrigated using four pressure-compensating emitters (3.7 L hr⁻¹) per microplot attached to a ring of spaghetti tubing (to disperse water evenly throughout the pots) with an independent shut-off valve installed for each microplot. Irrigation inputs were carefully managed based on soil water content and vine water status. Volumetric soil water content (θ_v) was monitored every two to three days during

the summer months using TDR, and irrigation was applied whenever θ_v approached the target soil water content desired. θ_v at field capacity and the permanent wilt point (soil $\Psi = -1.5$ MPa) was previously determined using the same soil mix at a bulk density of 1.3 g cm^{-3} . θ_v at field capacity was 31% and θ_v at the permanent wilt point was 9% as determined with a psychrometer (SC-10; Decagon Devices, Pullman, WA).

In 2006 and 2007, vines were irrigated to field capacity whenever θ_v approached 15% to avoid any significant water stress in these establishment years. In 2008 and 2009, irrigation prior to fruit set was also applied when θ_v approached 15%, but irrigation was withheld after fruit set (in early July) on two consecutive irrigation cycles until shoot tips began to wilt in each of the different rootstocks to control canopy growth. Wilt tip in the field was found to occur at θ_v of 11 to 12% (corresponding to soil $\Psi \sim 0.5$ MPa) based on actual TDR measurements in microplots of the different rootstocks. Thereafter until harvest in 2008 and 2009 vines were irrigated when θ_v reached 13 to 14% volumetric soil water content (θ_v). However, vines were occasionally irrigated before reaching this target to accommodate work schedules. Stomatal conductance (Gs) and leaf water potential (Ψ_{leaf}) were measured periodically (at the beginning and end of an irrigation cycle) to confirm that water stress was moderate for grapevines (Gs $> 75 \text{ mmol m}^{-2} \text{ s}^{-1}$, leaf $\Psi \geq 1.3$ MPa; see Lovisolo et al. 2010) between fruit set and harvest. After harvest, vines were irrigated whenever θ_v reached 15%. Fertilizer was applied in late spring of each year ~ 1 month after budbreak (early May). Each microplot received 50 g of a complete fertilizer (20-10-20 with micronutrients; Peters Professional, Scott Chemical Co., St Louis, MO).

Nematode population densities in soil. Ring nematode population densities were estimated in the spring (April) and fall (October) each year, beginning in October 2006, although the spring 2007 sampling was postponed until July as populations were very low in October 2006 (after a single growing season). Nematodes were extracted from two soil cores (1.5 cm diam x 45 cm deep) collected from each microplot; core holes were filled with a fumigated soil mix after each sampling. Nematodes were extracted from the entire soil sample (after obtaining total soil fresh mass and removing a 10 to 20 g subsample to determine gravimetric soil water content [θ_g]) by a wet-sieving sucrose flotation and centrifugation method (Jenkins 1964) and enumerated under a stereomicroscope.

Vine root growth and AMF colonization. Vine root samples were collected near the time of veraison (late August) in each year. Samples from each microplot were comprised of one or two soil cores (3.0 cm diam x 45 cm deep) collected from each microplot halfway between the vine trunk and side of the pot. Core holes were filled with a fumigated soil mix after each sampling. Soil samples were stored at 4°C until root extraction within four days of collection. A small subsample (20 to 40 g) of soil was removed prior to root extraction to determine θ_g .

Roots were retrieved by a wet-sieving method (Böhm 1979) and separated into woody and fine root fractions under a stereomicroscope as described by Schreiner (2003). Woody

roots were blotted dry on paper towels, weighed, and their length was determined with a ruler. Fine roots were blotted dry, fresh weights were recorded, and roots were stored in FAA (formaldehyde/acetic acid/ethanol, 5%:10%:50%) for up to four months before clearing and staining to evaluate AMF colonization. Roots were cleared using KOH and H_2O_2 and stained with trypan blue (Schreiner 2003).

Fine root length was determined by the gridline intercept method (Newman 1966). Colonization of fine roots by AMF was determined on randomly selected root fragments mounted on slides using the method of McGonigle et al. (1990) as modified by Schreiner (2003). The proportion of fine root length containing any AMF structures (aseptate hyphae, vesicles, or arbuscules) and separate counts of only arbuscules or only vesicles was determined.

Soil respiration. Soil respiration was determined in 2007 and 2008 in the first week of July, August, and September. The alkaline trapping method (method 3.2; Anderson 1982) was used taking care to ensure that less than 20% of KOH had reacted with CO_2 released from the soil surface. CO_2 respired from the soil surface was expressed as $\mu\text{mol m}^{-2} \text{ s}^{-1}$.

Vine vigor. Shoot lengths were measured at bloom in each year. All shoots per vine were measured with a flexible tape measure. Dormant season pruning (fresh) weights from all vines were determined in the winter following 2006, 2008, and 2009 seasons by weighing the count shoots from the previous season. Data were not available after the 2007 season as we established the head that year in midsummer. Shoot fresh weights of the portion of the shoot removed in 2007 (to establish the head) were recorded.

Vine water status and gas exchange. Midday leaf water potential (Ψ_{leaf}) was measured periodically using a pressure chamber (model 610; PMS Instrument Co., Corvallis, OR). A fully sun-exposed, undamaged leaf was selected from the midcanopy within each plot and placed in a plastic bag prior to cutting the petiole with a razor blade. Leaves were measured within 1.5 hr of solar noon. Gas exchange (Gs) was measured periodically in the summer months, when possible on consecutive days at the beginning/end of an irrigation cycle, and was determined with a porometer (Li-Cor 1600, Li-Cor Inc., Lincoln, NE) or with a portable IRGA photosynthesis system (Li-Cor 6400). For both types of measurements, only fully exposed leaves (PAR $> 1700 \mu\text{mol m}^{-2} \text{ s}^{-1}$) were measured. Whenever possible, Ψ_{leaf} was measured immediately following gas exchange on the same leaves.

