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Distribution of Plant–parasitic Nematodes in Missouri and Arkansas, USA, Vineyards

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Abstract. **A nematode survey was conducted from 30 vineyards in Missouri and Arkansas (USA) comprising 107 samples among 21 grape cultivars (*Vitis aestivalis*, *Vitis labruscana*, *Vitis vinifera*, *Vitis* hybrids, and *Muscadinia rotundifolia*). All the samples tested positive for nematode presence. Eleven different nematode taxa were isolated and identified, five of which have economic importance to grapevines: *Xiphinema americanum*, *Meloidogyne* spp., *Pratylenchus* spp., *Criconemoides* spp., and *Tylenchulus* spp. *Xiphinema americanum* was detected at all but two sites, with 58% of sites having populations at or above levels with expected biological and economic impact. This is primarily a concern because of the ability of *X. americanum* to transmit *Tomato ringspot virus* and other viruses. The other four nematode taxa of concern were present in fewer samples and at much lower population densities. *Xiphinema index*, known to vector *Grapevine fanleaf virus* was not identified in any of the samples collected.**

Grapevines (*Vitis* and *Muscadinia* spp.) are hosts to a variety of nematodes (phylum Nematoda) around the world, but most are of unknown or insignificant concern in grape production. Although our knowledge of grapevine–nematode interactions is expanding, a comprehensive understanding of the potential impact of different nematode taxa in viticulture remains elusive. Increasingly, both grape growers and scientists believe the importance of nematodes in viticulture has likely been underestimated (Khan 2023). The major plant–parasitic nematodes that are currently known to threaten grapevines in North America are dagger nematodes (*Xiphinema index* and *Xiphinema americanum*), root-knot nematodes (*Meloidogyne* spp.), and lesion nematodes (*Pratylenchus* spp.) (Andret-Link et al. 2017; Brown et al. 1993; Garcia et al. 2019). Other notable taxa of concern are ring nematodes (*Criconemella* and *Criconemoides* spp.) and citrus nematodes (*Tylenchulus* spp.) (McHenry and Bettiga 2013).

The threats of plant–parasitic nematode feeding activity in vineyards are 2-fold: 1) physical injury to roots and 2) virus transmission. Physical damage from *Xiphinema* species can be particularly detrimental in the case of *X. index*, which feeds ectoparasitically on the root tips, resulting in swelling, gall formation, stunting of the root system, death of feeder root tips, and overall decline in vine vigor and growth (Brown et al. 1993; Garcia et al. 2019; Nicol et al. 1999; Raski and Lider 1959). A study in the state of Washington, USA, showed that *Xiphinema* spp. are deeply distributed in the vineyard soil profile (≥122 cm) and thus are very difficult to manage through traditional methods of soil treatment such as fumigation (East et al. 2019). *Meloidogyne* spp. are more prevalent in sandy soils, with high infestations reducing yields as a result of restrictions in water and nutrient uptake caused by root damage and production of galls (Brown et al. 1993; Nicol et al. 1999). Patches of growth-stunted vines are symptoms of feeding by *Pratylenchus* spp., which damage roots by feeding on root cortical tissues and forming lesions (Brown et al. 1993).

Although damage caused by root feeding can be economically significant, the viruses vectored by nematodes can be of greater concern. Of the five taxa previously listed, only the dagger nematodes (*Xiphinema* spp.) are currently known to vector viruses. *Xiphinema index* has been documented in transmitting the devastating *Grapevine fanleaf virus* (GFLV) (Garcia et al. 2019), whereas *X. americanum* has been associated with *Tomato ringspot virus* (ToRSV; which causes grape yellow vein disease), *Tobacco ringspot virus* (TRSV), *Peach rosette mosaic virus* (Andret-Link et al. 2017; Brown et al. 1993; Taylor and Brown 1997), and *Arabis mosaic virus* (ArMV) (Milkus 2001). Symptoms observed for GFLV and the yellow vein disease strain of ToRSV are in many ways similar, requiring diagnosis of the virus through laboratory testing. Common symptoms of these two viruses are poor growth and fruit set, overall vine decline with leaves displaying an oak leaf pattern, yellow mosaic coloration, and vein banding (Golino et al. 1992).

