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Spatial Distribution of Plant-Parasitic Nematodes in Semi-Arid *Vitis vinifera* Vineyards in Washington

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Abstract: The most commonly encountered plant-parasitic nematodes in eastern Washington *Vitis vinifera* vineyards are *Meloidogyne hapla*, *Mesocriconema xenoplax*, *Pratylenchus* spp., *Xiphinema americanum*, and *Paratylenchus* sp.; however, little is known about their distribution in the soil profile. The vertical and horizontal spatial distribution of plant-parasitic nematodes was determined in two Washington *V. vinifera* vineyards. Others variables measured in these vineyards included soil moisture content, fine root biomass, and root colonization by arbuscular mycorhizal fungi (AMF). *Meloidogyne hapla* and *M. xenoplax* were aggregated under irrigation emitters within the vine row and decreased with soil depth. Conversely, *Pratylenchus* spp. populations were primarily concentrated in vineyard alleyways and decreased with depth. *Paratylenchus* sp. and *X. americanum* were randomly distributed within the vineyards. Soil water content played a dominant role in the distribution of fine roots and plant-parasitic nematodes. Colonization of fine roots by AMF decreased directly under irrigation emitters; in addition, galled roots had lower levels of AMF colonization compared with healthy roots. These findings will help facilitate sampling and management decisions for plant-parasitic nematodes in Washington semi-arid vineyards.

Key words: arbuscular mycorrhizal fungi colonization, management, plant-parasitic nematodes, semi-arid, spatial distribution, *Vitis vinifera*, Washington.

Plant-parasitic nematodes are common pests of global economic concern in *Vitis vinifera* vineyards. In grapevines, nematode feeding can cause premature decline of vineyards (Lider, 1960; Anwar and Van Gundy, 1989), reduced vine vigor (Nicol et al., 1999; Téliz, 2007), and an increased susceptibility to other biotic or abiotic stresses such as pests, diseases, viruses, and drought (Brown et al., 1993; Ramsdell et al., 1996; Téliz et al., 2007; Esmenjaud and Bouquet, 2009). Feeding by plant-parasitic nematodes can also result in reduced root and shoot growth (Anwar and Van Gundy, 1989; Nicol et al., 1999), water and nutrient uptake (Nicol et al., 1999), and yield (Lider, 1960; Esmenjaud and Bouquet, 2009). Yield losses because of plant-parasitic nematodes have been estimated to range from 7% to 60% (Nicol and van Heeswijck, 1997; Téliz et al., 2007).

Little is known about plant-parasitic nematodes in Washington vineyards even though Washington is the second-largest wine grape producing region in the United States. The Washington wine industry has an economic value of $236 million with 17,401 ha of vineyards including more than 30 different varieties (USDA, 2013). Washington's vineyards primarily occur on the eastern side of the state and receive approximately 16 hr of sunlight in the summer and an annual average rainfall of 20 cm. Because of limited rainfall, vineyards in eastern Washington rely on drip irrigation to maintain productivity. The majority of vineyards in Washington are grown as own-rooted *V. vinifera* vines because of potentially damaging winter temperatures (Keller et al., 2012).

Zasada et al. (2012) conducted surveys in Washington to determine the plant-parasitic nematodes associated with *V. vinifera* vineyards. The most commonly encountered plant-parasitic nematodes were *Meloidogyne hapla*, *Paratylenchus* spp., and *Xiphinema* sp., which were detected in 60%, 50%, and 59% of sampled vineyards, respectively. Other plant-parasitic nematodes found were *Pratylenchus* spp. detected in 45% of sampled vineyards and *Mesocriconema xenoplax* found in 14% of sampled vineyards. *Meloidogyne hapla* is a sedentary endoparasite, and remains stationary for most of its life feeding inside the roots of a host plant. This nematode can significantly reduce root system size (Brown et al., 1993), limit the plant's ability to acquire water and nutrients (Ramsdell et al., 1996), and reduce yield (Téliz et al., 2007). *Pratylenchus* spp. are migratory endoparasites that enter host roots and tunnel through cortical cells where they feed on the cytoplasm. *Pratylenchus* spp. cause necrotic lesions on the roots, reducing water and nutrient uptake, and can also make the root more susceptible to secondary infections (Corbett, 1973; Walker, 1984). *Xiphinema* spp. are migratory ectoparasites that move freely in soil and feed from the exterior surfaces of host roots. This nematode can induce the malformation and necrosis of root tips, which can inhibit root growth and reduce yield (Anwar and Van Gundy, 1989; Brown et al., 1993). *Xiphinema* spp. can also vector viruses (Anwar and Van Gundy, 1989); however, no nematode-transmitted viruses have been found in Washington vineyards associated with this nematode. *Mesocriconema xenoplax* is another migratory ectoparasite, feeding externally on roots. *Mesocriconema xenoplax* can significantly reduce shoot and root growth, yield, and arbuscular mycorrhizal fungi (AMF) colonization of roots (Pinkerton et al., 2004; Zasada et al., 2012). *Paratylenchus* spp. are also migratory

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ectoparasites that can reside in the soil for long periods of time but appear to have a minimal impact on grapevines (Pinkerton et al., 1999).

Although it has been demonstrated that plant-parasitic nematodes are abundant and widespread in Washington vineyards (Zasada et al., 2012), little is known about the distribution and pathogenicity of plant-parasitic nematodes in this production system. The spatial distribution of plant-parasitic nematodes within vineyards has been determined in other regions. For instance, Ferris and McKenry (1974) examined the spatial distribution of *X. americanum* and four *Meloidogyne* spp. in a 'Thompson Seedless' (*V. vinifera* L.) vineyard in California, and Quader et al. (2001, 2003) similarly investigated the distribution of *Meloidogyne* spp., *Xiphinema* spp., and *Pratylenchus* spp. in South Australian vineyards. With limited research focusing on plant-parasitic nematodes in Washington, growers are at a disadvantage in knowing how to best target plant-parasitic nematode control measures in their vineyards. The goal of this research was to help fill this void in knowledge to better guide plant-parasitic nematode management in Washington vineyards. The objectives of this study were to determine the horizontal and vertical distribution of plant-parasitic nematodes, and to better understand what may be affecting their distributions in eastern Washington *V. vinifera* vineyards.

