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Effects of *Mesocriconema xenoplax* on *Vitis vinifera* and Associated Mycorrhizal Fungi

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Abstract: Previous surveys of vineyards had indicated that *Mesocriconema xenoplax* was present in 85% of vineyards in western Oregon, but yields were not depressed in established vines. Microplot studies were initiated in 1997 in a Willamette Valley vineyard to determine the impact of *M. xenoplax* on vine establishment. Plots were infested with 0.03, 0.6, and 3.0 *M. xenoplax* g^{-1} soil and planted with self-rooted Chardonnay and Pinot Noir vines. In November 2000, four growing seasons after planting, pruning weights, fine root weights, and fruit yield of vines planted in infested soil were reduced by 58%, 75%, and 33%, respectively, relative to control vines (planted in noninfested soil). In 1998 with ca 2000 degree-day base 9 °C accumulation, population densities increased 32-fold and 44-fold on 1-year-old Chardonnay and Pinot Noir vines, respectively. Nematode population dynamics and pruning data suggested that the carrying capacity of vines in microplots was 5 to 8 *M. xenoplax* g^{-1} soil. In November 2000, more than 80% of the fine root length was colonized by arbuscular mycorrhizal fungi in all treatments. The frequency of fine roots containing arbuscules (the site of nutrient transfer between plant and fungus), however, was depressed from 5% to 65% in plants infested initially with *M. xenoplax* as compared to controls. Competition for photosynthate within the root system is proposed as a possible mechanism by which nematodes suppressed arbuscule frequency.

Key words: arbuscule frequency, grape, *Mesocriconema xenoplax,* mycorrhizae, plant disease loss, population dynamics, ring nematode, *Vitis vinifera.*

Mesocriconema xenoplax is widely distributed throughout vineyards in the United States, South Africa, and Europe. *Mesocriconema xenoplax* was found in 75% of the sampled vineyards in Germany (Weischer, 1961) and was the most abundant nematode in vineyards in Switzerland (Güntzel et al., 1987). It also was found in vineyards in Australia (Walker, 1995), Italy (Ambrogioni et al., 1980), Spain (Pinochet and Cisneros, 1986), and France (Scotto La Massese et al., 1973). Suppression of vine growth has been associated with *M. xenoplax* in European vineyards (Ambrogioni et al., 1980; Klingler, 1975; Klingler and Gerber, 1972). In California, McKenry (1992) reported 10% to 25% reduction in grapevine yields with greater than 500 *Mesocriconema xenoplax* kg^{-1} soil. *Mesocriconema xenoplax* was found in 85% of 70 Oregon vineyards surveyed, with population densities greater than 2,000 *M. xenoplax* kg^{-1} of soil in 20% of the vineyards (Pinkerton et al., 1999). However, no obvious relationship between population densities of *M. xenoplax* and fruit yield was found in Oregon. It was proposed that vines compensate for nematode parasitism in Oregon because vines are not often stressed by other factors. Stress on vines is low because western Oregon has a mild climate with relatively high annual average precipitation, and vines are managed for crop loads of ca. 4,500 kg ha^{-1}, 50% less than other western states (Anonymous, 2003). However, the long-term impact of *M. xenoplax* on grape production in Oregon is unknown because the majority of vineyards are less than 20 years old.

Vineyards are being replanted in Oregon in response to the presence or threat of phylloxera and changing markets for grape varieties. Many of these vineyards have high population densities of *M. xenoplax* (Pinkerton et al., 1999), which may impact the establishment and growth of young vines. Growers need to know if the cost of controlling nematodes is justified, and which management options may be the most cost effective. In Oregon, soil fumigation is used rarely before planting grapes because of its expense and the difficulty in preparing the soil for effective fumigation. Rootstocks that have resistance or tolerance to *M. xenoplax* (Pinkerton et al., 1998) may provide an attractive alternative to fumigation on sites with high *M. xenoplax* population densities.

Plant-parasitic nematodes and arbuscular mycorrhizal fungi (AMF) co-inhabit and interact in plant roots and in the rhizosphere. Research on their interactions has focused on determining whether AMF increase the tolerance or resistance of crop species to nematode parasitism (Borowicz, 2001; Caron, 1989; Hussey and Roncadori, 1982; Ingham, 1988; Pinochet et al., 1998). The outcomes of these interactions are dependent upon the design of specific experiments. Among the variables that affect plant-parasitic nematode-AMF interactions are the host plant itself, AMF and nematode species, the sequence of inoculation of nematodes and AMF, and nematode population densities. In many

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studies, penetration of roots by nematodes and their subsequent development were inhibited by AMF (Calvet, et al., 2001; Forge et al., 2001; Pinochet et al., 1995); in other studies AMF increased nematode reproduction (Atilano et al., 1981; Calvet et al., 1995) or had no effect on nematodes (MacGuidwin, et al., 1985; Pinochet et al., 1997). Generally, AMF appear to increase tolerance of host plants to nematodes by increasing plant vigor and nutrient uptake (Hussey and Roncadori, 1982; Smith et al., 1986).

The impact of nematodes on AMF colonization of roots or AMF spore population densities in soil most often has been negative (Atilano et al., 1981; Calvet et al., 1995; Deiderichs, 1987; Forge et al., 2001; Pinochet et al., 1998), although numerous cases have also shown no impact of nematodes on AMF colonization or spores (Kellam and Schenck, 1980; Lopez et al., 1997; Pinochet et al., 1997; Pinochet et al., 1995; Saleh and Sikora, 1984). While arbuscules have been observed in cortical cells adjacent to citrus nematode nurse cells (O'Bannon and Nemec, 1979) and adjacent to cells containing root lesion nematode eggs (Lopez et al., 1997), no quantitative assessment of arbuscule frequency in roots has been reported in nematode-AMF interactions. Since arbuscules are the primary site of nutrient transfer between AMF and plants (Blee and Anderson, 1998; Ferrol et al., 2002), their frequency in roots is more indicative of symbiotic function than vesicular or hyphal colonization of roots.

Mechanisms governing the interactions between AMF and plant-parasitic nematodes within plant roots are largely unknown but may involve competition for space or nutrients in the roots or alterations in root physiology and morphology by nematodes or AMF (Morandi, 1996; Smith et al., 1986). Previous research on AMF and nematodes has dealt solely with sedentary or migratory endoparasitic nematodes, making it difficult to separate morphological (structural) effects caused by nematodes (galls, feeding cells) from nutritional effects on the interaction. The sedentary ectoparasitic nematode *M. xenoplax* that causes minimal disruption to root cells (Hussey et al., 1992) may be a better model to examine the role of host nutrition on AMF and nematode interactions.