Vine nutrient status. Vine leaves used to determine nutrient status were examined at bloom (2008 and 2009) and at veraison (all years). Opposite cluster leaves were collected at bloom, and paired leaf samples comprising an opposite cluster leaf and a recently expanded leaf were collected at veraison from count shoots only. Leaf blades and petioles were separated, rinsed in distilled water, dried at 70°C for 48 hr, and ground in a Wiley mill to pass through a $425 \mu\text{m}$ sieve. Nitrogen was determined via combustion analysis (LECO, Inc., St. Louis, MO), and P, K, S, Ca, Mg, Mn, Cu, B, Zn, and Fe concentrations were measured by inductively coupled plasma-optical emission spectrometry (Optima 3000DV;

Perkin Elmer, Wellesley, MA) after microwave digestion in HNO_3 (Jones and Case 1990).

Fruit yield and composition. Yield data and fruit subsamples were collected on 13 Oct 2008 and 5 Oct 2009. All fruit clusters were removed from each vine, counted, and weighed. The average cluster weight was calculated by dividing the total yield per vine by the number of clusters. Subsamples consisting of five randomly selected clusters from each vine (selected after placing all clusters per vine on a large tray) were transported to the laboratory in coolers, stored at 4°C, and processed within two days. Berries were removed by hand and pressed in a small, stainless-steel, hand-crank press to obtain a juice yield of 625 mL kg⁻¹ fresh weight of clusters. Juice soluble solids (Brix) was measured with a hand-held refractometer (Leica Microsystems, Buffalo, NY) and pH was determined with a pH meter. Titratable acidity (TA) was determined by titration to a pH endpoint of 8.2, after cold storage of pressed samples overnight at 4°C.

Statistical analysis. Data were analyzed by analysis of variance (ANOVA) or by Kruskal–Wallis (K–W) nonparametric ANOVA by ranks for those variables that could not be transformed to satisfy assumptions of ANOVA (see below). θ_v (collected approximately every three days by TDR during the growing season) was analyzed as a repeated measure ANOVA within each year using rootstock and nematode treatment as factors. θ_g (assessed one time per year at veraison) was also analyzed by ANOVA in each year independently using rootstock and nematode treatment as factors. Ring nematode population densities were analyzed in the infested plots only (since noninfested plots remained nematode-free) using sample date and rootstock as factors. A Box–Cox transform and exclusion of the fall 2006 data (which was very low) was used to satisfy variance assumptions of ANOVA for ring nematode population densities. Fine root mass and AMF colonization parameters were analyzed within each rootstock independently using year and nematode as factors. Fine root mass was log-transformed to satisfy assumptions of homogeneity of variance. No transformations were needed to assess % AMF colonization, although AMF colonization in the self-rooted vines had to be analyzed using the K–W nonparametric test. Soil respiration was analyzed in each year separately using sample date (July, August, September), rootstock, and nematode treatments as factors, and was log-transformed to meet variance assumptions. Shoot length at bloom and dormant season pruning weights were analyzed in each year separately using rootstock and nematode treatment as factors. Gs, Ψ_{leaf} , and leaf and petiole nutrient concentrations were analyzed by ANOVA at each sampling time independently using rootstock and nematode treatment as factors. Fruit yield and berry parameters were analyzed using K–W nonparametric analysis in 2008 and standard ANOVA in 2009. In both cases, rootstock and nematode treatment were used as factors. Means were compared using Tukey's post-hoc test whenever ANOVA was used (standard error of the mean is shown in all tables following the mean values). Statistica software (version 8.0; Statsoft Inc., Tulsa, OK) was used for all analyses, and effects were considered significant at 95% confidence ($p < 0.05$).

Results

Weather and soil moisture. Weather patterns during the growing season (1 Apr to 30 Sept) over the four years of this study varied considerably. 2006 was warmer than usual with 1344 growing degree days (GDD) >10°C, 18 days with a maximum air temperature above 32°C, a daily average air temperature of 16.4°C, and 171 mm rainfall from April to September. 2006 was the warmest year in the region in the past 25 years. The following three growing seasons were closer to norms for the region. 2007 had 1212 GDD >10°C, six days with a maximum air temperature above 32°C, a daily average air temperature of 15.4°C, and 216 mm rain. 2008 had 1175 GDD >10°C, 13 days with a maximum air temperature above 32°C, daily average air temperature of 15.2°C, and 145 mm rain. 2009 was warmer, with 1282 GDD >10°C, 17 days with a maximum air temperature above 32°C, a daily average air temperature of 15.9°C, and 188 mm rain. Averages for the prior 10-year period (1996 to 2005) from April to September were 1239 GDD >10°C, 11 days with a maximum air temperature above 32°C, a daily average air temperature of 15.7°C, and 225 mm rainfall.

θ_v determined throughout each growing season by TDR was not affected ($p > 0.05$) by rootstock or nematode treatments in any year. Generally, θ_v (expressed as a percentage) declined over the growing season from high values of ~30% near budbreak to low values of 13 to 16% by the end of each irrigation cycle in mid- to late summer (data not shown). Gravimetric soil water content (θ_g) from the soil cores used for root collection was not altered ($p > 0.05$) by rootstock or nematode in 2006 or 2007, but was affected by rootstock ($p = 0.019$) and nematode ($p = 0.041$) in 2008. Self-rooted vines at veraison 2008 had slightly higher θ_g of 17.9 ± 0.9 % than vines on 101-14 (14.5 ± 0.4 %), while all other rootstocks were intermediate and did not differ between these two extremes. θ_g in nematode-infested plots (16.5 ± 0.5 %) was slightly higher than in noninfested plots (15.0 ± 0.3 %) in 2008. In 2009, θ_g was also affected by rootstock ($p = 0.031$) and nematode ($p = 0.019$) treatments, although differences due to rootstock were not supported by Tukey's means comparisons at 95% confidence. Nematode-infested vines at veraison 2009 also had slightly higher θ_g than noninfested vines (19.2 ± 0.5 % versus 18.0 ± 0.5 %). These small differences in θ_g were not apparent in the θ_v readings, possibly due to the fewer observations in TDR measurements (only half of experimental units were equipped with TDR waveguides).