Materials and Methods

Site description: Two vineyards in eastern Washington were sampled. The first vineyard was a 34-yr-old *V. vinifera* cv. Chardonnay on Hezel loamy fine sand soil with a slope of 0 to 30 degrees, located in Paterson, WA. The mean annual precipitation in this area is 15 to 25 cm and the mean annual air temperature is 11°C to 12°C. The vineyard has a frost-free period of 150 to 200 d (USDA, 2012). The second vineyard was located in Mattawa, WA, and vines were 38-year-old *V. vinifera* cv. Riesling grown on Warden silt loam soil with 0 to 5 percent slope. In this region, the mean annual precipitation is 15 to 23 cm and the mean annual air temperature is 9°C to 11°C. The area has a frost-free period of 135 to 200 d (USDA, 2012). Alleyway management in both vineyards consisted of resident vegetation and planted grass cover crops, such as orchardgrass (*Dactylis glomerata*) and crested wheatgrass (*Agropyron cristatum*), and both vineyards were irrigated using regulated deficit irrigation (Schreiner et al., 2007). Row orientation was north-south with in row vine spacing of 1.8 m and between vine row spacing of 2.7 m. Vines were managed according to industry standards in the area and irrigated using pressure-compensated emitters at a rate of 1.8 liter/h. Soil sampling for both experiments was conducted in mid-September.

Horizontal distribution of plant-parasitic nematodes in semi-arid vineyards: Five 1.2- × 1.8-m plots were randomly established at each vineyard (Fig. 1); each plot spanned between two vines and included two drip irrigation emitters. A grid system was overlaid on each plot with spatial sampling points located at every 30-cm intersections of x-y coordinates; each plot consisted of 35 sampling points (Fig. 1). A soil sample, 5-cm-diam. × 45-cm-deep, was collected at each grid intersection within a plot, placed in a bag, and transported to the laboratory for processing.

In the laboratory, each soil sample was initially passed through a 2.36-mm sieve with roots and debris being retained on the sieve. All roots with a diameter of ≤ 2 mm were collected, washed in tap water, blotted dry, weighed, and stored in AA (acetic acid:alcohol 10%:50% v/v) whereas larger woody roots (> 2-mm diam.) were discarded. Root samples from the Chardonnay vineyard were further partitioned into physiologically active fine roots (feeder roots) and small woody roots to accurately assess AMF colonization. Physiologically active fine roots were classified as roots with an intact cortex varying in color from white to brown (Class A and B) and woody roots were categorized as living roots with a periderm (Class C, D, and E) (Mohr, 1996). Only roots from samples in the vine row and 30 cm to either side of the vine row (Vine Row, Middle East, and Middle West, see Fig. 1) were cleared and stained for AMF quantification because insufficient quantities of roots were extracted from the edges of the sampling plots (Alley West and Alley East, see Fig. 1). AMF colonization was determined from 21 locations per plot for a total of 105 samples. After observing significant galling because of *M. hapla* feeding in numerous root samples, 47 of these samples (approximately 45%) were further split into nongalled and galled roots to examine the impact of *M. hapla* on AMF colonization. Feeder roots were cleared and stained to assess the percentage of feeder root length colonized by AMF (Schreiner, 2003).

Plant-parasitic nematodes were extracted from a 250-g subsample of each soil sample using a semi-automatic elutriator followed by sucrose centrifugation (Jenkins,

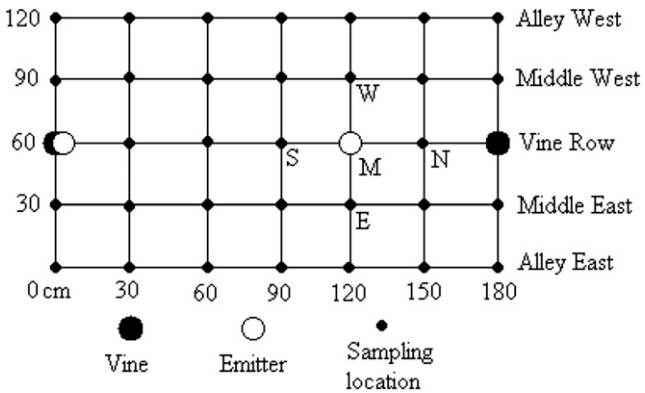

Fig. 1. Sampling scheme used to determine the horizontal and vertical distributions of plant-parasitic nematodes in semi-arid *Vitis vinifera* vineyards. Each point represents a sampling location; sampling locations were spaced 30 cm apart (n = 35).

1964; Byrd et al., 1976). Nematodes were identified based on morphological characteristics and counted under a stereo-microscope. Nematode extraction and quantification was performed at the Washington State University-Irrigated Agriculture Research and Extension Center, Prosser, WA. Soil water content was determined gravimetrically (Schmugge et al., 1980); each soil sample was dried in an oven at 105°C for 5 d. In addition, speciation of *Pratylenchus* at both vineyards was determined using β,1-4 endoglucanse species specific primers at the USDA-ARS Horticultural Crops Research Unit, Corvallis, OR (Peetz and Zasada, unpubl. data).