The objectives of this research were to (i) study the population biology of *M. xenoplax* on grapevines in the Pacific Northwest, (ii) determine the impact of *M. xenoplax* on vine establishment and early growth, and (iii) observe the impact of *M. xenoplax* on AMF colonization of grapevine roots.

Materials and Methods

Plant materials: Chardonnay-clone FPMS 29 (ENTAV-INRA No. 76) and Pinot Noir FPMS clone 2A were propagated from hardwood cuttings collected in February 1997 at the foundation blocks on the Lewis Brown Farm, Oregon State University. The cuttings were rooted in flats containing 30:70 (v:v) peat:perlite mix under intermittent mist with bottom heat. Rooted plants were transplanted into peat:perlite (30:70) mix in Deepot Cone-tainers (Stuewe and Sons, Corvallis, OR). Vines were grown in a greenhouse until July when they were transplanted directly from the Cone-tainers into field microplots.

Nematode source and inoculation: A population of *M. xenoplax* was collected at the Oregon State University Woodhall III Research Vineyard in Alpine, Oregon, in 1995. The population was presumed to be pathogenic on grape based on high nematode population densities (8 to 12 *M. xenoplax* g^{-1} soil sampled to 45 cm), vines with low vigor, and poor grape yields (1,600 kg ha^{-1}) compared to healthy areas of the vineyard with less than 0.2 *M. xenoplax* g^{-1} soil (yield of 4,500 kg ha^{-1}). Nematodes were extracted from the soil by wet-sieving sucrose flotation and centrifugation (Jenkins, 1964), and *M. xenoplax* were handpicked under a stereomicroscope to establish pure cultures. The nematode population was increased and maintained for 8 months on *Prunus* rootstock (GI 148/2) in greenhouse pot (8 liters) cultures grown in steam-pasteurized Willamette Valley alluvial loam mixed 2:1 (v:v) with washed river sand. These plants were fertilized twice a week with Long Ashton nutrient solution (Hewitt, 1966).

Nematode inoculum used to infest the microplots was prepared by bulking and mixing the soil from ca. 130 pot cultures (total of 520 liters of soil). Soil was screened (1-cm mesh) to remove large plant material. Twenty 250-g samples were collected randomly from this soil, processed by flotation-centrifugation, and *M. xenoplax* population densities were determined. Mean nematode density was 15.7 ± 0.3 g^{-1}. Three infestation densities were produced by blending different amounts of bulked infested soil from greenhouse cultures with pasteurized loam:sand mix to yield 15 liters of infested soil. This soil was stored in plastic bags at 4 °C for several days before infesting the plots. Each bag of infested soil was mixed by hand in wheelbarrows with 100 liters of fumigated field soil. Initial infestation densities (*Pi*) of *M. xenoplax* in the 115 liters of soil (microplot volume) were 0.03, 0.6, and 3.0 g^{-1} of soil. The control treatments consisted of 100 liters of fumigated field soil amended with 15 liters of pastuerized loam:sand mix.

Microplot experimental design: The 0.1-ha site was situated on Belpine silty clay soil at the Woodhall III Research Vineyard. It was previously planted with grasses and mixed weeds, and had never been planted with grapevines. The area was disked and rototilled in early May 1997. On 21 May, the areas where the vine rows were to be located were fumigated with metam sodium at 930 liters ha^{-1} in 2.7 cm water. The fumigant was applied through three parallel drip irrigation lines in each of the four rows, with a 1.5-m × 25-m treated area in each row. Immediately following fumigation, rows

were covered with 4-mil polyethylene tarps. Tarps were removed 10 days later on 31 May and laid on the ground next to the rows. Holes (60-cm-diam. × 70-cm) on 1.5-m spacing in the rows were dug with a tractor-powered auger. Rows were spaced 3 m apart. Soil removed from each hole was collected on and covered by the fumigation tarp to prevent contact with native soil and drying. Fiberglass sheets formed into 60-cm-diam. × 70-cm cylinders were set in each hole to form the walls of the microplots. On 15 July, 115 liters of *M. xenoplax* infested or noninfested soil was placed in each microplot.

The experimental design was a blocked split-plot design, with paired adjacent rows of microplots planted with self-rooted Chardonnay or Pinot Noir vines. Each of the nine blocks consisted of four microplots in adjacent rows of each cultivar, each infested with one of the three nematode densities or noninfested soil. Blocks were arranged on the slope, with replicate 1 at the top and replicate 9 at the bottom of the slope. On 25 July plots were fertilized with $CaNO_3$ at 34 kg ha^{-1}, and a single vine was planted in each microplot. Roots were dusted with whole-soil inoculum of the AM fungus *Glomus intraradices* consisting of spores, hyphae, and colonized root fragments from a pot-culture with *Vitis vinifera* (Linderman and Davis, 2001). Border vines were planted in nonfumigated soil at the ends of each row of microplots and in rows parallel to microplot rows on both sides of the experimental area.

A drip-irrigation system and trellis were installed. Vines were trained using a double Guyot training system. Drip irrigation was used to deliver between 7.6 and 13.7 liters of water per vine every 2 weeks from mid-June to mid-September. Vines were pruned to a height of approximately 2.5 m during the second week of July. Two shoots per vine were allowed to grow during the 1998 season. Four and 6 buds/vine were left at pruning during 1999 and 2000, respectively. Vines were sprayed with wettable sulfur and demethylation-inhibiting fungicides from the three-leaf stage until véraison (start of fruit coloration) for powdery mildew control.

Nematode analysis: Three soil cores, 2 × 45 cm, were collected from each microplot in June and November of 1998, 1999, and 2000. In November 2000, larger cores (4 × 45 cm) were collected to facilitate sampling of roots. The holes were filled with fumigated field soil after sampling. Cores from each microplot were bulked and processed by wet-sieving sucrose flotation and centrifugation, and *M. xenoplax* densities were determined. Nematode data were expressed as *M. xenoplax* g^{-1} soil and *M. xenoplax* mg^{-1} root.

Plant response: Vines in the microplots were pruned each February, and the prunings were weighed to evaluate vine vigor. The flowers were removed before fruit set in 1998. Fruit was harvested on 8 October 1999 and 10 October 2000. The number of clusters and fruit weight from each vine were determined. In 2000, the fruit from each vine was crushed at harvest and the juice used to measure soluble solids (Brix), pH, and titratable acidity (TA/g).