Ring nematode population densities. Population densities quickly increased on all three susceptible vines (self-rooted, 3309C, and 1103P) by the second year (2007) after showing no increase in 2006 (Figure 1). From July 2007 through April 2008, all three susceptible vines had significantly higher ($p < 0.001$) nematode population densities than the resistant rootstocks (420A, 101-14, and 110R). However, by October 2008 ring nematode population densities began to increase on 110R and 101-14, with no increase in nematode population densities on 420A. By the fourth year (April and October 2009), ring nematode population densities had still not increased significantly on 420A, while all other rootstocks

and self-rooted vines had statistically similar populations of ring nematode.

Fine roots and AMF colonization. Fine root density expressed as fresh weight g^{-1} dry soil (Figure 2) or as length g^{-1} dry soil (data not shown) generally increased in all rootstocks from 2006 to 2009, with the greatest increase from 2007 to 2008 when vines were transitioned from a single shoot to multiple shoots. Fine roots were not altered by ring nematode

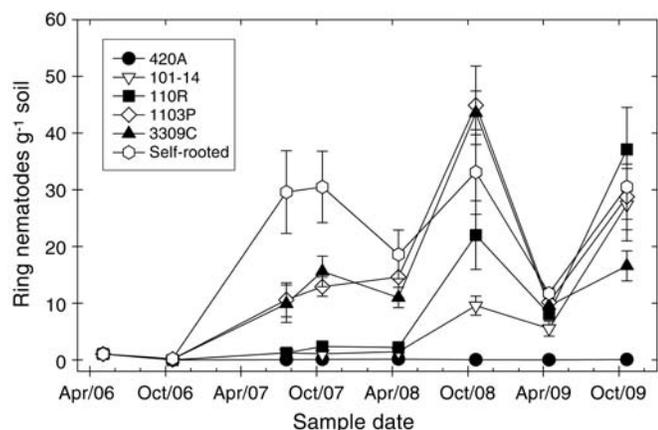


Figure 1 Ring nematode (*M. xenoplax*) population densities over four years in field microplots with different rootstocks and self-rooted vines. Data are mean values at each sampling date \pm SE ($n = 6$).

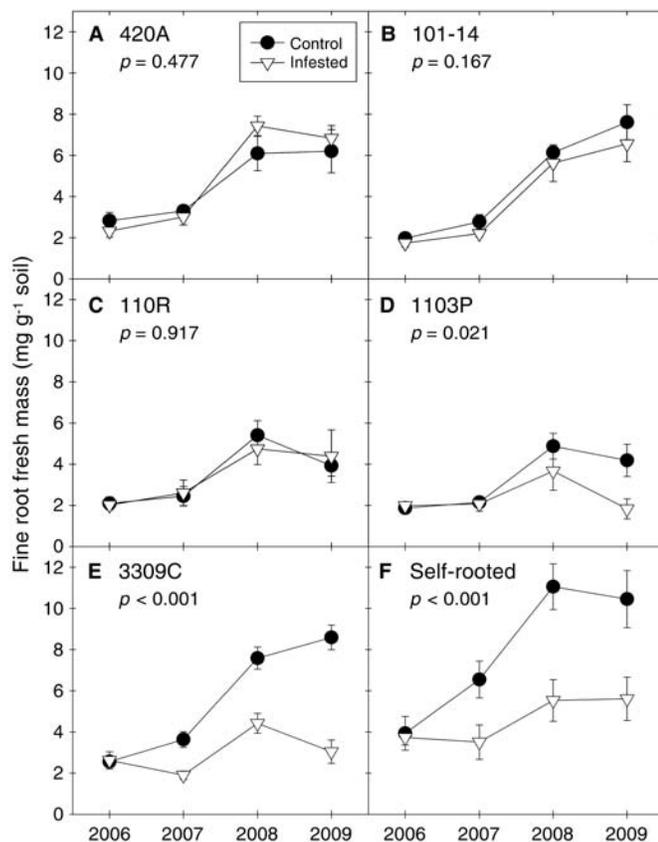


Figure 2 Changes in fine root fresh mass in different rootstocks and self-rooted vines at veraison over four years. Data are mean values for each year \pm SE ($n = 6$), and p values for the main effect of ring nematode (*M. xenoplax*) treatment are shown for each rootstock.

in any of the three resistant rootstocks (420A, 101-14, 110R), but ring nematode reduced fine root production in each of the susceptible rootstocks (1103P, 3309C, self-rooted). Woody root mass or length was reduced ($p = 0.016$) by ring nematode only in self-rooted vines (data not shown). Woody roots had similar range of fresh mass across the whole data set (2 to 12 mg g^{-1} dry soil) as compared to fine roots (2 to 11 mg g^{-1} dry soil), but the range of woody root length (1 to 8 mm g^{-1} dry soil) was much lower than the range for fine root length (7 to 40 mm g^{-1} dry soil). We did observe some very dark brown or black roots beginning in 2008 (year 3) and again in 2009 in some of the nematode-infested plots in the susceptible rootstocks. The percentage of dark-colored roots was quantified in 2008 and 2009, but differences due to ring nematode or the interaction between ring nematode and rootstock treatments were not significant (data not shown).