Vertical distribution of plant-parasitic nematodes in semi-arid vineyards: Five plots within each vineyard were established. Plots were selected based on the criteria of having an emitter equidistantly spaced between vines, an absence of weeds, and a level terrain. From each plot, five soil samples were collected to a depth of up to 90 cm. The locations sampled were directly underneath an emitter and 30 cm to the north, south, east, and west of the emitter (Fig. 1).

Soil samples were collected using a demolition hammer (Bosch, Farmington Hills, MI). The hammer was attached to a 5-cm-diam. × 1.2-m-long stainless steel soil collection tube lined with a 4.5-cm-diam. × 1.2-m-long removable polyethylene terephthalate (PTEG) plastic liner (Giddings Machine, Windsor, CO). A high-lift jack was used to remove the collection tube from the ground; each plastic tube was capped on both ends, stored in a cooler, and transported to the laboratory. In the laboratory, each soil core sample was cut into depth increments of 0 to 15, 16 to 30, 31 to 45, 46 to 60, 61 to 75, and 76 to 90 cm. Plant-parasitic nematodes were extracted from a 250-g subsample from each depth, quantified, and identified as described above. Soil moisture content of each sample was also determined as described above.

Statistical analyses: Data from each vineyard within the horizontal and vertical distribution studies was analyzed separately. To facilitate statistical analysis of plant-parasitic nematode populations across the horizontal sampling plots, areas within the plots were designated as Alley West, Middle West, Vine Row, Middle East, and Alley East (Fig. 1). Differences in nematode population densities across the plot were determined using the Kruskal-Wallis Rank Sum Test (R Studio v0.98, Boston, MA). In addition, contour plots of the horizontal distribution of plant-parasitic nematodes, soil water content, fine root biomass, and AMF colonization were created using the mean values for each unique sampling point from all five plots per vineyard (SigmaPlot 12.0, San Jose, CA). The relationships between soil water content and fine root biomass to each plant-parasitic nematode ($\log_{10}$ (x + 1) transformed data) were also determined using linear regression analysis (JMP 9.0.0, SAS Institute, Cary, NC). AMF colonization of galled versus healthy fine feeder roots was analyzed by a paired t-test in matching samples from each individual sampling point within each replicate. Plant-parasitic nematode data from the vertical distribution studies was $\log_{10}$ (x + 1) transformed before analysis to meet normality and variance assumptions of the model (JMP 9.0.0). A one-way analysis of variance was performed for each plant-parasitic nematode in relation to depth as well as location; each plant-parasitic nematode was also linearly regressed with soil water content. Paired t-tests were conducted to compare soil water content and fine root biomass (when measured) between vineyards in both the horizontal and vertical distribution studies. Means were separated using Tukey's honestly significant difference test ($P \leq 0.05$).

Results

Plant-parasitic nematodes found in the Chardonnay vineyard were *M. hapla, M. xenoplax, P. neglectus*, *X. americanum*, and *Paratylenchus* sp. In the Riesling vineyard, *M. hapla, X. americanum, Paratylenchus* sp., and a mixed population of *Pratylenchus* spp. (*P. neglectus* and *P. thornei*) were found. *Tylenchorhynchus* sp. and *Helicotylenchus* sp. were also found in both vineyards at very low densities (<5 nematodes/250-cm^3 soil); therefore, these species were not included in the analyses.

Horizontal distribution of plant-parasitic nematodes in semi-arid vineyards: In the Chardonnay vineyard, the mean (± standard error) population density of each major plant-parasitic nematode across all grid locations was 191 (± 22) *M. hapla*/250-cm^3 soil, 110 (± 14) *Paratylenchus* sp./250-cm^3 soil, 33 (± 4) *P. neglectus*/250-cm^3 soil, 295 (± 45) *M. xenoplax*/250-cm^3 soil, and 50 (± 7) *X. americanum*/250-cm^3 soil. The contour plots showed that *M. hapla* was concentrated under the emitters in the vine row (Fig. 2A). This was statistically supported with more *M. hapla* in the vine row as compared with the alleyways (Table 1). The distribution of *Mesocriconema xenoplax* was similar to that of *M. hapla*, with higher population densities of this nematode located in the vine row and lower population densities 30 cm away from the vine row toward the alleyways (Table 1; Fig. 2B). *Pratylenchus neglectus* was concentrated near the alleyways, with higher population densities located in the western alleyway (Table 1; Fig. 2C). *Paratylenchus* sp. was randomly distributed within the sampling area (Fig. 2D), with few differences in population densities across the sampling area (Table 1). In this vineyard, *X. americanum* had no uniform distribution (Fig. 2E) and there was no difference in population densities across the sampling area (Table 1). Both soil water content and fine root biomass were concentrated in a 60-cm band in the center of the vine row, with higher concentrations located directly under the irrigation emitters (Table 1; Fig. 2F,G). AMF colonization of fine roots was lowest directly under the drip emitters and increased in areas of lower soil water content closer to the alleyways (Fig. 2H).