Root and mycorrhizal analysis: In November 1999, roots were collected on a 1-mm sieve while processing soil to extract nematodes. Roots from the nine replicates of each infestation density were combined in a single observation to obtain enough material for mycorrhizal assessments. In November 2000 roots were collected in a similar manner, except that roots from two replicates (1–2, 3–4, 5–6, and 7–8) in each treatment were combined. Fine roots were handpicked from the samples and examined for cortex quality and color using a dissecting microscope. Fine roots were defined as primary roots with an intact cortex varying in color from white to brown (class A and B sensu Mohr, 1996). Roots were blotted dry, weighed to determine fresh mass, and stored in FAA (formaldehyde:acetic acid:alcohol 5%: 10%:50% v/v) prior to clearing and staining for mycorrhizal fungi. Roots were cleared and stained to reveal AMF according to Schreiner (2003).

Fine root length was determined by the grid-line intercept method (Newman, 1966) using a dissecting microscope. The proportion of root length colonized by AMF was determined on randomly selected root fragments using the method of McGonigle et al. (1990). Roots were considered mycorrhizal if they contained vesicles, arbuscules, coils, or nonseptate hyphae within the cortex. The proportion of roots containing arbuscules (the site of nutrient transfer between plant and fungus) was counted separately. A minimum of 100 root intersections was examined for each sample.

Statistical analysis: For each sample date, population densities of *M. xenoplax,* pruning, and yield data for each cultivar were analyzed statistically using one-way analysis of variance (ANOVA). Nematode, plant, and AMF data collected in November 2000 were analyzed statistically using a blocked split-plot ANOVA. Variety was evaluated as the whole-plot factor, and *M. xenoplax* inoculum density was treated as the sub-plot factor. Means were separated using Fisher's Protected LSD at 95% confidence. Linear regression models were used to analyze the relationships between population densities of *M. xenoplax* and root length and mass (Statgraphics Plus version 3, Manugistics Inc., Rockville, MD).

Results

Population dynamics: Annual population dynamics patterns of *M. xenoplax* were similar for both varieties; the cultivar-Pi interaction was not significant for any nematode population variable (Table 1). Ten months after the microplots were infested, the population densities of *M. xenoplax* were not different between the two highest initial infestation levels for either cultivar, but these were greater than densities in the noninfested controls and in the lowest infestation level ($P < 0.01$)

TABLE 1. Significance of explanatory variables in analysis of variance of interactions of initial population densities (Pi) of *Mesocriconema xenoplax* and two grape varieties on root growth, colonization of mycorrhizae, and nematode densities.[a]

	Model variables					
	Cultivar		Pi		Cultivar × *Pi*	
	F value	*P* value	*F* value	*P* value	*F* value	*P* value
M. xenoplax mg^{-1} root	15.944	0.001	6.017	0.005	1.947	0.149
M. xenoplax g^{-1} soil	3.513	0.073	6.010	0.003	0.287	0.834
Fine root length g^{-1} soil	32.182	0.001	103.094	0.005	2.097	0.430
Fine root wt g^{-1} soil	17.601	0.001	40.395	0.001	1.062	0.384
Percent colonization	0.550	0.465	3.227	0.040	1.293	0.300
Percent arbuscular	11.293	0.003	12.375	0.001	3.952	0.020

[a] Data were collected in November 2000, 40 months after Pinot Noir and Chardonnay vines were planted. Model degrees of freedom for cultivar, initial nematode population density (*Pi*), cultivar × *Pi*, and error were 1, 3, 3, and 24, respectively.

(Fig. 1). Population densities increased 32× in Chardonnay and 44× in Pinot Noir plots from March through November 1998. During this period, the degree-day accumulation (base 9 °C) was estimated from soil temperatures collected at Hyslop Research Farm in Corvallis, Oregon, at ca. 2,000 DD (Westcott and Burrows, 1991). Population densities increased in the second year to 6 to 8 *M. xenoplax* g^{-1} in all infested plots, and these densities were maintained through November 2000 (Fig. 1). The highest densities were observed during the second and third years in plots initially infested with 0.03 nematodes g^{-1}. Mean population densities in the control plots remained less than 0.01 g^{-1} until June 2000. However, densities increased rapidly in the noninfested control plots in the final year of the study, with densities exceeding 2 g^{-1} and 5 g^{-1} in the Chardonnay and Pinot Noir plots, respectively, in November 2000. At that time, there were more *M. xenoplax* mg^{-1} root ($P < 0.01$) in Chardonnay plants than in Pinot Noir plants (Table 1, Fig. 2A).

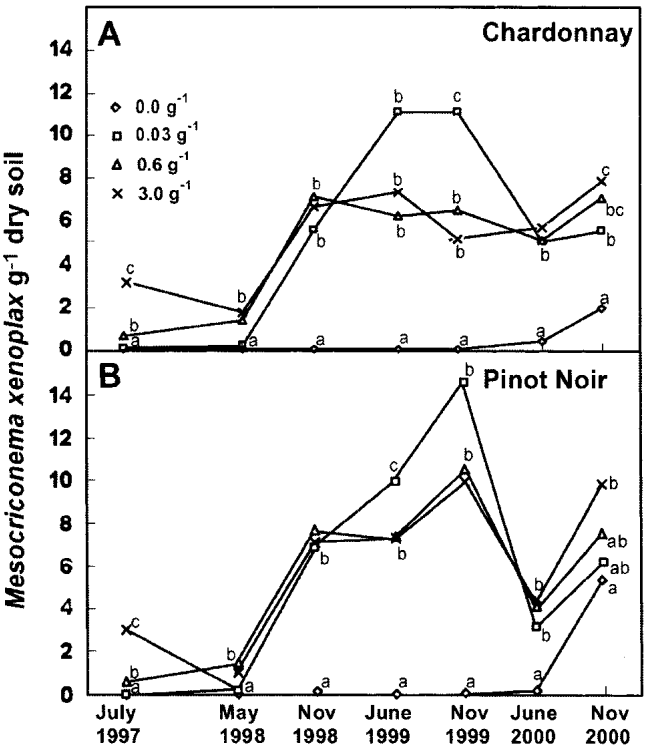

FIG. 1. Seasonal population dynamics of *Mesocriconema xenoplax* on *Vitis vinifera* varieties in microplots located in Alpine, Oregon. Microplots were infested with 0.0, 0.03, 0.6, or 3.0 *M. xenoplax* g^{-1} soil on 15 July 1997. Self-rooted Chardonnay (A) and Pinot Noir (B) vines were planted on 25 July 1997. Mean values of data for each cultivar collected at each date that were different ($P < 0.01$) according to Fisher's LSD are signified by different letters to the right of the symbols.