Colonization of fine roots by AMF was differentially affected by ring nematode in the different rootstocks and self-rooted vines. Total AMF colonization was reduced in all susceptible vines (self-rooted, 1103P, 3309C), but not in any of the resistant rootstocks despite the high ring nematode population densities that occurred on 110R and 101-14 (Figure 3). The frequency of arbuscules in fine roots was not consistently altered by the presence of ring nematode. Arbuscules in roots were reduced by ring nematode only in 2008 as a main effect

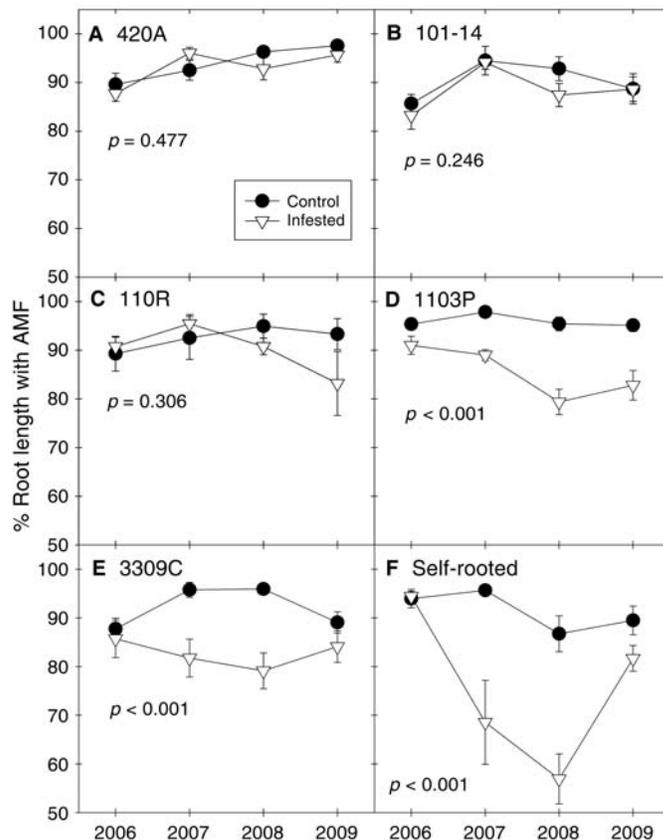


Figure 3 Changes in total arbuscular mycorrhizal fungi (AMF) colonization of fine roots in different rootstocks at veraison over four years. Data are mean values for each year \pm SE ($n = 6$) and p values for the main effect of ring nematode (*M. xenoplax*) treatment are shown for each rootstock.

across all rootstocks ($p = 0.04$), but that was not found in any other year nor were arbuscule levels altered by the interaction between ring nematode and rootstock treatments (data not shown). However, the frequency of vesicles in fine roots was consistently altered by ring nematode in all susceptible vines, and interestingly also in 110R and 101-14 roots (Figure 4). Vesicles were not altered in 420A roots.

Soil respiration. Soil CO_2 flux, indicative of root + microbial + faunal respiration, was significantly altered by sample date and rootstock in both 2007 and 2008. Respiration increased in both years from July to September, and in both years respiration was highest in self-rooted vines. Respiration was higher in nematode-infested versus noninfested vines across all rootstock treatments only in 2007 (Table 1), which was driven mainly by self-rooted vines leading to a significant interaction between rootstock and nematode treatments (Figure 5). Ring nematode did not significantly alter soil respiration in 2008.

Shoot growth and vigor. Ring nematode did not affect shoot growth in the first two years, but by the third (2008) and fourth (2009) years, shoot length was affected by the interaction between rootstock and nematode (Table 2). In 2008, shoot length of self-rooted vines was reduced by ring nematode, and in 2009 shoot length of 3309C vines was reduced by nematode. Although the mean comparison of shoot length was not sig-

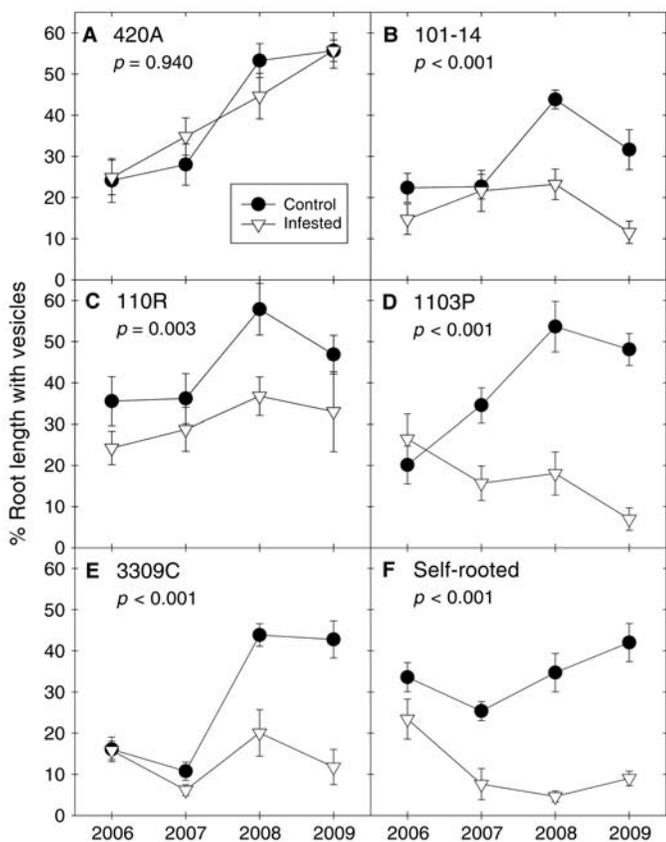


Figure 4 Changes in vesicle colonization of fine roots in different rootstocks and self-rooted vines at veraison over four years. Data are mean values for each year \pm SE ($n = 6$) and p values for the main effect of ring nematode (*M. xenoplax*) treatment are shown for each rootstock.

nificant for all three susceptible rootstocks (self-rooted, 3309, 1103P) in 2009, there was a difference between these vines and the resistant vines in terms of nematode impact on shoot length. Vines on 420A, 101-14, and 110R showed little reduction in shoot length in nematode-infested versus noninfested plots (1 to 6 cm), while shoot length of vines on the three susceptible rootstocks was reduced by 18, 23, and 42 cm by ring nematode compared to noninfested vines. Dormant season pruning weights of count shoots was not affected by either rootstock or nematode in 2006, but the interaction between rootstock and nematode drove differences in pruning weights in 2008 and 2009 (Table 3). In 2008, pruning weights of both 3309C and self-rooted vines were reduced by ring nematode,

