Progress Report

2022 Request for Applications

Progress Report Title:	Final Report
Applicant Name:	Devin Rippner
Application Title:	The effect of soil parameters on plant-parasitic nematodes of wine grapes in Washington and Oregon
Application ID:	142
Review Deadline:	01/11/2024 11:59 PM

Final Report

Please fill out the following information by inserting text directly onto the space provided. Please do not write your report on a separate sheet. There are files that need to be filled out and uploaded in the last sections (this includes the 2023 Conference proceedings form). NOTE: Material from this final report will be used to create a NCSFR Factsheet circulated to the PNW industry.

Please email info@nwberries.org if you have received this final reporting request in error. Provide proof of No Cost Extension or other timeline in your email.

Deadline for submission is Oct.27, 2023 at 4pm PST.

Oral presentations of findings will take place during the NCSFR Confrerence on Nov **13-15** in **Corvallis, OR**. You will be receiving a mailing with more conference information shortly.

Please note: Failure to submit final project reports and research impact statements, as well as to present a final oral presentation at the NCSFR conference, may result in disqualification for future proposals considered for funding through this program. PI must present in person at the conference.

Research Reporting

Project Title:	The effect of soil parameters on plant-parasitic nematodes of wine grapes in Washington and Oregon	
Principle Investigator & Cooperator(s): :	Devin Rippner; Katherine East	
Full Project Reporting Period Covered (M/D/Y-M/D/Y):	Start Date --	End Date
Full Project Reporting Period Covered (M/D/Y-M/D/Y):	Start Date 05/1/2022	End Date 05/31/2023
Is this a final report?:	--	
Is this a final report?:	Yes	
Abstract:		

Abstract:

Plant parasitic nematodes are costly pests that cause global crop loss of over $100 billion dollars. Previously it was thought that the large populations of ring nematode in Oregon and Northern root-knot nematode in Washington vineyards were caused by differences in soil characteristics. We found that soil texture had no influence on both nematodes' population growth. We found that Northern root-knot nematodes that live inside of the roots thrived in acidic (low pH) soil than alkaline (high pH) soil. Soil pH had no effect on ring nematodes that live outside of the roots. We also generated a computer model to automate nematode egg counting. These results will help generate parasitism risk maps, help wine grape growers make better vineyard planting decisions, and increase the speed with which scientists can identify plant parasitic nematode eggs.

Objectives:

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Objective 1. Determine soil parameters that affect Meloidogyne hapla (Northern root-knot nematode) invasion and success in vineyards. Wine and Juice Grape Viticulture Priority 3C – Biology and management of soil-borne pests.

Objective 2. Determine the effect of soil pH and texture on M. hapla and Mesocriconema xenoplax (ring nematode) invasion and success. Wine and Juice Grape Viticulture Priority 3C – Biology and management of soil-borne pests

Objective 3. Develop a protocol for using machine-learning to count M. hapla eggs.

Wine and Juice Grape Viticulture Priority 3C – Biology and management of soil-borne pests

Accomplishments:

Accomplishments:

Objective 1: we identified permanganate oxidizable carbon as an important indicator nematode parasitism resistance in soils. The results of this work are in the final stages of writing before submission for publication.

Objective 2: We identified pH as a driver of plant parasitic nematode success, with root knot nematode plant parasitism being more effected by soil pH than parasitism by ring nematodes. The results of this work were published in Agrosystems, Geosciences, and Environment (https://doi.org/10.1002/agg2.20450).

Objective 3: A machine learning model was developed to count M. Hapla eggs; the results were presented at the 2023 NCSFR conference. Work continues on this project to turn it into a publication.

Reasons why goals and objectives were not met (when applicable): :

Reasons why goals and objectives were not met (when applicable): :

NA-all objectives completed.

Industry Significance:

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1: Vineyard establishment is the largest one time cost for vineyard owners, ranging between 10,000 and $85,000+ an acre. Young vine success is crucial to vineyard profitability; however young vines are most susceptible to soil born parasites like plant parasitic nematodes. The parasitic success of Northern Root Knot Nematode (M. Hapla) was negatively associated permanganate oxidizable carbon in soils. Permanganate oxidizable carbon is an easily measured soil health metric that is associated with plant derived polyphenolic compounds, like lignin or tanins. Increasing permanganate oxidizable carbon in young vineyards is hypothesized to decrease plant parasitic nematode success.