Plant evaluations: Mesocriconema xenoplax suppressed shoot and root growth. In 1998 and 1999, pruning weights of Chardonnay vines were greater ($P < 0.01$) in the control and 0.03 nematodes g^{-1} treatment than in the 0.6 and 3.0 nematodes g^{-1} treatments (Fig. 3A). A similar trend was observed for Pinot Noir vines, but these differences were not significant. Pruning weights in the control plots increased to 215 and 233 g/vine for Pinot Noir and Chardonnay, respectively, in the last year of the study, whereas vines in all nematode-infested treatments had pruning weights less than 100 g/vine. Similar trends were observed in the Pinot Noir plots (Fig. 3B); however, pruning weights of control vines did not increase from 1999 to 2000.

The effect of *M. xenoplax* on the density of fine roots collected in November 2000 corresponded to observations of pruning weights, i.e. mm root g^{-1} soil of both cultivars was lower ($P > 0.01$) in all nematode-infested microplots than the control in both cultivars (Fig. 2B). Pinot Noir had greater overall fine root length (mm g^{-1} soil) and mass (mg g^{-1} soil) than Chardonnay plants (Table 1; Fig. 2B). Root lengths in the control microplots of both cultivars were between 8 and 10 mm g^{-1} soil compared to 0.5 to 4 mm g^{-1} in infested plots (Fig. 2B). Regression analysis revealed negative correlations for root mass and root length with *M. xenoplax* mg^{-1} root in November 2000. The r^2 values for relationships between nematodes mg^{-1} root and root mass or length were 0.496 and 0.540 for Pinot Noir and 0.536 and 0.546 for Chardonnay, respectively. Nematodes g^{-1} soil in November 2000 was negatively related with root mass and length for Chardonnay only, with r^2 values of 0.670 and 0.634, respectively.

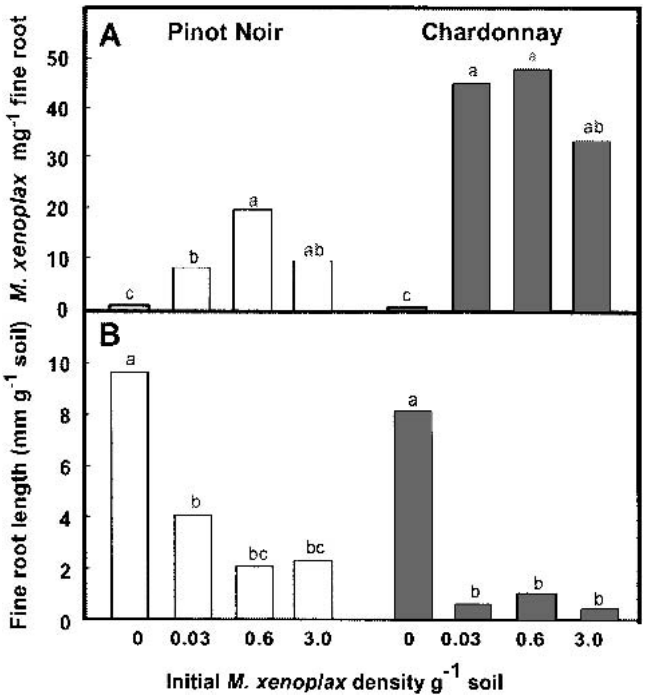

FIG. 2. Relationship between *Mesocriconema xenoplax* initial population densities and root growth. A) Number of *M. xenoplax* mg^{-1} fine root. B) Length of fine roots g^{-1} root. Roots were collected in November 2000. Microplots were infested with 0.0, 0.03, 0.6, or 3.0 *M. xenoplax* g^{-1} soil on 15 July 1997, and self-rooted Chardonnay and Pinot Noir vines were planted on 25 July 1997. Means for each cultivar that differ ($P < 0.01$) according to Fisher's LSD are indicated by different letters.

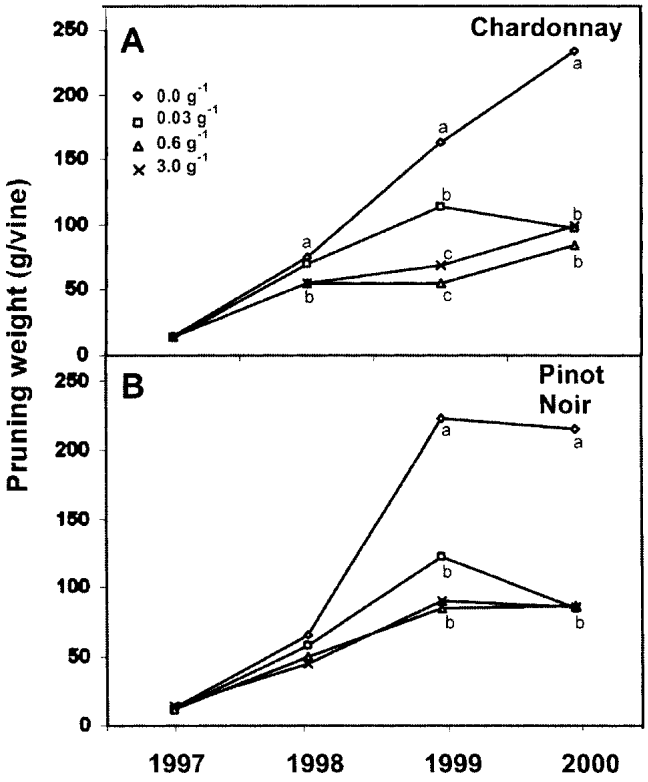

FIG. 3. Pruning weights of *Vitis vinifera* vines growing in microplots infested with *Mesocriconema xenoplax*. Data representing each year were collected in February of the subsequent year. Microplots were infested with 0.0, 0.03, 0.6, or 3.0 *M. xenoplax* g^{-1} soil on 15 July 1997. Self-rooted Chardonnay (A) and Pinot Noir (B) vines were planted on 25 July 1997. Mean values at each date that differ ($P < 0.01$) according to Fisher's LSD are signified by different letters to the right of the symbols.