Table 1 Main effects of sample time, Pinot noir rootstock treatment, and ring nematode (*M. xenoplax*) treatment on soil respiration in 2007 and 2008.

| Main factor ^a | Soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) | |
|--------------------------------|--|-----------------|
| | 2007 | 2008 |
| Sample date (n = 72) | | |
| July | 2.37 (0.06) c ^b | 4.52 (0.09) b |
| Aug | 2.95 (0.08) b | 5.71 (0.12) a |
| Sept | 4.64 (0.11) a | 5.39 (0.13) a |
| ANOVA signif | <0.001 | <0.001 |
| Rootstock (n = 36) | | |
| 420A | 2.87 (0.18) i | 4.71 (0.20) h |
| 101-14 | 3.00 (0.16) hi | 4.93 (0.15) gh |
| 110R | 3.15 (0.17) ghi | 5.07 (0.15) fgh |
| 1103P | 3.38 (0.25) fg | 5.16 (0.18) fgh |
| 3309C | 3.27 (0.19) gh | 5.57 (0.19) fg |
| Self-rooted | 3.70 (0.24) f | 5.64 (0.18) f |
| ANOVA signif | <0.001 | <0.001 |
| Ring nematode (n = 108) | | |
| No | 3.06 (0.10) z | 5.08 (0.10) |
| Yes | 3.39 (0.13) y | 5.27 (0.11) |
| ANOVA signif | <0.001 | 0.123 |

^aNo interactions among factors were significant ($p > 0.05$) in 2008.

^bMeans within a column followed by the same letter are not significantly different (Tukey's HSD at 95% confidence).

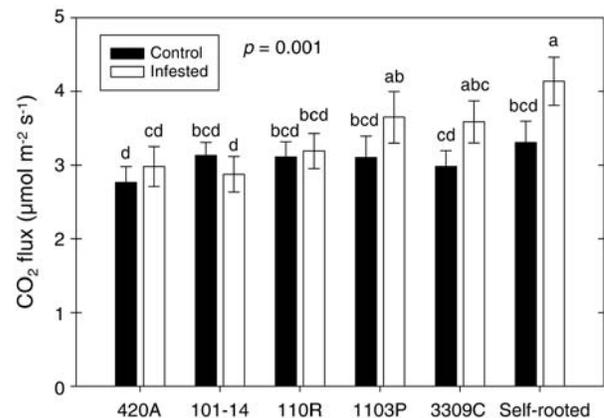


Figure 5 Soil respiration from microplots averaged over July, August, and September 2007 in different rootstocks and self-rooted vines. Data are mean values \pm SE ($n = 18$).

and in 2009 pruning weights of 3309C, 1103P, and self-rooted vines were reduced by ring nematode. Pruning weights were not reduced by ring nematode in the three resistant rootstocks in any year, but mean pruning weights in nematode-infested vines in 2008 and 2009 were always numerically lower than noninfested vines, giving high significance to the main effect of nematode treatment on vine pruning weight ($p < 0.001$).

Table 2 Interactive effects of Pinot noir rootstock treatment and ring nematode (*M. xenoplax*) treatment on shoot length (cm) at bloom over four years (n = 6).

| Rootstock | Ring nematode | 2006 (1) ^a | 2007 (1) ^a | 2008 (10) ^a | 2009 (16) ^a |
|-------------|---------------|-----------------------|-----------------------|------------------------|------------------------|
| 420A | No | 74 (4) | 116 (5) | 93 (3) ab ^b | 89 (4) ab |
| | Yes | 68 (5) | 120 (6) | 97 (3) ab | 90 (4) ab |
| 101-14 | No | 102 (5) | 107 (8) | 101 (4) ab | 94 (4) a |
| | Yes | 111 (7) | 117 (5) | 99 (3) ab | 92 (4) a |
| 110R | No | 83 (6) | 116 (8) | 92 (5) ab | 88 (3) ab |
| | Yes | 76 (6) | 124 (6) | 94 (3) ab | 82 (4) abc |
| 1103P | No | 98 (4) | 113 (10) | 103 (5) ab | 95 (6) a |
| | Yes | 94 (7) | 110 (9) | 101 (4) ab | 77 (4) abc |
| 3309C | No | 81 (5) | 121 (6) | 106 (3) ab | 96 (5) a |
| | Yes | 90 (5) | 115 (5) | 90 (4) b | 54 (6) c |
| Self-rooted | No | 94 (6) | 128 (7) | 110 (3) a | 88 (3) ab |
| | Yes | 88 (4) | 122 (10) | 90 (4) b | 65 (7) bc |
| ANOVA signf | | | | | |
| Rootstock | | <0.001 | 0.567 | 0.167 | 0.013 |
| Nematode | | 0.777 | 0.792 | 0.018 | <0.001 |
| R x N | | 0.468 | 0.847 | 0.004 | 0.003 |

^aNumber in parentheses below each year indicates the number of shoots retained on each vine.

^bMeans within a column followed by the same letter are not significantly different (Tukey's HSD at 95% confidence).

Table 3 Interactive effects of Pinot noir rootstock treatment and ring nematode (*M. xenoplax*) treatment on dormant season pruning mass of shoots (g, fresh weight) over a 4-year period (n = 6). (No data were collected in 2007, when the head was established.)

| Rootstock | Ring nematode | 2006 | 2008 | 2009 |
|-------------|---------------|----------|--------------------------|--------------|
| 420A | No | 173 (14) | 291 (19) ab ^a | 394 (32) ab |
| | Yes | 188 (11) | 273 (18) abc | 379 (35) ab |
| 101-14 | No | 202 (8) | 324 (13) ab | 431 (31) a |
| | Yes | 203 (9) | 308 (12) ab | 392 (12) ab |
| 110R | No | 174 (18) | 273 (11) abc | 330 (31) abc |
| | Yes | 223 (17) | 258 (24) abc | 250 (29) bcd |
| 1103P | No | 210 (18) | 329 (24) ab | 378 (41) ab |
| | Yes | 192 (14) | 243 (12) bcd | 192 (17) cd |
| 3309C | No | 178 (16) | 337 (18) a | 381 (26) ab |
| | Yes | 217 (15) | 198 (15) cd | 172 (13) d |
| Self-rooted | No | 167 (17) | 296 (21) ab | 382 (23) ab |
| | Yes | 174 (19) | 165 (13) d | 200 (29) cd |
| ANOVA signf | | | | |
| Rootstock | | 0.213 | 0.001 | <0.001 |
| Nematode | | 0.073 | <0.001 | <0.001 |
| R x N | | 0.225 | <0.001 | 0.016 |

^aMeans within a column followed by the same letter are not significantly different (Tukey's HSD at 95% confidence).