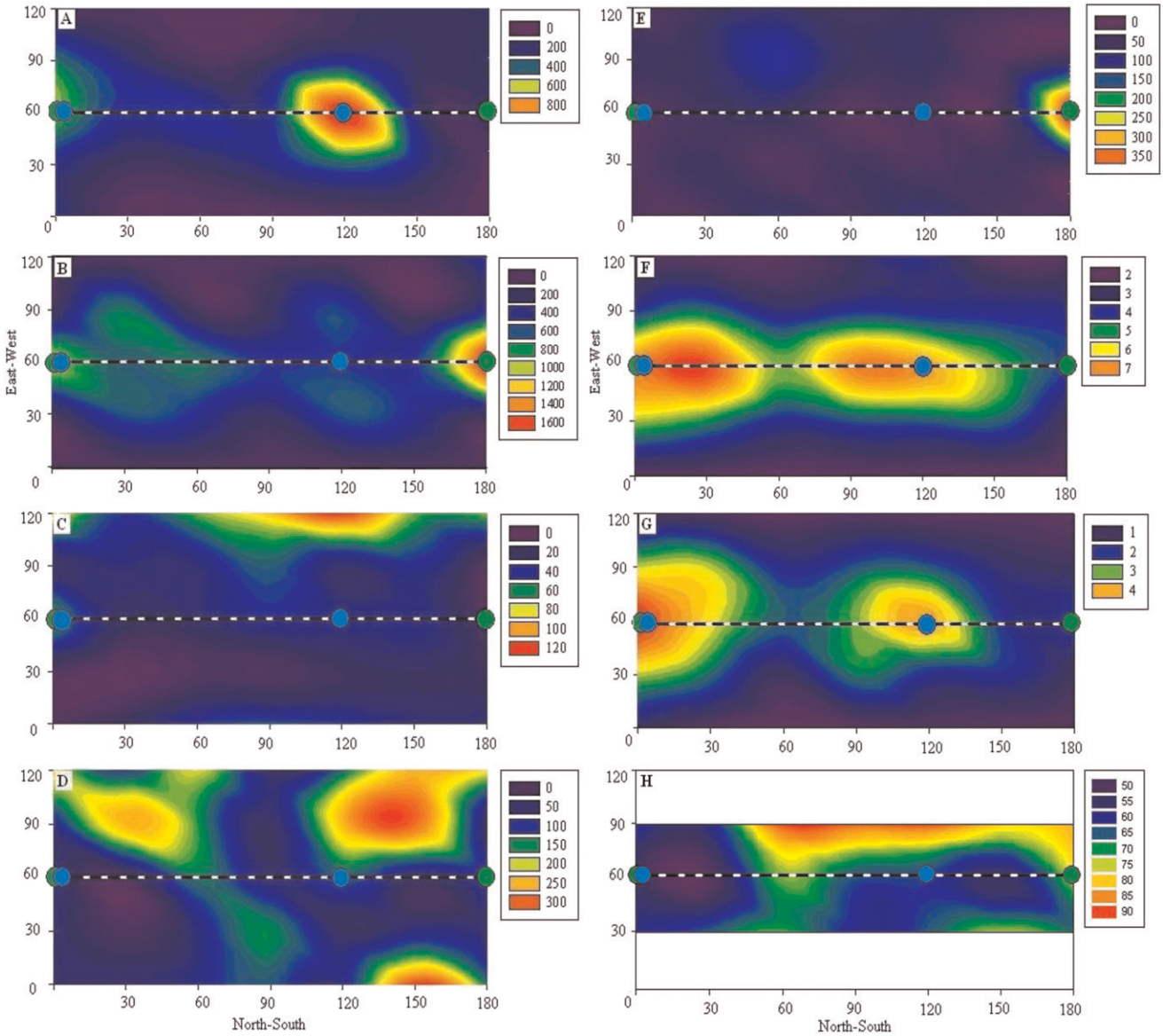

FIG. 2. Horizontal distribution of (A) *Meloidogyne hapla*, (B) *Mesocriconema xenoplax*, (C) *Pratylenchus neglectus*, (D) *Paratylenchus* sp., (E) *Xiphinema americanum*, (F) soil water content, (G) fine root biomass, and (H) % of root length colonized by arbuscular mycorrhizal fungi in a Chardonnay vineyard, Paterson, WA. Contour plots were generated from the average of five observations. Soil water content (g/cm^3) was determined gravimetrically. Fine root (≤ 2 mm) biomass is expressed as grams (g) fresh weight. Plant-parasitic nematode population densities are nematodes/250-cm^3 dry soil. Green circles represent vines, blue circles represent emitters, and the dotted line represents the vine row.

AMF colonization of roots was negatively correlated to soil water content ($P < 0.05$). In addition, AMF colonization was reduced by 8% in galled roots, caused by *M. hapla* infection, as compared with healthy roots from matching samples ($P = 0.017$).

In the Riesling vineyard, the mean (± standard error) population densities of plant-parasitic nematodes across all grid locations was 1,011 (± 95) *M. hapla*/250-cm^3 soil, 207 (± 34) *Paratylenchus* sp./250-cm^3 soil, 135 (± 19) *Pratylenchus* spp./250-cm^3 soil, and 9 (± 1) *X. americanum*/250-cm^3 soil. *Meloidogyne hapla* was concentrated in a 60-cm band in the center of the vine row (Fig. 3A). Statistically, the highest population densities of this nematode were in the vine row and 30 cm west of the vine row with the lowest population densities in both alleyways (Table 1). Similar to the results from the Chardonnay vineyard, population densities of *Pratylenchus* spp. were highest in the alleyways compared with other locations (Table 1; Fig. 3B). There were significantly higher population densities of *Paratylenchus* sp. 90 cm east of the vine row with no other differences in population densities detected within the sampling area (Fig 3C; Table 1). *Xiphinema americanum* was randomly distributed across this vineyard (Fig. 3D) and there were no differences in population densities in the sampling area (Table 1). Soil water content and fine root biomass were again concentrated in a 60-cm band down the center of the vine row (Fig. 3E,F). The highest soil water content and fine root biomass were

TABLE 1. Population densities of plant-parasitic nematodes/250-cm^3 soil in two Washington vineyards corresponding to each row destination in the horizontal study.