Yields in 1999 were low, and there was no difference between *M. xenoplax*-infested and noninfested vines. In 2000, infested vines yielded 1,000–1,200 kg ha^{-1}, whereas vines planted in noninfested plots yielded 1,500–1,800 kg ha^{-1}. For Chardonnay, nematode infestation reduced yield per vine and clusters per vine by more than 32% ($P > 0.01$) and 29% ($P > 0.01$), respectively (Table 2). Trends were similar for Pinot Noir, for which nematode infestation reduced yield and clusters per vine by at least 32% ($P > 0.09$) and 28% ($P > 0.01$), respectively (Table 2). In this study, juice quality was not greatly affected by nematode parasitism (Table 2). Juice from berries harvested from control Chardonnay vines had slightly higher pH ($P < 0.01$) and lower titratable acidity ($P < 0.01$) than juice from infested treatments.

Mycorrhizal colonization: Roots collected in November 1999 showed a trend of reduced frequency of arbuscules with increasing nematode infestation, but no differences in the proportion of roots colonized by mycorrhizal hyphae and (or) vesicles were found (data not shown). In November 2000, nematodes affected ($P > 0.01$) the fine root length colonized by AMF (Table 1), but roots from all treatments had greater than 80% colonization (Fig. 4). For Pinot Noir, average colonization by AMF was less than ($P > 0.01$) control microplots only in microplots infested at the highest nematode density. However, the proportion of fine root length containing arbuscules was depressed ($P > 0.01$) in roots collected from microplots infested at all inoculum densities, except for Pinot Noir microplots at the lowest infestation level (Fig. 4). Arbuscule frequency was re-

TABLE 2. Yield and juice quality of grapes harvested in October 2000 from Chardonnay and Pinot Noir vines in microplots infested with different population densities of *Mesocriconema xenoplax*.[a]

Variety	Pi	kg/vine	Clusters/vine	Brix[b]	pH	TA/g[c]
Chardonnay	0.0 g^{-1}	0.84[a]	14.3[a]	24.9	3.2[a]	5.8[a]
	0.03 g^{-1}	0.53[b]	9.0[b]	25.3	3.1[b]	6.4[b]
	0.6 g^{-1}	0.58[b]	10.1[b]	24.8	3.1[b]	6.4[b]
	3.0 g^{-1}	0.57[b]	9.4[b]	24.9	3.1[b]	6.6[b]
	P =	0.008	0.003	0.031	0.008	0.002
Pinot Noir	0.0 g^{-1}	1.02	18.6[a]	25.1	3.1	6.6
	0.03 g^{-1}	0.69	13.4[b]	24.8	3.0	7.0
	0.6 g^{-1}	0.65	11.4[b]	25.2	3.1	6.5
	3.0 g^{-1}	0.67	12.1[b]	25.1	3.0	6.9
	P =	0.086	0.010	0.284	0.906	0.513

[a] Microplot soil was infested with initial nematode densities (Pi) of 0.0, 0.03, 0.6, or 3.0 *M. xenoplax* g^{-1} soil in July 1997 when the vines were planted. Within a column, means followed by different letters are significantly different according to Fisher's LSD procedure.

[b] Units measuring soluble solids or sugar content.

[c] Titratable acidity.

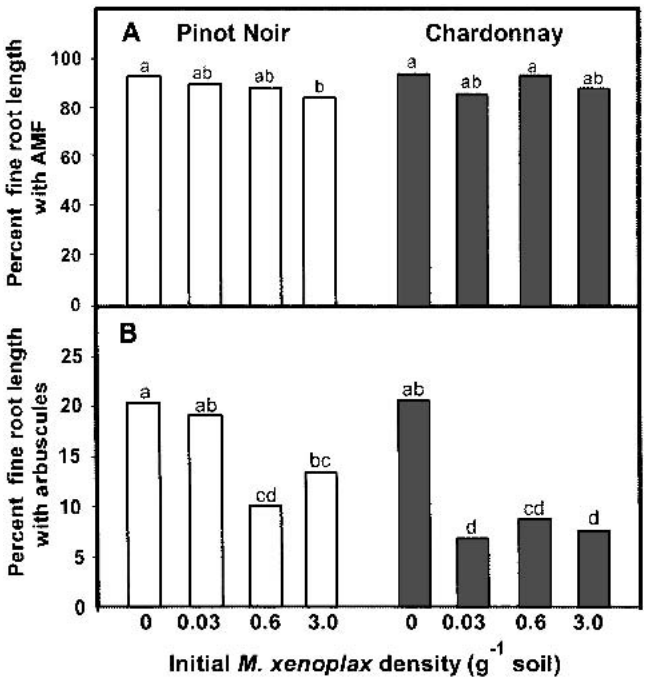

FIG. 4. Effect of *Mesocriconema xenoplax* on mycorrhizial colonization of the roots of self-rooted Chardonnay and Pinot Noir vines in microplots. A) Percent of fine root length colonized by AMF. B) Percent of fine root length with arbuscules. Roots were collected in November 2000. Microplots were infested with 0.0, 0.03, 0.6, or 3.0 *M. xenoplax* g^{-1} soil on 15 July 1997, and vines were planted on 25 July 1997. Means for each cultivar that differ ($P < 0.01$) according to Fisher's LSD are signified by different letters.

duced more by nematodes in Chardonnay vines than Pinot Noir vines, leading to an interaction ($P < 0.02$) between cultivar and Pi (Table 1). The proportion of fine roots with arbuscules was negatively related to both *M. xenoplax* g^{-1} soil and mg^{-1} root ($P < 0.02$), with R^2 values between 0.313 and 0.436, respectively. Nematode population densities were not correlated with total AMF colonization.