Vine water status and gas exchange. Ring nematode treatment did not influence either measure of leaf water status (Ψ_{leaf} and Gs) in any year, nor did it influence rates of photosynthesis (data not shown). Vine water status based on Ψ_{leaf} and Gs measurements were occasionally altered by rootstock treatment, but effects were not consistent across sampling dates within a given year or across years. The lowest average Ψ_{leaf} (-1.32 MPa) and Gs (90 mmol m⁻² s⁻¹) values occurred on the same hot day at the end of an irrigation cycle on 2 August 2007. Subsequent values for these parameters in 2008 and 2009 when vines carried a crop were never less than these values.

Vine nutrient status. Leaf and or petiole nutrient concentrations were not measured until veraison in the first two years. Effects of ring nematode on vine nutrient status were not consistent across years. In 2007, leaf N was higher ($p < 0.05$) in nematode-infested vines at veraison, but this was not supported by higher levels in petioles at the same time. Ring nematode did not affect any other nutrients in 2007. In 2008, ring nematode resulted in lower [K] and [Cu] in both leaves and petioles at both bloom and veraison. For example, leaf [K] at bloom was 12.5 g kg⁻¹ in noninfested vines and 11.6 g kg⁻¹ in infested vines, and leaf [Cu] was 13.1 mg kg⁻¹ in control vines and 10.8 mg kg⁻¹ in nematode-infested vines. In 2009, ring nematode also reduced leaf and petiole [K] compared to noninfested vines ($p < 0.001$). Leaf [K] was 11.9 g kg⁻¹ in noninfested vines and 10.8 g kg⁻¹ in infested vines at bloom in 2009. There was an interaction between rootstock and nematode treatments for leaf [N] at bloom in 2009, such that self-rooted, noninfested vines had higher N (38.9 g kg⁻¹ ± 1.0) than self-rooted, infested vines (30.1 g kg⁻¹ ± 2.8), with all other infested or noninfested rootstocks intermediate between these two extremes. This effect on N was not observed at veraison in 2009. All nutrients, except for P which was close to deficiency levels in 3309C and 101-14 vines (see below), were generally in sufficient concentration ranges deemed to be healthy for grapevines, based on known leaf and petiole standards (Christensen et al. 1978, Robinson 1992, Gärtel 1996).

Nutrient status of vines was altered by rootstock treatments in a consistent manner beginning in 2007. Vines on 101-14 roots had the highest leaf or petiole [K] and these were consistently higher than self-rooted, 1103P, and 420A vines. For example, at bloom in 2008 vines on 101-14 had 14.4 g kg⁻¹ leaf [K], while vines on 1103P had 10.1 g kg⁻¹ leaf [K], self-rooted had 11.4 g kg⁻¹ leaf [K], and 420A had 11.2 g kg⁻¹ leaf [K]. Self-rooted vines consistently had the highest leaf or petiole [Ca], differing from 101-14 vines that always had the lowest [Ca] at all sampling times in 2007 to 2009 (data not shown). Leaf and petiole [P] was most often lowest in 3309C and 101-14 vines and most often highest in self-rooted and 110R vines. For example, at bloom in 2008 self-rooted vines had higher leaf [P] (3.5 g kg⁻¹) than 3309C (2.3 g kg⁻¹) and 101-14 (2.2 g kg⁻¹). The consistently low [P] in vines on 3309C and 101-14 roots was supported by observations of P deficiency symptoms ($p < 0.001$) that developed on basal leaves in late summer 2007 only on these two rootstocks.

Fruit yield and composition. Fruit produced in 2008 (first year, small crop) was highly variable and could not be transformed to suit analysis by ANOVA. Nonparametric analysis revealed that the only fruit parameter affected by ring nematode in 2008 was juice pH, with lower values found in nematode-infested vines compared to noninfested vines (Table 4). Yield in 2009 was about double that of 2008, and both rootstock and nematode treatments affected yield and cluster weights. Ring nematode reduced both yield and cluster weights by ~12% in 2009, but did not affect other fruit parameters.

Discussion

The salient finding from this study was that ring nematode eventually reproduced well and reached high populations on two (110R and 101-14) of three grape rootstocks that were previously identified as resistant to this population from western Oregon under glasshouse and field conditions (Pinkerton et al. 2005). Only 420A remained resistant to this population of ring nematode throughout the duration of this trial. Nematodes increased more rapidly on the three susceptible rootstocks and vines (self-rooted, 3309C, and 1103P) examined here, reaching high populations during the second growing season (2007), while nematodes did not reproduce significantly on the two resistant roots (110R and 101-14) until the third growing season. The reason for this apparent loss of resistance in 110R and 101-14 roots is presently unknown, but two differences between this study and the previous work