To date (including this study), *X. index* has not been detected in any vineyard in Missouri or Arkansas, USA, whereas *X. americanum* is widely distributed throughout the region where the nepoviruses ToRSV and ArMV have been documented (Milkus 2001; Milkus and Goodman 1999; Qiu et al. 2006). A more recent virus survey (Schoelz et al. 2021), however, consisting of 400 samples from 25 grape cultivars across Missouri, USA, did not detect any known nepoviruses (GFLV, ToRSV, TRSV, ArMV). Decline and virus-like symptoms of 'Chardonnay' in a Missouri, USA, vineyard in 2004 prompted research into virus sampling and testing (Lunden et al. 2010; Qiu et al. 2007). Symptoms included short internodes, stunted and crinkled leaves, leaf mosaic, vein clearing, leaf curling, decline in vine size, and reduced cluster size and set. The positive identification of GFLV in that study (Qiu et al. 2007), along with the discovery of a complex of GFLV and ToRSV

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Fig. 1. Locations (Missouri and Arkansas, USA) where vineyard soil/root samples were collected for plant–parasitic nematode analysis.

yellow vein strain in combination with *Grapevine rupestris stem pitting-associated virus* (Lunden et al. 2010), prompted our study to determine whether the vector *X. index* is present in Missouri or Arkansas, USA, vineyards and to identify other nematodes that may be consequential in regional viticulture.

The objectives of our study were to conduct a widespread nematode survey across the major viticulture regions of Missouri and Arkansas, USA, encompassing diverse environments, vineyard ages, grape cultivars, and production methods, and, more specifically, to determine whether the documented presence of GFLV in the region may be a result of the heretofore-unknown presence of the nematode vector *X. index*.

Materials and Methods

A survey for plant–parasitic nematodes was conducted among 21 grape cultivars at 30 vineyards in Missouri and Arkansas, USA, during Oct and Nov 2008. Sampling at this time of year is expected to yield the greatest populations of nematodes present, especially *Xiphinema* species (McHenry and Bettiga 2013). Sites (22 in Missouri and 8 in Arkansas, USA) represented the major regions of grape production in both states as well as the diversity of cultivars grown (Fig. 1). A broad, region-wide assessment of the soils indicates that the central and southern Arkansas sites generally feature fine-sandy loams, whereas the northwestern Arkansas and Missouri sites largely encompass a variety of silt loam soils (US Department of Agriculture, Natural Resources Conservation Service 2024). Samples were collected from 21 cultivars among *Vitis aestivalis*, *Vitis labruscana*, *Vitis vinifera*, *Vitis* hybrids, and *Muscadinia rotundifolia*. All the *V. vinifera* cultivars were grafted to various rootstocks (which may or may not impart nematode resistance), whereas only ∼3% of the other cultivars were grafted (both are typical viticulture practices in the region). A total of 107 samples were collected in descending order by grape species/hybrid: *Vitis* hybrid (n = 59 samples), *V. aestivalis* (n = 21), *V. vinifera* (n = 12), *M. rotundifolia* (n = 10), and *V. labruscana* (n = 5). This sampling is representative of grape production in the region.

One or more sampling blocks within each vineyard were delineated. These blocks mostly encompassed distinct cultivars; but, in some cases, the same cultivar was sampled from different areas (blocks) within a vineyard. Sampling blocks ranged from 1 to 8 ha, with additional variables of grafted status, irrigation status, and vineyard age recorded for each block/sample. The sampling used a walked W pattern through each block, selected to alleviate block-scale variability concerns (soil type, soil depth, fertility changes, etc.). Because vine-to-vine variability, even among neighboring vines, can be high as a result of a variety of factors, individual vines were selected for sampling based on a visual assessment of their size and health relative to surrounding vines within the block, with the most representative vines selected. Six to 10 vines within a sampling block were selected for subsample collection, and soil cores (∼15 cm in diameter × 30 cm deep) were hand-dug with a metal "sharpshooter" spade. Subsamples, consisting of both soil and roots, were collected ∼30 cm from the vine trunk, avoiding areas directly below irrigation emitters. These 6 to 10 subsamples were placed in a clean bucket and mixed thoroughly, and a representative experimental sample (>250 cm^3) was collected. Samples were placed in zippered plastic bags, cooled immediately, then transported to the University of Arkansas Nematology Laboratory (Fayetteville, AR, USA) within 2 d for analysis.