Row designation with a plot[a]	*Meloidogyne hapla*	*Mesocriconema xenoplax*	*Pratylenchus* spp.	*Paratylenchus* sp.	*Xiphinema americanum*	Soil water content	Fine root biomass
			Chardonnay				
Alley East	59 c[b]	16 b	77 a	185 a	43 a	2.56 c	0.46 b
Middle East	241 ab	302 b	24 b	127 ab	54 a	3.99 b	2.08 a
Vine Row	353 a	712 a	27 b	62 b	79 a	6.65 a	2.98 a
Middle West	217 abc	321 b	11 b	87 ab	40 a	4.52 b	1.90 a
Alley West	83 bc	126 b	27 b	90 ab	35 a	2.06 c	0.51 b
P-value[c]	<0.01	<0.01	<0.01	0.04	0.32	<0.01	<0.01
			Riesling				
Alley East	86 d	–[d]	294 a	33 b	7 a	3.28 c	0.70 c
Middle East	1,117 bc	–	57 b	205 b	10 a	5.38 b	2.06 b
Vine Row	1,922 a	–	15 b	159 b	5 a	7.50 a	2.85 ab
Middle West	1,419 ab	–	13 b	109 b	9 a	7.51 a	3.50 a
Alley West	623 cd	–	317 a	521 a	13 a	5.34 b	1.86 b
P-value	<0.01	–	<0.01	<0.01	0.64	<0.01	<0.01

[a] Areas within the sampling plots were split into five row categories: the sampling locations along the plot borders were designated as Alley, the next row in were designated Middle, and the sampling locations along the vine row were designated as the Vine Row (Fig. 1).
[b] Means within a column followed by the same letter are not significantly different according to Tukey's honestly significant difference test ($P \leq 0.05$); $n = 35$.
[c] P-values were obtained from Kruskal-Wallis Rank Sum Test.
[d] – = Nematode not found at this vineyard.

found in the vine row and in the middle western locations (Table 1); the lowest soil water content and fine root biomass was found in the eastern alleyway.

Meloidogyne hapla, *M. xenoplax,* and *P. neglectus* population densities were related to soil water content and fine root biomass in the Chardonnay vineyard (Table 2). However, *M. hapla* and *M. xenoplax* were positively correlated to soil water and fine root biomass, whereas *P. neglectus* was negatively correlated. Population densities of *Paratylenchus* sp. and *X. americanum* were not related to either soil water content or fine root biomass. In the Riesling vineyard, *M. hapla* and *Pratylenchus* spp. population densities were also related to soil water content and fine root biomass (Table 2). *Meloidogyne hapla* was positively correlated to soil water content and fine root biomass, whereas *Pratylenchus* spp. were negatively correlated to soil water content and fine root biomass. Similar to the Chardonnay vineyard, *Paratylenchus* sp. and *X. americanum* were not related to either soil water content or the distribution of fine roots. The majority of the sampling locations in the Riesling vineyard had soil water contents > 7%; this was wetter than the Chardonnay vineyard where soil water contents were > 7% in only a few sampling locations. The average soil water content was 3.98% (± 0.20%) and 5.85% (± 0.17%) at the Chardonnay and Riesling vineyards, respectively. Soil water content between the two vineyards was significantly different ($P < 0.001$); fine root biomass did not differ across the vineyards ($P > 0.05$).

Vertical distribution of plant-parasitic nematodes in semi-arid vineyards: In the Chardonnay vineyard, the average population densities of plant-parasitic nematodes across all locations and depths were 106 (± 19) *M. hapla*/250-cm^3 soil, 409 (± 57) *Paratylenchus* sp./250-cm^3 soil, 22 (± 3) *P. neglectus*/250-cm^3 soil, 56 (± 18) *M. xenoplax*/250-cm^3 soil, and 91 (± 10) *X. americanum*/250-cm^3 soil. Depth was significant for *M. hapla, M. xenoplax*, *P. neglectus*, and *Paratylenchus* sp. (Table 3). Higher population densities of *M. hapla* were discovered at the 0- to 45-cm soil depths, whereas the highest population densities of *M. xenoplax* were in the upper 30 cm of the soil profile; higher population densities of *P. neglectus* were also in the upper 30 cm of soil. In contrast, population densities of *Paratylenchus* sp. increased with soil depth with more nematodes discovered at a depth of 46 to 60 cm. *Xiphinema americanum* was evenly distributed throughout the soil profile with depth having no significant effect (Table 3). Soil water content also significantly decreased with depth (Table 3), with the upper 30 cm of soil having the highest soil water content; only soil water content varied among sampling location ($P = 0.02$). All the plant-parasitic nematodes were significantly related to soil water content except for *Paratylenchus* sp. (Table 3).

In the Riesling vineyard, the average population densities of plant-parasitic nematodes across all locations and depths were: 566 (± 100) *M. hapla*/250-cm^3 soil, 26 (± 10) *Paratylenchus* sp./250-cm^3 soil, 9 (± 3) *Pratylenchus* spp./250-cm^3 soil, and 14 (± 3) *X. americanum*/250-cm^3 soil. The vertical distribution of plant-parasitic nematodes and soil water content in the Riesling vineyard were similar to those observed in the Chardonnay vineyard. Depth was significant for *M. hapla*, *Pratylenchus* spp., and *Paratylenchus* sp. but not for *X. americanum* (Table 4). Population densities of *M. hapla* decreased with depth, with more nematodes recovered at shallower (0 to 30 cm) than deeper (31 to 90 cm) depths (Table 4). The same trend was observed for *Pratylenchus* spp.; however, similar densities were detected down to 45 cm for this nematode with no *Pratylenchus* spp. found lower (61 to 90 cm) in the soil profile. *Paratylenchus* sp. decreased with depth until 60 cm and no *Paratylenchus* sp. were found at the lower depths in the soil profile. The