(Pinkerton et al. 2005) may explain why these rootstocks failed to limit ring nematode reproduction here. The previous greenhouse trials were of short duration (~7 months) compared to this trial (4 years), which may have limited the time needed for this population to adjust to feeding on a less favorable host. Our findings here indicate that short-term greenhouse trials examining rootstock-ring nematode interactions must be interpreted with caution. Similar findings are known from evaluations of *Prunus* rootstocks as suitable hosts for *M. xenoplax* (Okie et al. 1994, Westcott et al. 1994). Secondly, the previous field examination of these same rootstocks was carried out in a naturally infested vineyard site where roots were not confined to microplots. We suspect that the high fine root density in the microplots of this study (7 to 40 mm g⁻¹ dry soil), as compared to much lower fine root density found in the infested vineyard site (0.4 to 1 mm g⁻¹ dry soil; see Schreiner 2003), provided much easier access to fine roots for nematodes. In addition, the frequent irrigation applied to our microplots in this study probably resulted in a greater proportion of fine roots that did not become suberized or accumulate oxidized phenolics (turning brown in color) and thus may have been more palatable to ring nematode. Fine roots of grapevines are known to turn brown and accumulate more suberin in response to lower soil moisture levels (Richards 1983). Higher soil moisture regimes in our microplots as compared to natural vineyards may have also facilitated greater nematode movement through soil. In essence, our microplot study may have represented a best-case scenario for favoring

Table 4 Main effects of Pinot noir rootstock treatment and ring nematode (*M. xenoplax*) treatment on fruit parameters in 2008 and 2009.

| Main factor ^a | Level | Yield (kg) | Cluster mass (g) | Berry mass (g) | Soluble solids (Brix) | pH | Titrateable acidity (g L ⁻¹) |
|--------------------------|--------------|----------------------------|------------------|-----------------|-----------------------|----------------|--|
| 2008 | | | | | | | |
| Rootstock (n = 12) | 420A | 1.64 (0.06) a ^b | 169 (6) a | nd ^c | 21.7 (0.4) ab | 3.32 (0.03) b | 7.26 (0.21) a |
| | 101-14 | 1.03 (0.05) b | 107 (4) b | nd | 20.6 (0.2) b | 3.45 (0.01) ab | 6.56 (0.15) ab |
| | 110R | 1.31 (0.07) ab | 132 (7) ab | nd | 21.3 (0.5) ab | 3.33 (0.03) b | 7.33 (0.24) a |
| | 1103P | 1.31 (0.10) ab | 135 (11) ab | nd | 23.7 (0.4) a | 3.44 (0.03) ab | 5.99 (0.18) b |
| | 3309C | 1.17 (0.07) b | 119 (8) b | nd | 22.7 (0.5) ab | 3.46 (0.06) a | 6.51 (0.44) ab |
| | Self-rooted | 1.30 (0.02) ab | 135 (2) ab | nd | 23.8 (0.6) a | 3.47 (0.02) a | 5.91 (0.19) b |
| | K-W signif | | <0.001 | <0.001 | | <0.001 | 0.002 |
| Nematode (n = 36) | No | 1.26 (0.06) | 128 (6) | nd | 22.0 (0.2) | 3.46 (0.02) y | 6.44 (0.12) |
| | Yes | 1.32 (0.03) | 137 (3) | nd | 22.6 (0.4) | 3.37 (0.02) z | 6.75 (0.20) |
| K-W signif | | 0.189 | 0.091 | | 0.248 | 0.004 | 0.295 |
| 2009 | | | | | | | |
| Rootstock (n = 12) | 420A | 2.69 (0.11) a | 168 (7) a | 1.07 (0.03) ab | 25.8 (0.4) ab | 3.39 (0.02) ab | 4.80 (0.21) a |
| | 101-14 | 2.16 (0.14) bc | 134 (9) bc | 1.09 (0.03) ab | 24.2 (0.3) b | 3.45 (0.02) ab | 4.61 (0.15) ab |
| | 110R | 2.33 (0.15) ab | 146 (9) ab | 1.13 (0.03) a | 24.6 (0.3) b | 3.37 (0.03) b | 4.93 (0.14) a |
| | 1103P | 1.94 (0.10) bc | 122 (6) bc | 1.06 (0.03) ab | 25.7 (0.6) ab | 3.53 (0.04) a | 4.40 (0.20) ab |
| | 3309C | 1.85 (0.08) c | 114 (4) c | 1.01 (0.03) ab | 25.6 (0.5) ab | 3.53 (0.04) a | 4.36 (0.21) ab |
| | Self-rooted | 1.81 (0.010) c | 113 (6) c | 0.98 (0.04) b | 26.5 (0.4) a | 3.54 (0.04) a | 3.95 (0.15) b |
| | ANOVA signif | | <0.001 | <0.001 | 0.025 | 0.002 | 0.002 |
| Nematode (n = 36) | No | 2.27 (0.09) y | 142 (5) y | 1.04 (0.02) | 25.0 (0.3) | 3.50 (0.02) | 4.41 (0.11) |
| | Yes | 1.99 (0.08) z | 123 (4) z | 1.07 (0.02) | 25.7 (0.2) | 3.44 (0.02) | 4.63 (0.12) |
| ANOVA signif | | 0.003 | 0.001 | 0.209 | 0.068 | 0.051 | 0.099 |

^aInteractions between rootstock and nematode factors were not significant ($p > 0.05$) in either year.

^bMeans within a year in a column followed by the same letter are not significantly different (based on nonparametric comparison in 2008 or on Tukey's HSD in 2009 at 95% confidence).

^cnd: not determined.

ring nematode development on less favorable roots. It should be noted that even though 420A roots remained resistant to this population of ring nematode from western Oregon in this trial, a population of ring nematode from the California Central Valley did reproduce slightly better (but not statistically significant) than five populations from the Pacific Northwest on 420A roots (Pinkerton et al. 2005).