Nematodes were extracted from samples by suspending in water and filtering through an 850-µm sieve over a 75-µm sieve to separate plant and soil particles from nematodes. Extracted nematodes were isolated using centrifugation–flotation (Jenkins 1964), killed by heat relaxation, fixed with 37% formalin, and mounted onto glass microscope slides (Hooper 1986). Identification and counting were performed using a Nikon Optiphot 2 compound microscope (Nikon, Tokyo, Japan) and a scanning electron microscope. *Xiphinema* nematodes were identified to species level, whereas all other nematodes were identified to genus (Ye 1996). The nematode population density was reported as number of nematodes per 250 cm^3 of sample.

The total nematode population per sample was ascertained by adding the population density of each nematode taxon found in each sample. Frequency tables and descriptive statistics were calculated and created in Excel (Microsoft 365; Microsoft Corporation, Redmond, WA, USA). Data transformations were determined using the Box-Cox transformation procedure to meet assumptions of normal distribution, independence, and variance homogeneity (Supplemental Table 1). Transformed data were used to conduct an analysis of variance using the general linear model in SAS (SAS version 9.4; SAS Institute, Cary, NC, USA) to determine whether nematode population densities were affected by the independent variables in the survey: grape species/hybrid, cultivar, grafted status, irrigation status, and vineyard age. Relationships between vineyard age and nematode density were determined by creating scatterplots with 95% prediction ellipses using the SGPLOT procedure in SAS (SAS version 9.4; SAS Institute, Cary, NC, USA). Mean separations were performed using Tukey's

Table 1. The incidence of plant–parasitic nematodes by grape species/hybrid in 107 samples collected among 30 Missouri and Arkansas, USA, vineyards.

Nematode taxa	Common name	Nematode frequency (% of positive samples by grape species/hybrid)				
		Vitis aestivalis (n = 21)	*Vitis labruscana* (n = 5)	*Vitis vinifera* (n = 12)	*Vitis* hybrids (n = 59)	*Muscadinia rotundifolia* (n = 10)
Xiphinema americanum[i]	Dagger	100	100	92	98	100
Meloidogyne spp.[i]	Root-knot	14	20	17	5	0
Pratylenchus spp.[i]	Root-lesion	38	40	8	17	40
Criconemoides spp.[i]	Ring	33	80	42	51	40
Tylenchulus spp.[i]	Citrus	14	20	0	15	0
Paratylenchus spp.	Pin	43	60	50	44	20
Hemicycliophora spp.	Sheath	0	20	0	2	10
Helicotylenchus spp.	Spiral	57	100	92	85	80
Tylenchorynchus spp.	Stunt	14	0	17	17	20
Paratrichodorus spp.	Stubby-root	10	0	0	0	0
Dorolaimus spp.	—	0	0	0	2	0

[i] These five nematode taxa are of the greatest concern in Missouri and Arkansas, USA, viticulture.

honestly significant difference test at $P \leq 0.05$.