Changes to standard production practices :

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Changes to standard production practices :

-Increase soil carbon to decrease root knot nematode success

-In acid soils, lime to decrease root knot nematode success

-Return winery waste to the vineyard to increase soil POX carbon

-Prevent spread of nematodes to new locations to help prevent parasitism.

New grower recommendations:

New grower recommendations:

New grower recommendations:

-Identify sites with good drainage and high permangate oxidizable carbon to reduce risk from northern root knot nematodes

-If you have nematodes, plant on rootstock to avoid parasitism.

-Amending soils with winery waste prior to planting may decrease northern root knot nematode pressure.

Provide a list of all scientific citations and papers that have been published because of the funding you received from NCSFR :

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East, K.E., Zasada, I.A., Lee, J., Schreiner, R.P. and Rippner, D.A., 2023. Vineyard soil texture and pH effects on Meloidogyne hapla and Mesocriconema xenoplax. Agrosystems, Geosciences & Environment, 6(4), p.e20450.

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None

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Nematodes, Soil Health, Plant Parasites

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ORIGINAL ARTICLE

Agrosystems

Vineyard soil texture and pH effects on *Meloidogyne hapla* and *Mesocriconema xenoplax*

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Abstract

Northern root-knot nematode (*Meloidogyne hapla*) and ring nematode (*Mesocriconema xenoplax*) are the most prevalent plant-parasitic nematodes of wine grapes in the Pacific Northwest, but *M. hapla* is most important in eastern Washington and *M. xenoplax* in western Oregon. These regions differ edaphically where Washington soils are minimally weathered and alkaline while Oregon soils are highly weathered and acidic. To examine the effect of soil texture and pH on nematode reproduction, an alkaline, sandy loam soil (pH 7.9) from Washington and an acidic loam soil from Oregon (pH 5.4) were modified to the other pH extreme, and to a middle pH of 6.9. Tomatoes were planted into each soil/pH combination, and either 500 *M. hapla* second-stage juveniles or *M. xenoplax* individuals were added to each pot. After 7 weeks, plants were harvested, three roots collected for analysis, remaining roots and leaves dried and weighed, and nematode population densities determined as eggs on roots (*M. hapla*) and nematodes in soil (*M. xenoplax*). Soil texture (sandy loam or loam) had no effect on either nematode, but *M. hapla* reproduction was greater in the lowest pH soil while *M. xenoplax* was unaffected by soil pH. *Mesocriconema xenoplax* parasitism reduced root length and root tip number, whereas *M. hapla* increased root mass in the highest pH Washington soil. Under these experimental conditions, it appears vineyard soil texture in the Pacific Northwest is not a determining factor in population growth of these nematodes, but *M. hapla* performed better at low pH.

1 | INTRODUCTION

Plant-parasitic nematodes cause in excess of $100 billion crop loss globally per year and have the potential to parasitize almost all plant species (Bernard et al., 2017). They can either be endoparasites, residing predominantly in plant roots, or ectoparasites, always residing in soils. Among the most damaging of the endoparasitic nematodes are root-knot nematodes (*Meloidogyne* spp.), including *Meloidogyne hapla* (Olsen, 2011). Occupying a completely different parasitic niche, ectoparasitic nematodes from the family Criconematidae, including *Mesocriconema xenoplax*, can be problematic in perennial cropping systems such as wine grapes (Pinkerton

Abbreviations: ACE, autoclaved citrate-extractable; DTPA, diethylenetriamine pentaacetic acid; MinC, mineralizable carbon; POXC, permanganate oxidizable carbon; SOM, soil organic matter.

et al., 1999; Schreiner et al., 2012). *Meloidogyne hapla* and *M. xenoplax* are two of the most problematic plant-parasitic nematode species for wine grapes in the Pacific Northwest (Idaho, Oregon, and Washington) of the United States (Howland et al., 2014; Pinkerton et al., 1999). Plant-parasitic nematodes are often difficult to deal with in perennial cropping systems, where their density increases over time and parasitism eventually decreases crop yield and vineyard life span (East et al., 2021; Raski et al., 1973). Resistant rootstocks are often the best approach for managing grape production in nematode-infested soils, but resistance varies depending on the nematode species, and there are few rootstocks that have broad-spectrum resistance against all plant-parasitic nematodes that coexist in vineyards (East et al., 2021; Ferris et al., 2012; Pinkerton et al., 2005; Zasada, Howland et al., 2019).