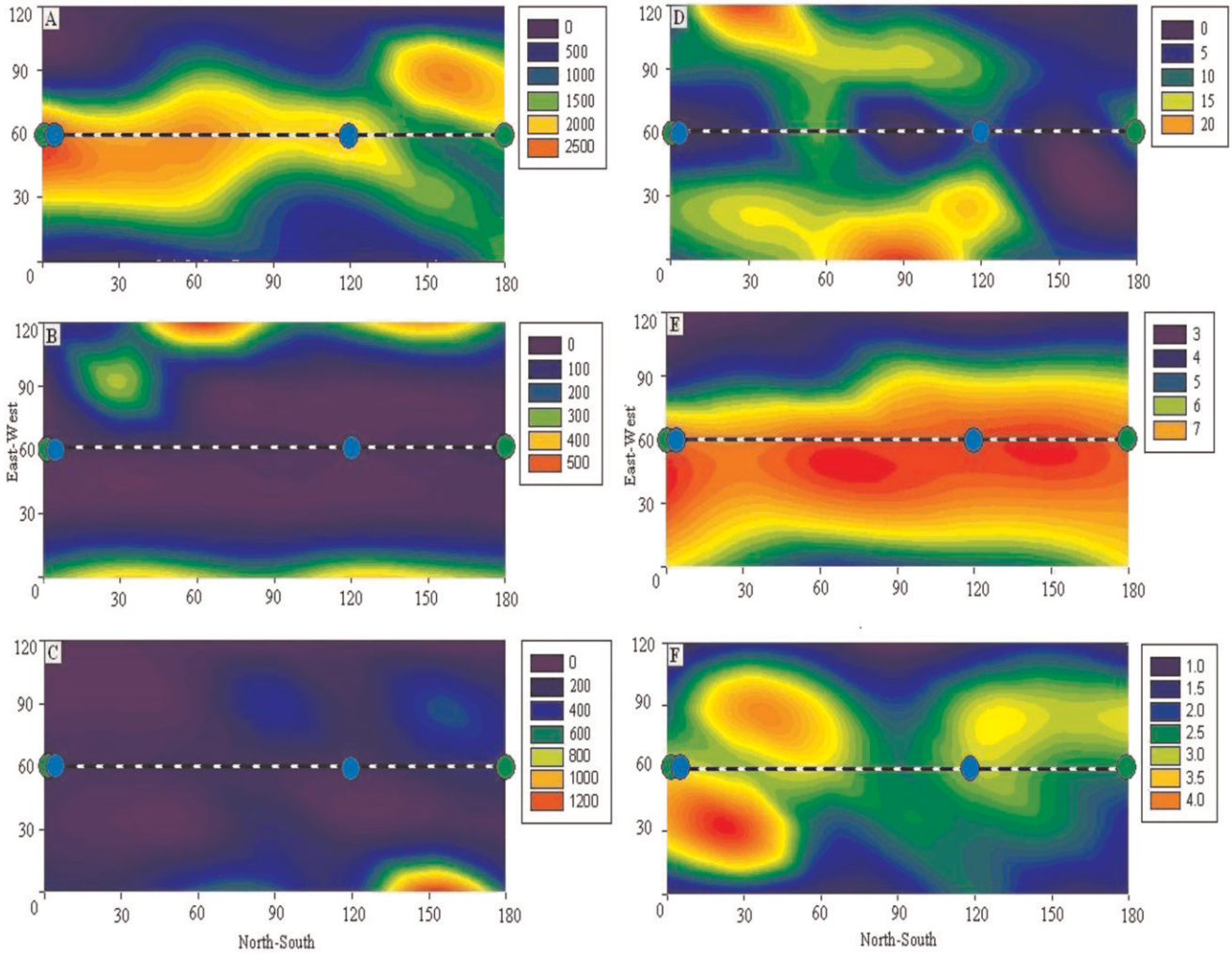

FIG. 3. Horizontal distribution of (A) *Meloidogyne hapla*, (B) *Pratylenchus* spp., (C) *Paratylenchus* sp., (D) *Xiphinema americanum*, (E) soil water content, and (F) fine root biomass in a Riesling vineyard, Mattawa, WA. Contour plots were generated from the average of five observations. Soil water content (g/cm^3) was determined gravimetrically. Fine root (≤ 2 mm) biomass is expressed as grams (g) fresh weight. Plant-parasitic nematode population densities are nematodes/250-cm^3 dry soil. Green circles represent vines, blue circles represent emitters, and the dotted line represents the vine row.

distribution of *X. americanum* was not influenced by depth. Soil water content in the Riesling vineyard also decreased with depth (Table 4) and differed at different sampling locations ($P = 0.01$). Only *M. hapla* and *Pratylenchus* spp. were significantly related to soil water content. The average soil water contents were 10.57% (± 0.46%) and 11.73% (± 0.44%) at the Chardonnay and Riesling vineyards, respectively; soil water content was different between the two vineyards ($P < 0.001$).

DISCUSSION

The horizontal and vertical distributions of plant-parasitic nematodes in semi-arid, drip-irrigated Washington *V. vinifera*

TABLE 2. Test of significance of plant-parasitic nematodes/250-cm^3 soil to soil moisture and fine root biomass in a Chardonnay and Riesling vineyard, Washington.

	Meloidogyne hapla	*Mesocriconema xenoplax*	*Pratylenchus* spp.	*Paratylenchus* sp.	*Xiphinema americanum*
		Chardonnay			
Soil moisture	<0.01[a]	<0.01	0.04	0.19	0.25
Fine root biomass	<0.01	<0.01	0.01	0.12	0.44
		Riesling			
Soil moisture	<0.01	–[b]	<0.01	0.29	0.70
Fine root biomass	<0.01	–	0.01	0.07	0.75

[a] *P*-values were determined using a simple linear regression; $n = 175$.
[b] – = Nematode not found at this vineyard.

TABLE 3. Vertical distribution of plant-parasitic nematodes/250 cm^3 and the summary of significance of their relationship to depth and soil water content in a Chardonnay vineyard, Washington.