The impact of ring nematode parasitism on vines was most evident in the three susceptible roots, with self-rooted varieties showing the earliest and most dramatic responses consistent with the most rapid nematode population increase. The first response to ring nematode that we detected was an increase in soil respiration in self-rooted vines during the second summer after planting (2007). Since our microplots were weed-free and harbored high levels of fine roots, the increase in CO₂ flux from infested soils can be largely attributed to an increase in grape root respiration when ring nematode was present. Even in forest ecosystems with a well-developed litter layer, roots are known to dominate soil respiration (Högberg et al. 2001). Indeed, the higher rates of soil respiration that occurred in 2007 and 2008 due to rootstock treatment were related to higher fine root densities in those treatments. What is interesting from the data set in 2007 was that soil respiration was higher in the infested self-rooted vines than noninfested self-rooted vines, but root density was already lower in the nematode-infested plots, suggesting that roots parasitized by ring nematode have a higher rate of respiration per unit root mass. The reason for this increased respiration in the self-rooted vines was not determined here, but we suspect it was related to an increase in primary metabolism in response to feeding site modifications brought about by the nematode (Hussey et al. 1992) or possibly also an increase in secondary metabolites (defense response to nematode feeding), as was shown in *Plantago lanceolata* when challenged with nematodes (Wurst et al. 2010). It is also possible that ring nematode feeding increased root exudation of sugars and other metabolites that stimulated microbial activity in the rhizosphere of infested roots. The rates of soil respiration that we found were ~50% higher than rates found directly under the vine row in a California vineyard (Carlisle et al. 2006), but that can most likely be attributed to the high root densities in our microplots.

Ring nematode decreased fine root production and colonization of those roots by AMF in all three susceptible rootstock/vine treatments, but had no influence on root growth in the three resistant rootstocks. The self-rooted vines were affected earlier and to a greater degree than the two susceptible rootstocks. Fine root growth was reduced as early as the second growing season (2007) in self-rooted and 3309C vines, and AMF colonization was reduced in all three susceptible rootstocks as soon as the second growing season. Reduction of root growth is consistent with previous results in both microplot and greenhouse studies using self-rooted vines exposed to this population of ring nematode (Pinkerton et al. 2004, Schreiner and Pinkerton 2008). Ring nematode has not consistently reduced root growth of grapevines in other trials and has even stimulated aboveground vine growth in

some cases (Raski and Radewald 1958, Nigh 1965, McKenry et al. 2001).

Our findings here on the nature of effects on AMF colonization were different than what we observed in previous trials. Previous studies with ring nematode showed that arbuscules were specifically reduced in roots without necessarily reducing total (hyphae, arbuscules, or vesicles) AMF colonization (Pinkerton et al. 2004, Schreiner and Pinkerton 2008). We did not see a consistent reduction of arbuscules in roots as a result of ring nematode feeding here, but rather a consistent reduction in total colonization by AMF in all three susceptible rootstock treatments. Moreover, we found that vesicles were reduced by ring nematode in all five of the rootstock treatments where ring nematode populations had eventually increased (including 101-14 and 110R). The more pronounced effect here on vesicles in roots may be a result of high levels of root colonization by *R. intraradices* in this experiment, which is known to form copious vesicles and spores in roots (Schenck and Smith 1982). We previously attributed the loss of arbuscules in roots to carbohydrate competition between AMF and ring nematode (Pinkerton et al. 2004), but the same could apply to vesicles since they function as carbon storage for AMF (Smith and Read 1997). Why we saw a clear effect here on vesicles but not on arbuscules as in previous studies is unknown.

A reduction in aboveground vine performance due to ring nematode was not apparent until the third growing season (2008), when both shoot lengths and pruning weights of self-rooted vines were reduced by ring nematode. Pruning weights were more consistently altered by ring nematode as compared to shoot lengths. We suspect that pruning weights may have been reduced by ring nematode as early as the second growing season, but this data was not available since we established the head that year. Yield of grapes was only affected by ring nematode in 2009, as a main effect across all rootstock treatments. The lower yield in ring nematode infested vines was due to lower cluster weights (berries per cluster), as berry weights were not altered. Ring nematode did not affect leaf water status of vines or any measure of single leaf gas exchange at any time during the experiment.

Ring nematode altered vine nutrient status in leaves or petioles as early as the second growing season (2007), but most effects on nutrients were not consistent in both tissues at the same time, nor were they consistent across years. A reduction in leaf and petiole [K] in both 2008 and 2009 was the most reproducible effect on nutrients attributed to ring nematode, which was also observed in greenhouse-grown vines in the same soil type (Schreiner and Pinkerton 2008). However, the magnitude of the reduction of K status was relatively small and unlikely to be a good indicator for nematode parasitism. For example leaf [K] at bloom was reduced by 7% in 2008 and 9% in 2009 by ring nematode.

The effect of rootstock treatments on vine nutrient status generally agreed with past comparisons of grapevine rootstocks. Our observation of higher [K] in vines on 101-14 and lower [K] in vines on 420A and 1103P is well known (Ruhl 1989, Tardáguila et al. 1995, Wolpert et al. 2005). The higher

[P] in vines on 110R and lower [P] in vines on 101-14 has also been reported (Grant and Matthews 1996, Nikolaou et al. 2003, Ibacache and Sierra 2009). Low [K], high [P], and high [Ca] in self-rooted vines in comparison to some of the rootstocks examined here is not supported in the literature, but there have been few cases where nutrients are monitored simultaneously in self-rooted and grafted vines.

Conclusions

The results show that only 420A has durable resistance to this western Oregon isolate of ring nematode. The rootstocks 101-14 and 110R, previously shown to have good resistance to ring nematode, should be avoided on sites with this nematode. The effects of ring nematode parasitism on grapevines occurred below ground first, and included increased soil respiration, decreased root growth, and decreased AMF colonization. The first effect on vines aboveground, with reduced growth as indicated by pruning weights, was not apparent until the third year. Yield was reduced by ring nematode by ~12% in the fourth year. Nutrient effects on vines were not great or consistent enough to be a reliable indicator of ring nematode damage. Soil water content was not consistently altered by ring nematode, nor was leaf water status or gas exchange at the single-leaf level. Pruning weights appear to be the most likely tool that growers could use to understand when infested vineyards are significantly impacted by ring nematode. However, even that may be difficult to detect in a commercial vineyard where noninfested vines may not be available for comparison. Therefore, a combination of nematode population assessment and vigor assessment (most likely as pruning weights) will be required to best manage vineyards infested by ring nematode.

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