Once a vineyard is heavily infested with *M. hapla* or *M. xenoplax*, newly planted vines may suffer, limiting establishment success and delaying time to first harvest and subsequent yield (Forge et al., 2021; Zasada, Kitner et al., 2019). While both *M. hapla* and *M. xenoplax* are found in both Washington and Oregon, *M. hapla* is the most prevalent nematode pest of eastern Washington vineyards, and *M. xenoplax* is the most prevalent nematode pest of western Oregon vineyards (Pinkerton et al., 1999; Zasada et al., 2012). From a 2012 survey in eastern Washington, 60% of vineyards had *M. hapla* present, and 26% of vineyards had population densities above a damage threshold of 100 *M. hapla* juveniles per 250 g soil (Zasada et al., 2012). In contrast, only 10% of western Oregon vineyards had any *M. hapla*, and only 1% had population densities above a damage threshold of 50 juveniles per 250 g soil (Pinkerton et al., 1999). The opposite was true for *M. xenoplax*; only 14% of vineyards in eastern Washington had *M. xenoplax* present, where 81% of Oregon vineyards had *M. xenoplax*, and 20% with population densities above the damage threshold of 125 individuals per 250 g soil (Pinkerton et al., 1999; Zasada et al., 2012). It is unclear why these two nematode species are so different in their distribution in vineyards between these regions.

One potential influence may be the attributes of the soil itself. Soil physical and chemical properties are thought to play a significant role in the distribution and successful parasitism of plant-parasitic nematodes (Taylor et al., 1982). However, given the large number of plant-parasitic nematode species, these results are not comprehensive (Martin et al., 2022; Melakeberhan et al., 2004; Mulder et al., 2003; Wang et al., 2004). No information exists about the role of soil properties on *M. hapla* specifically, but there are some examples with other *Meloidogyne* species. *Meloidogyne incognita* population densities were negatively correlated with soil electrical conductivity (EC) and positively correlated to percentage of sand content in cotton fields (Monfort et al., 2007; Ortiz et al., 2010). Soil texture also influenced *Meloidogyne javanica* juvenile movement, where the optimum soil pore size was between 75 and 120 μm, typical of coarse sandy soils (Wallace, 1966). Soil pH may also play a role. When parasitizing grapevines in acid soils in Georgia, *Meloidogyne* spp. populations were positively correlated with pH, % sand, and lime buffer capacity (LBC), a measure of a soil's pH buffering capacity driven by exchangeable aluminum (Al^{3+}) (Martin et al., 2022). *Meloidogyne incognita* infection of soybean was positively correlated with pH in acid soils (Melakeberhan et al., 2004). However, the relationship between *Meloidogyne* spp. and pH can be site dependent or species dependent as they were only weakly negatively correlated across eight different cropping systems, including fallow and maize/beans in western Kenya (Kandji et al., 2001). Similarly, there was no influence of soil pH ranging from 4.0 to 8.0 on *M. javanica* movement in soil (Wallace, 1966).

A gap in the literature also exists for *M. xenoplax*, especially in alkaline soils. *Mesocriconema xenoplax* densities in wine grape vineyards were positively correlated to percentage of sand and LBC, but not soil pH in Georgia (Martin et al., 2022). *Mesocriconema xenoplax* densities were also positively correlated to percentage of sand content in the Okanagan Valley of Canada, but were not correlated with pH in that study (Forge et al., 2021). A study in corn found no correlation of *M. xenoplax* densities with EC, pH, or % silt, though densities were correlated to soils with lower organic matter and/or lower clay content (Simon et al., 2018). Similarly, *M. xenoplax* densities in vegetable crops were not correlated with soil physical or chemical properties (Marquez et al., 2021). As vineyard soils in western Oregon are generally acidic and those in eastern Washington are mostly alkaline, this offers an opportunity to examine the effect of soil texture and pH on reproduction of these two plant-parasitic nematode species.