Sampling depth (cm)	*Meloidogyne hapla*	*Mesocriconema xenoplax*	*Pratylenchus neglectus*	*Paratylenchus* sp.	*Xiphinema americanum*	Soil water content
0-15	166 ab[a]	177 a	58 a	62 b	75 a	17.20 a
16-30	256 a	121 a	45 a	327 ab	127 a	15.16 a
31-45	115 ab	14 ab	9 b	494 ab	110 a	10.06 b
46-60	33 b	6 ab	4 b	673 a	78 a	7.98 bc
61-75	20 b	0 b	2 b	529 ab	80 a	6.12 c
76-90	9 b	2 ab	0 b	343 ab	58 a	5.12 c
Depth[b] *P-value*	<0.01	0.01	<0.01	<0.01	0.10	<0.01
Soil moisture *P-value*	<0.01	<0.01	<0.01	0.05	0.04	

[a]Nematode population densities at each depth are the mean of $n = 25$. Means within a column followed by the same letter are not significantly different according to Tukey's honestly significant difference test ($P \leq 0.05$).
[b]*P*-values were obtained from one-way analysis of variance.

vineyards were consistent across the two vineyard locations considered in this study. In general, soil water content and fine root biomass were concentrated under the irrigation emitters and decreased with soil depth. The distribution of *M. hapla* and *M. xenoplax* were significantly related to soil water content and fine root biomass, and population densities of these nematodes were aggregated under the emitters within the vine row and decreased with depth. *Pratylenchus* spp. were concentrated along the alleyways with very few *Pratylenchus* spp. found in the vine rows with population densities decreasing with depth. *Paratylenchus* sp. and *X. americanum* had nonuniform distribution patterns within the vineyards and population densities of these nematodes were not influenced by root density or soil water content.

A noticeable difference observed between the two vineyards was the amount and distribution of water in the soil profile. The Riesling vineyard had higher soil water contents than the Chardonnay vineyard in both spatial studies, and soil water content was distributed further away from the drip emitters in the Riesling vineyard. The differing water status between the two vineyards was attributable in part to different irrigation schedules in relation to time of sampling and to different soil types present at each site. In both studies, sampling at the Riesling vineyard was conducted the day after irrigation was applied, whereas sampling in the Chardonnay vineyard occurred 4 d after irrigating. In addition, the silt loam soil in the Riesling vineyard has a higher water holding capacity of 30 g/cm^3 than the sandy loam soil in the Chardonnay vineyard that has water holding capacity of 23 g/cm^3 (NRCS, 2014). The larger pore spaces of the sandy loam soil in the Chardonnay vineyard would have allowed irrigation water to percolate more readily through the soil at this site as opposed to silt loam soil in the Riesling vineyard. This was apparent when comparing the horizontal spread of soil water content at both sites, where water did not disperse as far away from the irrigation emitters at the Chardonnay vineyard. The same trend was shown with fine roots, which were also aggregated directly under the emitters at the Chardonnay vineyard, whereas roots were more widely dispersed in the Riesling vineyard. This implies that soil water content controls the distribution of fine roots in these vineyards.

AMF colonization of roots at the Chardonnay vineyard was reduced in these pockets of higher soil water content and higher root biomass directly under emitters. It is difficult to say whether the higher soil water content or the higher *M. hapla* densities directly under the emitters was primarily responsible for reduced levels of AMF under the emitters. It is likely that both factors played a role. AMF colonization of roots was reduced

TABLE 4. Vertical distribution of plant-parasitic nematodes/250 cm^3 and the summary of significance of their relationship to depth and soil water content in a Riesling vineyard, Washington.

Sampling depth (cm)	*Meloidogyne hapla*	*Pratylenchus* spp.	*Paratylenchus* sp.	*Xiphinema americanum*	Soil water content
0-15	1,406 a[a]	26 a	67 a	7 a	16.65 a
16-30	1,427 a	17 ab	59 ab	20 a	14.98 ab
31-45	366 b	9 ab	14 ab	29 a	12.37 bc
46-60	9 b	2 b	6 ab	5 a	10.12 cd
61-75	0 b	0 b	0 b	6 a	8.13 d
76-90	4 b	0 b	0 b	12 a	6.72 d
Depth *P-value*[b]	<0.01	<0.01	0.01	0.20	<0.01
Soil water content *P-value*	<0.01	<0.01	0.32	0.40	

[a] Nematode population densities at each depth are the mean of $n = 25$. Means within a column followed by the same letter are not significantly different according to Tukey's honestly significant difference test ($P \leq 0.05$).
[b] *P*-values were were determined using one-way analysis of variance.

when more water was applied in a deficit irrigated Cabernet vineyard in eastern Washington (Schreiner et al., 2007); however, in the current study, colonization was reduced also in roots with apparent galls. Most of the samples with galled roots were located directly under the drip emitters in the Chardonnay vineyard.

Meloidogyne hapla population densities were positively related to soil water content and fine root biomass. In both vineyards, *M. hapla* population densities were concentrated in a 60-cm band along the vine row, indicating that *M. hapla* aggregates in the root zone. This finding conforms to the biology of *Meloidogyne* spp.; fine roots are the preferred site for entry of second-stage juveniles, which invade right behind the root tip (Anwar and McKenry, 2002). Population densities of *M. hapla* also decreased with depth. Numerically, higher population densities were recovered in the upper 45 cm of the soil profile in both vineyards, where soil moisture and fine root biomass were the highest, although this data was not always statistically supported. Our results for *M. hapla* are similar to results from previous studies evaluating *Meloidogyne* spp. distribution in vineyards. *Meloidogyne* spp. population densities were highest in the upper 60 cm of soil in the vine row and declined with depth in a 'Thompson Seedless' vineyard in California (Ferris and McKenry, 1974). The same study also found that *Meloidogyne* spp. population densities followed root distribution, which was highest in the vine row. Quader et al. (2001) investigated the distribution of *Meloidogyne* spp. in five South Australian vineyards and similarly found that highest population densities occurred in the vine rows where the majority of roots were located.