Discussion

Population densities of *M. xenoplax* increased rapidly in the microplots, which had soil type, environmental conditions, and management practices typical of hillside vineyards in the Willamette valley. The largest seasonal increase in population density was observed in the microplots in the low infestation treatment the second year. The rate of increase of 32× to 44× was less than the ca. 250× at 2000 DD 9 predicted by a model developed in growth chamber experiments for *M. xenoplax* on peach (Westcott and Burrows, 1991). Different host species, variable temperature and soil moisture conditions in the field microplots, losses to predation, and reduced carrying capacity of the plants under increasing nematode feeding may account for overestimation of the model. The microplot data, however, are consistent with data reported for *M. xenoplax* on grape from greenhouse experiments. In a greenhouse study, we observed a 50× population increase on Chardonnay and Pinot Noir after 8 months and ca. 2900 DD 9 (Pinkerton et al., 1998). Lownsberry (1961) reported a 30× increase in *M. xenoplax* densities after 4 months at 26 °C (ca. 2050 DD 9) on Thompson seedless grapes, whereas other studies reported 60× increase (Raski and Radewald, 1958) and 52× increase (Nigh, 1965) after 5 and 7 months on Thompson seedless. Santo and Bolander (1977) reported greater than 100-fold increase to densities of 16 nematodes g^{-1} soil in 4 months on Concord grape, *Vitis labrusca,* infested with 0.1 *M. xenoplax* g^{-1} soil.

The rate of increase in nematode population densities was similar in all infested treatments during 1998. The nematode population data suggest that the carrying capacity of grapevine in the microplots was 6 to 8 *M. xenoplax* g^{-1} soil. This value is similar to the population density in the low-vigor vineyard from which the population of *M. xenoplax* used in the study was collected originally. This value is somewhat higher than commercial vineyards surveyed in Oregon, in which the highest population density observed was 5.2 *M. xenoplax* g^{-1} and densities greater than 2 g^{-1} were observed only in 8% of vineyards (Pinkerton et al., 1999). The density of fine roots was greater in the microplots than observed in the soil under vines in commercial vineyards (Schreiner, unpubl. data). This may explain the higher population densities of *M. xenoplax* in microplots compared to surveyed vineyards. Fumigation of the soil before planting also may have eliminated natural antagonists that regulate nematode populations. While the carrying capacity of vines for *M. xenoplax* should be related to the amount and quality of roots in the soil, this may be affected by cultivar. Nematodes mg^{-1} root were higher and fine root length was lower in Chardonnay plots compared to Pinot Noir plots. Neither cultivar appeared to be tolerant to *M. xenoplax,* as growth and yield were reduced by the nematode (Roberts, 2002).

Grapevine is a good host for *M. xenoplax,* but roots parasitized by *M. xenoplax* do not display the extensive physical damage that is observed with roots of *Prunus* spp. (Lownsberry, 1961; Nigh, 1965; Raski and Radewald, 1958; Schreiner, unpubl. data). The effect of *M. xenoplax* on grapevines appears to vary among different geographic regions, soil characteristics, and management regimes. In California, *M. xenoplax* can reduce yield and vine vigor at 0.5 nematodes g^{-1} soil, population densities commonly found in Oregon vineyards. In contrast, *M. xenoplax* did not affect cane length, pruning weight, and fruit yield of 10 French-American varieties in a 5-year microplot study conducted in Michigan (Ramsdell et al., 1996). In our study, however, the impact of *M. xenoplax* on vine growth became evident in the second season and persisted through the study. Vine damage was not proportional to the initial population density, in part because population densities rapidly converged to a common carrying capacity. Based

on pruning weights, vine growth reached an asymptote when nematode population densities reached 4.0 to 8.0 g^{-1} soil. In June 2000, the final year of the study, *M. xenoplax* was recovered from some noninfested control micoplots. It is probable that nematodes were introduced into noninfested plots with surface water running downhill, since most of the controls which became infested were located near the bottom of the slope. Population densities in Pinot Noir control plots increased rapidly to nearly 5.0 *M. xenoplax* g^{-1} soil in 2000 and resulted in no net increase in pruning weight from the previous season.

It is difficult to extrapolate the impact of *M. xenoplax* on grape production in commercial vineyards from these microplot data. Commercial vineyards seldom have population densities as high as those attained in microplots (Pinkerton et al., 1999). Because roots were restricted in the microplots, growth potential of vines may have been reduced, exacerbating effects of *M. xenoplax* during the third and fourth years. It is clear that *M. xenoplax* has the potential to damage roots, reduce vine vigor and yield, and delay establishment of vines. However, *M. xenoplax* at densities greater than 4.0 g^{-1} soil have not been associated with unthrifty vines in older, established vineyards in Oregon (Pinkerton et al., 1999). Vineyard managers strive to reduce vine vigor and crop load to permit ripening of the fruit. It is likely that vines compensate for nematode parasitism under conditions in Oregon. On sites with high population densities of *M. xenoplax,* growers can plant vines on rootstocks that have resistance to *M. xenoplax,* such as MG 420A, MG 101-14 (Pinkerton et al., 1998), or Schwarzmann (McKenry et al., 2001).

Our findings are consistent with the hypothesis that ring nematodes compete with AMF for photosynthate in roots. Reductions in arbuscule frequency with relatively little effect on total mycorrhizal colonization were most likely due to decreased carbohydrate availability in roots where nematodes were feeding. *Mesocriconema xenoplax* is a fastidious ectoparasite and may feed from a single cortical cell for up to 8 days (Hussey et al., 1992). Root cortical cells near the feeding cell have modified plasmodesmata that probably increase nutrient flows to the feeding cell (Hussey et al., 1992). Such elaborate modifications of root cortical cells by *M. xenoplax* could lead to an overall reduction in carbohydrate concentrations of nearby root cortical cells. Since AMF also colonize cells of the cortex, the added carbohydrate drain in the presence of nematodes could have suppressed either arbuscule formation or arbuscule lifespan in our study. A carbohydrate partitioning hypothesis is consistent with research results on peach tree short life in which parasitism by *M. xenoplax* decreased reducing sugars in roots (Nyczepir et al., 1987) or shoots (Olien et al., 1995), thus predisposing tree trunks to injury or death from environmental or biological stresses.

While it is generally accepted that arbuscules are the primary site of phosphorus transfer to the host plant (Smith and Read, 1997), it is becoming increasingly evident that arbuscules are also the site for carbohydrate uptake by the fungus (Blee and Anderson, 1998; Ferrol et al., 2002). Reducing the carbohydrate supply to roots is known to reduce the extent of mycorrhizal colonization of roots when soil P is low (Hayman, 1974; Schwab et al., 1991). However, the role of root carbohydrates in the specific regulation of arbuscules has not been reported. We have observed a rapid decline in arbuscule frequency in grape roots in response to reduced photosynthate supply (defoliated vines) with no change in hyphal or vesicular colonization (Schreiner, unpubl.). Our findings in the nematode-infested plots are consistent with these observations.