Results and Discussion

Eleven different taxa of plant parasitic nematodes were identified in this survey (Table 1), including five of economic concern for grapevines: *X. americanum*, *Meloidogyne* spp., *Pratylenchus* spp., *Criconemoides* spp., and *Tylenchulus* spp. Frequency of nematodes among samples was greatest for *X. americanum*, found in 98% of the 107 samples and at all but 2 of the 30 vineyards [one planted with 'Chambourcin' (*Vitis* hybrid) and the other with 'Muscat Canelli' (*V. vinifera*)]. Nematode frequency followed with *Helicotylenchus* spp. (80% of samples), *Criconemoides* spp. (47%), *Paratylenchus* spp. (43%), *Pratylenchus* spp. (23%), *Tylenchorynchus* spp. (16%), *Tylenchulus* spp. (12%), *Meloidogyne* spp. (8%), *Hemicycliophora* spp. (3%), *Paratrichodorus* spp. (2%), and *Aorolaimus* spp. (1%). *Xiphinema index* was not identified in any of the vineyard sites sampled. Nematode frequency was separated further by grape species/hybrid (Table 1). For example, *Meloidogyne* spp. and *Tylenchulus* spp. nematodes were not found in any *M. rotundifolia* vineyards, whereas 100% of samples from *M. rotundifolia*, *V. aestivalis*, and *V. labruscana* were positive for *X. americanum* nematodes.

The most abundant nematode throughout the survey was *Helicotylenchus* spp., with a mean population density of 139 per 250-cm^3 sample, and with a maximum count of 2800 individuals in a sample (Table 2). *Criconemoides* spp., *Paratylenchus* spp., and *X. americanum* were also abundant, with mean numbers of 89, 84, and 48, and maximum counts of 3800, 2064, and 492 individuals, respectively, per 250-cm^3 sample. McHenry and Bettiga (2013) state that nematode populations from a single grapevine may range from 0 to 10 million individuals; hence, sampling results are often inconsistent. In terms of nematodes of particular concern for grapevines, *X. americanum* was most abundant in number, followed by *Meloidogyne* spp. and *Pratylenchus* spp. *Pratylenchus* spp. were present among all grapevine species/hybrid, although in very low numbers on *V. vinifera*. The presence of *X. americanum* at nearly all sites raises concern for the spread of ToRSV and other nepoviruses, especially among sensitive cultivars.

The economic threshold (ET) for nematodes in agriculture is defined as the nematode population at which a crop's potential loss in value is equal to the cost of nematode control (Ferris 1978). Although ET levels for nematodes have been developed for many crops, especially annuals [e.g., corn, soybean, cotton, peanut (Mehl 2024)], true nematode ET levels are largely undeveloped in viticulture worldwide. Some university extension publications [e.g., Dickerson et al. 2000 (for South Carolina)] propose detrimental nematode population levels for grapes; however, most of the data do not appear to be based on published peer-reviewed or easily accessible research, nor are they true ET figures based on the cost of

Table 2. The incidence of plant–parasitic nematodes across all grape taxa in 107 samples collected among 30 Missouri and Arkansas, USA, vineyards.[i]

Nematode	No. of positive samples	Frequency of positive samples (%)	Avg population density (no. per 250-cm^3 sample)	*SD*	95% CI	Maximum observed density (no. per 250-cm^3 sample)	Threshold (nematodes per 1-kg sample)[ii]	No. of samples above threshold	Samples above threshold (%) In total samples	In positive samples
Xiphinema americanum[iii]	105	98.1	48	66	13	492	20	62	57.9	59.0
Meloidogyne spp.[iii]	9	8.4	14	61	12	420	75	6	5.6	66.7
Pratylenchus spp.[iii]	25	23.4	6	18	3	144	20	10	9.3	40.0
Criconemoides spp.[iii]	50	46.7	89	399	76	3800	50	22	20.6	44.0
Tylenchulus spp.[iii]	13	12.1	20	81	16	672	1000	0	0	0
Paratylenchus spp.	46	43.0	84	257	49	2064	—	—	—	—
Hemicycliophora spp.	3	2.8	4	40	8	408	—	—	—	—
Helicotylenchus spp.	86	80.4	139	355	68	2800	—	—	—	—
Tylenchorynchus spp.	17	15.9	10	49	9	420	—	—	—	—
Paratrichodorus spp.	2	1.9	0	3	1	24	—	—	—	—
Aorolaimus spp.	1	0.9	0	3	1	32	—	—	—	—
Empty cysts	1	0.9	0	0	0	5	—	—	—	—
Total	107	100	—	—	—	—	—	—	—	—

[i] Note that raw (nontransformed) data were used for this table.
[ii] Nematode critical threshold levels are based on the low end of medium population-level ranges associated with notable grapevine damage from McHenry and Bettiga (2013). The potential damage severity may depend on soil type, climate, and nematode susceptibility (or resistance) of the vine root system and cultivar.
[iii] These five nematode taxa are of the greatest concern in Missouri/Arkansas viticulture.
CI = confidence interval; *SD* = standard deviation.