Similar to *M. hapla*, population densities of *M. xenoplax* were positively related to soil water content and fine root biomass in the Chardonnay vineyard. The majority of the *M. xenoplax* were located in the wetting zone in the center of the vine row with higher levels directly under the vine, suggesting that *M. xenoplax* follows fine root distribution. *Mesocriconema xenoplax* also decreased with soil depth with the highest population densities found between 0 and 30 cm in the soil. These results are similar to those of Smolik and Dodd (1983) where *M. xenoplax* decreased with soil depth in short-grass prairie with the highest population densities of this nematode found in the upper 20 cm of the soil profile. *Mesocriconema xenoplax* was not found in the Riesling vineyard. This discrepancy could be attributable to differences in cropping history at the two vineyards. The Chardonnay vineyard was established in an old pivot irrigation field that was previously cropped with annual crops such as potato, wheat, alfalfa, and mint; both wheat and mint are hosts for *M. xenoplax* (Nyczepir and Bertrand, 1990; Hafez et al., 2010). Because of the intensive crop production in this area, it is possible that *M. xenoplax* was introduced into this field through infected planting material or unclean machinery. In contrast, the Riesling vineyard was planted into a virgin site dominated by native stands of rabbitbrush (*Chrysothamnus nauseosus*) and sagebrush (*Artemisia* spp.) (Weaver, 1917). The geographic isolation of the Riesling vineyard from other vineyards and agricultural fields would also be expected to reduce the likelihood of accidental contamination with plant-parasitic nematodes. *Mesocriconema xenoplax* was present in only 14% of the 157 sampled vineyards in eastern Washington (Zasada et al., 2012), showing that although *M. xenoplax* is present in eastern Washington vineyards, it does not have a widespread distribution.

Pratylenchus spp. had a similar distribution pattern in both vineyards, being aggregated on the edge of our sampling plots in the vineyard alleyways. Quader et al. (2003) found *Pratylenchus* spp. to be distributed evenly across a commercial vineyard. Their results suggested that both the grapevine and cover crops planted in the alleys were hosts for *Pratylenchus* spp.; our study suggests that the alleyway vegetation, but not the grapevines, were hosts for this nematode in eastern Washington vineyards. We also found that *Pratylenchus* spp. population densities declined with soil depth. Likewise, Quader et al. (2003) reported that *Pratylenchus* spp. population densities decreased with depth, especially below approximately 45 cm. This further supports the idea that shallow-rooted plants, and not the deep-rooted grapevines, are the preferred host for *Pratylenchus* spp. in eastern Washington vineyards. The species present in both vineyards, *P. neglectus* and *P. thornei*, have not been reported as significant parasites to grapes; only *P. vulnus* has been reported to cause significant damage in vineyards. This further supports the idea that grapevines are not the preferred host in this system (Pinochet et al., 1976). However, because of the limited sample size it is not possible to state whether additional species of *Pratylenchus* may be present in eastern Washington vineyards. Smiley et al. (2013) reported that *Pratylenchus* spp. was present in 90% of semi-arid fields in eastern Washington.

There were no clear spatial effects horizontally or vertically in the distribution of *X. americanum* in these studies. Other researchers have reported a similar, non-uniform distribution of *Xiphinema* spp. in vineyards (Ponchillia, 1972; Ferris and McKenry, 1974; Quader et al., 2003). Contrary to our results, Ferris and McKenry (1974) found that population densities of *X. americanum* were higher in the upper 45 cm of undisturbed soil in the vine row and Quader et al. (2003) reported that the highest densities of *X. americanum* occurred in the top 15 cm of soil.

Similar to *X. americanum, Paratylenchus* sp. had an inconsistent horizontal distribution within the vineyards. Ferris and McKenry (1976) similarly found that *Paratylenchus* spp. had the most variable distribution among the plant-parasitic nematodes found in a *V. vinifera* 'Thompson seedless' vineyard. In our study, population densities of *Paratylenchus* sp. were only influenced by depth at both vineyards. In the Riesling vineyard, *Paratylenchus* sp. decreased with depth with no nematodes detected below

61 cm. Verschoor et al. (2001) also found *Paratylenchus* spp. population densities to decrease with depth in four grasslands. Conversely, in the Chardonnay vineyard *Paratylenchus* sp. increased with soil depth to 60 cm. This may be explained by the fact that this nematode has been shown to follow the distribution of roots (Verschoor et al., 2001), which may extend further in the Chardonnay vineyard because of the larger pore spaces of the sandy soil. Although *Paratylenchus* sp. had high population densities in both sampled vineyards, the effect that *Paratylenchus* sp. has on grapevines is minimal (Pinkerton et al., 1999).

The results of this study will facilitate management decisions regarding plant parasitic nematodes for eastern Washington grape growers. When targeting plant-parasitic nematodes, grape growers should concentrate their management efforts to approximately a 60-cm horizontal band around the vine row and to the upper 45 cm of the soil profile, where the majority of fine roots and two economically important plant-parasitic nematodes, *M. hapla* and *M. xenoplax*, are located. Possible nematode management strategies could include off-set planting (replanting grapevines in the old alleyways as opposed to the old vine rows) when replanting a vineyard, or altering the emitter spacing in vineyards with sandy soils. From a postplant nematode management perspective, our data demonstrates that the application of nematicides through the drip line to specifically target nematodes in the vine row would be effective. This research also indicates that the use of specific cover crops known to suppress plant-parasitic nematodes populations as a means of control would be ineffective because the economically important plant-parasitic nematodes present in these vineyards are not located in the alleyway. *Pratylenchus* spp. were predominately found in the alleyways indicating *V. vinifera* is not the primary host for this nematode in the region.

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