Had we not examined arbuscule frequency, we would have concluded that *M. xenoplax* has little impact on AMF. Indeed, arbuscule frequency may have been reduced by nematodes in many of the prior studies that have reported no impact of nematodes on AMF. Since arbuscules are the site of nutrient transfer between plant and fungus (and hence should be a good measure of function in mycorrhizas), a re-evaluation of plant-parasitic nematode effects on symbiotic effectiveness in AMF is needed (Borowicz, 2001).

Mesocriconema xenoplax appears to disrupt root function in at least two important ways—by reducing root elongation and hence exploration of greater soil volume, and by reducing the nutrient transfer between AMF and the host plant. These effects should manifest themselves above ground by making plants more sensitive to water and nutrient stress.

All microplots became infested with AMF in this study, so our experiment could test only the effect of the nematode on AMF and not vice versa. Effects of AMF on plant-parasitic nematodes have often led to reduced nematode populations in roots or soils, and to a reduced impact of nematodes on the host plant (Ingham, 1988; Pinochet et al., 1996). It appears from this study that AMF had little impact on the development of ring nematodes in grapevines, because all plants were heavily colonized by AMF and nematodes reached exceptionally high densities. However, had plants not been colonized by AMF during this study, vines would have grown poorly and *M. xenoplax* may have had a more immediate impact on plant growth and vigor.

Studies are under way to investigate the proposed role of root carbohydrates in mediating ring nematode-AMF interactions in grapevines, and to investigate the potential impact of AMF on ring nematode development.

Literature Cited

Ambrogioni, L., F. P. D'Errico, A. M. Palmisano, and M. Talamé. 1980. Nematodi Criconematidae dei vigneti italiani. Atti Giornate Nematologiche 1980. Ascoli, Piceno, Italy, 46–57.

Anonymous. 2003. Noncitrus fruits and nuts: 2003 Preliminary summary. Fr Nt 1–3 (03). Agricultural Statistics Board. National Agricultural Statistics Service. USDA. Washington, DC.

Atilano, R. A., J. A. Menge, and S. D. Van Gundy. 1981. Interaction between *Meloidogyne arenaria* and *Glomus fasiculatus* in grape. Journal of Nematology 13:52–57.

Blee, K. A., and A. J. Anderson. 1998. Regulation of arbuscule formation by carbon in the plant. Plant Journal for Cell and Molecular Biology 16:523–530.

Borowicz, V. A. 2001. Do arbuscular mycorrhizal fungi alter plant-pathogen relations? Ecology 82:3057–3068.

Calvet, C., J. Pinochet, A. Camprubi, and C. Fernandez. 1995. Increased tolerance to the root-lesion nematode *Pratylenchus vulnus* in mycorrhizal micropropagated BA-29 quince rootstock. Mycorrhiza 5: 253–258.

Calvet, C., J. Pinochet, A. Hernandez-Dorrego, V. Estaun, and A. Camprubi. 2001. Field microplot performance of the peach-almond hybrid GF-677 after inoculation with arbuscular mycorrhizal fungi in a replant soil infested with root-knot nematodes. Mycorrhiza 10:295–300.

Caron, M. 1989. Problematique del l'utilisation des champignons endomycorhiziens comme agents de lutte biolgique. Phytoprotection 70:43–49.

Diederichs, C. 1987. Interaction between five endomycorrhizal fungi and the root-knot nematode *Meloidogyne javanica* on chickpea under tropical conditions. Tropical Agriculture 64:353–355.

Ferrol, N., J. M. Barea, and C. Azcon-Aguilar. 2002. Mechanisms of nutrient transport across interfaces in arbuscular mycorrhizas. Plant and Soil 244:231–237.

Forge, T., A. Muehlchen, C. Hackenberg, G. Neilsen, and T. Vrain. 2001. Effects of preplant inoculation of apple (*Malus domestica* Borkh.) with arbuscular mycorrhizal fungi on population growth of the root-lesion nematode, *Pratylenchus penetrans*. Plant and Soil 236: 185–196.

Güntzel, O., J. Klingler, and V. Delucchi. 1987. Tylenchids (Nematoda) extracted from soil of Swiss vineyards north of the Alps. Revue de Nématologie 10:361–368.

Hayman, D. S. 1974. Plant growth responses to vesicular-arbuscular mycorrhiza. IV. Effect of light and temperature. New Phytologist 73: 71–80.

Hewitt, E. J. 1966. Sand and water culture techniques used in the study of plant nutrition. Technical Communication. No 22 (2nd ed. rev.). London: Commonwealth Agriculture Bureau.

Hussey, R. S., C. W. Mims, and S. W. Westcott III. 1992. Ultrastructure of root cortical cells parasitized by the ring nematode *Criconemella xenoplax*. Protoplasma 167:55–65.

Hussey, R. S., and R. W. Roncadori. 1982. Vesicular-arbuscular mycorrhizae may limit nematode activity and improve plant growth. Plant Disease 66:9–14.

Ingham, R. E. 1988. Interactions between nematodes and vesicular-arbuscular mycorrhizae. Agriculture, Ecosystems & Environment 24: 169–182.

Jenkins, W. R. 1964. A rapid centrifugation flotation technique for separating nematodes from soil. Plant Disease Reporter 48:692.

Kellam, M. K., and N. C. Schenck. 1980. Interaction between a vesicular-arbuscular mycorrhizal fungus and root-knot nematode on soybean. Phytopathology 70:293–296.

Klingler, J. 1975. Beobachtungen über die parasitische Aktivität des Nematoden *Macroposthonia xenoplax* an Rebenwurzeln. Pflanzenkr Planzenschutz 82:722–728.

Klingler, J., and B. Gerber. 1972. Beobachtungen über die parasitische Aktivität des Nematoden *Macroposthonia xenoplax* an Rebenwurzeln. Schweizerische Zeitschrift für Obst- und Weinbau 108:217–223.

Linderman, R. G., and E. A. Davis. 2001. Comparative response of selected grapevine rootstocks and cultivars to inoculation with different mycorrhizal fungi. American Journal of Encology and Viticulture 52:8–11.

Lopez, A., J. Pinochet, C. Fernandez, C. Calvet, and A. Camprubi. 1997. Growth response of OHF-333 pear rootstock to arbuscular mycorrhizal fungi, phosphorus nutrition, and *Pratylenchus vulnus* infection. Fundamental and Applied Nematology 20:87–93.

Lownsberry, B. F. 1961. Factors affecting population levels of *Criconemoides xenoplax*. Phytopathology 51:101–103.