Table 3. P values for the independent variables grape species/hybrid, cultivar, grafted status, irrigation status, and vineyard age determined for total nematodes and among individual nematode taxa from 30 Missouri and Arkansas, USA, vineyards.[i]

Independent variable	Total nematode	*X. americanum*	*Paratylenchus*	*Criconemoides*	*Helicotylenchus*	*Pratylenchus*	*Tylenchorynchus*	*Hemicycliophora*	*Meloidogyne*	*Tylenchulus*
Grape species/hybrid	0.0751	0.1040	0.3638	0.2780	0.0015	0.2084	0.8245	0.0039	0.4055	0.4510
Cultivar	0.3089	0.0407	0.8257	0.5028	0.0540	0.0497	0.6144	0.0001	0.0282	0.9997
Grafted status	0.0933	0.3591	0.5616	0.1265	0.0011	0.4039	0.1261	0.9981	0.7799	0.9432
Irrigation status	0.0498	0.8810	0.8339	0.4208	0.1335	0.0507	0.3543	0.5702	0.5402	—
Vineyard age	0.1327	0.6380	0.4592	0.0265	0.0200	0.2393	0.3175	0.8307	0.5625	0.0109

[i]Transformed data (Supplemental Table 1) were used for this analysis of variance. Mean separations by Tukey's honestly significant difference test. P values $\leq$ 0.05 are considered statistically significant.

control. Rather, they tend to propose levels of expected vine damage in relation to defined nematode population levels. McHenry and Bettiga (2013) proposed low–medium–high nematode population numbers (per kilogram of sample) for important nematode taxa in California viticulture, and outlined the potential degrees of grapevine damage and crop loss associated with the various population levels; however, they did not define ET levels specifically. Because the work by McHenry and Bettiga (2013) is one of the most-cited resources on critical nematode population levels in viticulture, we used their data as a benchmark for comparison with our data.

Nematode density in our study is reported on a by-volume basis. Factors such as soil moisture, soil bulk density, and the inherent variability among soils sampled make direct volume-to-mass comparisons of our samples (250 cm^3) with the 1-kg figures in McHenry and Bettiga (2013) imprecise; however, for the purpose of developing the best possible understanding of the nematode threshold status in the study region, populations in our samples were multiplied by four to approximate 1 kg. Nematode population numbers at the low end of the medium population density range in McHenry and Bettiga (2013) were then designated as critical threshold levels for the purpose of assessing our data.

For *X. americana,* 57.9% of samples had population levels at or above threshold, whereas concerning levels of the citrus nematodes (*Tylenchulus* spp.) were not found in any samples (Table 2). *Meloidogyne* spp. were low in frequency among sites and density within samples, with only a handful of sites above threshold levels. *Muscadinia rotundifolia* was the only grapevine species/hybrid where no *Meloidogyne* spp. were found, which may indicate some level of resistance. A survey of *M. rotundifolia* vineyards in Georgia and North Carolina, USA (Jagdale et al. 2019), also found very low numbers of *Meloidogyne* spp. nematodes (9% of samples) compared with *Helicotylenchus* spp. (90%) and *Xiphinema* spp. (58%).

Table 3 elucidates statistical differences ($P \leq 0.05$) among nematode taxa in response to the independent variables grape species/hybrid, cultivar, grafted status, irrigation status, and vineyard age. The independent variables did not impart consistent trends or effects across all nematode taxa, but of note are that *X. americanum*, *Meloidogyne* spp., and *Pratylenchus* spp. populations varied significantly by cultivar; *Tylenchulus* spp., *Criconemoides* spp., and *Helicotylenchus* spp. populations depended on vineyard age; *Helicotylenchus* spp. was the only nematode taxon potentially influenced by grafting; and irrigated vineyards in general had greater nematode populations, but effects of irrigation (or not) on specific nematode taxa were not discerned.

Among the independent variables in this study, we chose vineyard age as an example for correlation analysis to determine whether there might be a relationship between vineyard age and nematode population density. Nonlinear regression analysis was used to fit the data to an exponential population decay model based on the scatterplot in Fig. 2. Although the relationship between the predictor (vineyard age) and the response (nematode density) was statistically significant ($P < 0.0001$), the model only explained a small portion of the variability. This suggests that vineyard age had a real but nevertheless weak influence on nematode density in our study, and that other factors (or combinations of factors) may account for most of the variability. Certainly, additional factors external

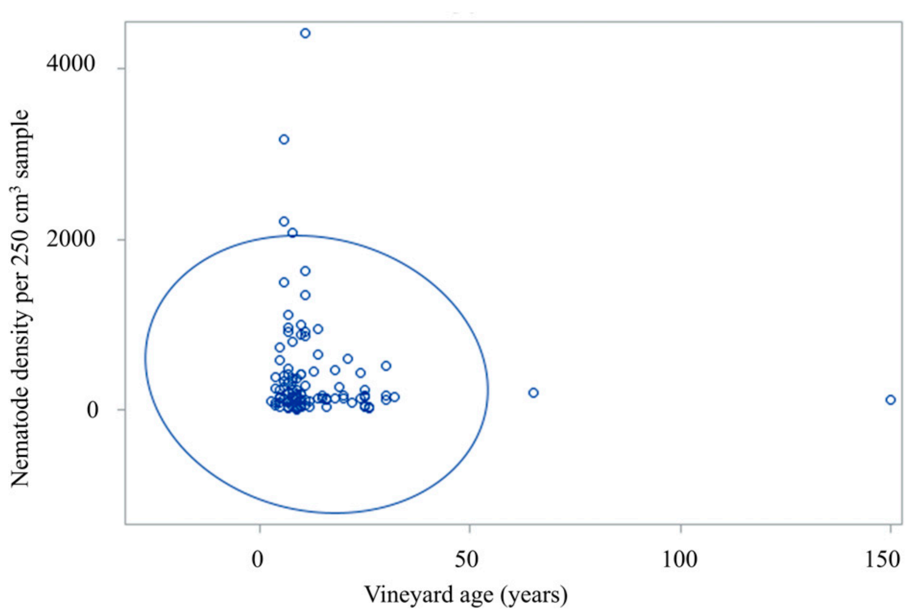

Fig. 2. Relationship between vineyard age and total nematode density, with a 95% prediction ellipse, from 107 vineyard nematode samples in Missouri and Arkansas. Transformed data (Supplemental Table 1) were used for this analysis.

to our study also influence nematode presence in vineyards.

Conclusion

Our survey underscores the diversity of plant–parasitic nematodes in Missouri and Arkansas, USA, vineyards and confirms the presence of five nematode taxa of economic importance to grapevines. The most concerning of these is *X. americanum*, which is known to vector several viruses. Fortunately, *X. index*, the worrisome vector of the nepovirus GFLV, was not identified in any samples. The lack of *X. index* in any of the samples collected raises questions as to how GFLV was established in Missouri vineyards (Kovacs and Qiu 2002; Qiu et al. 2006); we are not aware of any surveys having been conducted for GFLV in Arkansas, USA. Although GFLV may have been introduced on infected planting material, further research into other potential vectors of GFLV is needed to determine how this nepovirus is spread. Although this survey was conducted in 2008, we are not aware of any subsequent viticulture-based nematode surveys conducted or published from the region; therefore, our results remain relevant as a critical foundation for viticulture management and for additional needed research. More research on grapevine–nematode dynamics in the Missouri–Arkansas, USA, region is needed as the industry continues to expand, especially in terms of alleviating risks while developing mitigation and management strategies.

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