MacGuidwin, A. F., G. W. Bird, and G. R. Safir. 1985. Influence of *Glomus fasciculatum* on *Meloidogyne hapla* infecting *Allium cepa*. Journal of Nematology 17:389–395.

McGonigle, T. P., M. H. Miller, D. G. Evans, G. L. Fairchild, and J. A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phytologist 115:495–501.

McKenry, M. V. 1992. Nematodes. Pp. 281–293 *in* D. L. Flaherty, L. P. Christensen, W. T. Lanini, J. J. Marois, P. A. Phillips, and L. T. Wilson, eds. Grape pest management. 2nd ed. Publication No. 3343. Oakland, CA: Division of Agricultural Science, University of California.

McKenry, M. V., J. O. Kretsch, and S. A. Anwar. 2001. Interactions of selected rootstocks with ectoparasitic nematodes. American Journal of Encology and Viticulture 52:304–309.

Mohr, H. D. 1996. Periodicity of root tip growth of vines in the Moselle valley. Viticultural and Enological Sciences 51:83–90.

Morandi, D. 1996. Occurrence of phytoalexins and phenolic compounds in endomycorrhizal interactions, and their potential role in biological control. Plant and Soil 185:241–251.

Newman, E. I. 1966. A method of estimating the total length of root in a sample. Journal of Applied Ecology 3:139–145.

Nigh, E. L. 1965. Effects of *Criconemoides xenoplax, Longidorus elongatus,* and *Xiphinema americanum* on root development and growth of Thompson seedless grape. Phytopathology 55:1070.

Nyczepir, A. P., C. C. Reilly, and W. R. Okie. 1987. Effects of initial population density of *Criconemella xenoplax* on reducing sugars, free amino acids, and survival of peach seedlings over time. Journal of Nematology 19:296–303.

O'Bannon, J. H., and S. Nemec. 1979. The response of *Citrus limon* seedlings to a symbiont, *Glomus etunicatus,* and a pathogen, *Radopholus similis*. Journal of Nematology 11:270–275.

Olien, W. C., C. J. Graham, M. E. Hardin, and W. C. Bridges, Jr. 1995. Peach rootstock differences in ring nematode tolerance related to effects on tree dry weight, carbohydrates, and prunasin content. Physiologia Plantarum 94:117–123.

Pinochet, J., C. Calvet, A. Camprubí, and C. Fernández. 1995. Growth and nutritional response of Nemared peach rootstock infected with *Pratylenchus vulnus* and the mycorrhizal fungus *Glomus mosseae*. Fundamental and Applied Nematology 18:205–210.

Pinochet, J., C. Calvet, A. Camprubi, and C. Fernández. 1996. Interaction between migratory endoparasitic nematodes and arbuscular mycorrhizal fungi in perennial crops: A review. Plant and Soil Science 185:183–190.

Pinochet, J., A. Camprubí, C. Calvet, C. Fernández, and R. Rodriguez Kábana. 1998. Inducing tolerance to the root-lesion nematode *Pratylenchus vulnus* by early mycorrhizal inoculation of micropropagated Myrobalan 29 C plum rootstock. Journal of American Society of Horticultural Science 123:324–347.

Pinochet, J., and T. Cisneros. 1986. Seasonal fluctuations of nematode populations in three Spanish vineyards. Revue de Nématologie 9:391–398.

Pinochet, J, C. Fernández, M. de Carmen Jaizme, and P. Tenoury. 1997. Micropropagated banana infected with *Meloidogyne javanica* responds to *Glomus intraradices* and phosphorus. HortScience 32:101–1–3.

Pinkerton, J. N., T. A. Forge, K. L. Ivors, and R. E. Ingham. 1999. Distribution of plant-parasitic nematodes in Oregon vineyards. Journal of Nematology 31:624–634.

Pinkerton, J. N., K. L. Ivors, and C. M. Candolfi-Vasconcelos. 1998. Reaction of grape rootstocks to *Criconemella xenoplax*. Journal of Nematology 30:510.

Ramsdell, D. C., G. W. Bird, F. W. Warner, J. F. Davenport, C. J. Diamond, and J. M. Gillett. 1996. Field pathogenicity studies of four species of plant-parasitic nematodes on French-American hybrid grapevine cultivars in Michigan. Plant Disease 80:334–338.

Raski, D. J., and R. D. Radewald. 1958. Reproduction and sympto-

mology of certain ectoparasitic nematodes on roots of Thompson seedless grape. Plant Disease Reporter 42:941–943.

Roberts, P. A. 2002. Concepts and consequences of resistance. Pp. 23–41 *in* J. L. Starr, R. Cook, and J. Bridge, eds. Plant resistance to parasitic nematodes. Wallingford, UK: CABI.

Saleh, H., and R. A. Sikora. 1984. Relationship between *Glomus fasciculatum* root colonization of cotton and its effect on *Meloidogyne incognita*. Nematologica 30:230–237.

Santo, G. S., and W. J. Bolander. 1977. Effects of *Macroposthonia xenoplax* on the growth of Concord grape. Journal of Nematology 9:215–217.

Schreiner, R. P. 2003. Mycorrhizal colonization of grapevine rootstocks under field conditions. American Journal of Enology and Viticulture 54:143–149.

Schwab, S. M., J. A. Menge, and P. B. Tinker. 1991. Regulation of nutrient transfer between host and fungus in vesicular-arbuscular mycorrhizas. New Phytologist 117:387–398.

Scotto La Massese, C., C. Marenaud, and J. Dunez. 1973. Analyse d'un phénomène de dégénérescence du pêcher dans la Vallée de l'Eyrieux. Comptes Rendus de l'Académie d'Agriculture de France 59:327–339.

Smith, G. S., R. S. Hussey, and R. W. Roncadori. 1986. Penetration and postinfection development of *Meloidogyne incognita* on cotton as affected by *Glomus intraradices* and phosphorus. Journal of Nematology 18:429–435.

Smith, S. E., and D. J. Read. 1997. Mycorrhizal symbiosis. San Diego: Academic Press.

Walker, G. 1995. Nematode associated with grapevine foundation plantings at Loxton. Australian Grapegrower and Winemaker 381: 34–40.

Westcott, S. W., III, and P. M. Burrows. 1991. Degree-day models for predicting egg hatch and population increase by *Criconemella xenoplax*. Journal of Nematology 23:386–392.

Weischer, B. 1961. Nematoden in Weinbau. Weinberg und Keller 8:33–49.