The current study was conducted to evaluate the impact of soil texture and pH on *M. hapla* and *M. xenoplax* parasitism in vineyard soil, using a tomato plant model system. Two soils, collected from vineyards in Washington and Oregon, differing in soil texture and pH, were adjusted to three matching pH

Core Ideas

- The effect of soil pH and texture on two vineyard nematode pests in Washington and Oregon was tested.
- Soil texture had no effect on *Meloidogyne hapla* or *Mesocriconema xenoplax* reproduction.
- Only *M. hapla* reproduction was increased in the low pH (5.4) soil, and *M. xenoplax* was unaffected by pH.
- It is still unclear how soil impacts these nematodes' distribution and regional prominence.

endpoints to decouple the effects of soil texture and pH on nematode parasitism. The objectives were to (1) determine the role of pH on *M. hapla* and *M. xenoplax* population dynamics and impact on plant growth parameters, and (2) determine if there was an interaction between soil texture and pH on *M. hapla* and *M. xenoplax* reproduction and plant response.

2 | MATERIALS AND METHODS

2.1 | Soil pH modification

Two soils, one from a vineyard in Washington state (latitude 45.882391, longitude −119.741048) and one from an Oregon vineyard (latitude 44.340528, longitude −123.407291), representative of those areas and with a wide range of soil pH (2.5 pH units), were chosen for this experiment. The Washington soil was a Burbank loamy fine sand (Sandy-skeletal, mixed, mesic Xeric Torriorthent), characterized as a sandy loam by laboratory analysis (Soiltest Farm Consultants, Inc.), with 68:30:2% sand:silt:clay, and a pH of 7.9. The Oregon soil was a Jory silty clay loam (fine, mixed, active, mesic Xeric Palehumult), characterized as loam by laboratory analysis, with 52:28:20% sand:silt:clay, and a pH of 5.4. Soils were collected from the top 40 cm of the soil profile and passed through a 6-mm sieve to remove rocks or large debris. To obtain a consistent pH gradient across soils, a portion of each soil was modified to the other extreme; that is, the more basic Washington soil was acidified and the Oregon acid soil was alkalized. Multiple small-scale soil incubations were performed to determine the amounts of sulfuric acid (H_2SO_4) or calcium hydroxide ($Ca(OH)_2$) that would be needed to alter soil pH to achieve one of three pHs (Figure S1): low (pH 5.4) to match the natural pH of the Oregon soil, high (pH 7.9) to match the Washington soil, and a middle neutral pH (pH 6.9).

To decrease the pH of the basic soil, 2 M H_2SO_4 (2.0 L for pH 5.4, 1.5 L for pH 6.9) and a volume of deionized (DI) water (2.0 L for pH 5.4, 2.5 L for pH 6.9; to hydrate soil to 100% field capacity) was added to 10 L Washington soil in a 20-L bucket, and was incorporated until smooth with a spiral paint mixer attached to a hand drill. The same volume of DI water (4.0 L) was added to keep conditions the same for the pH 7.9 Washington soil. To increase the pH of the Oregon soil, 10 L of soil was placed in a 20-L bucket and $Ca(OH)_2$ as a powder was added in amounts of 0 g (no change; pH 5.4), 20 g (0.2 moles $Ca(OH)_2$; pH 6.9), or 60 g (0.6 moles $Ca(OH)_2$; pH 7.9), mixed in with a trowel, then wetted with 2.9 L of DI water and mixed as above.

All soils were left at least 7 weeks to equilibrate before the next stage of the experiment. Soil pH was measured four–five times per treatment approximately every 10 days between adjusting and planting to monitor the change in pH by taking a small subsample and measuring pH of a 1:1 w:w suspension of soil and water (Thermo Scientific Orion EA940 pH meter; Thermo Fisher Scientific Inc.). Prior to planting, all soils were steam-pasteurized for 1 h at 74°C to eliminate any background plant-parasitic nematodes.

2.2 | Soil property testing

Soil properties of air-dried and sieved (2 mm) soils were determined after adjustment, incubation, and pasteurization. One sample from each pH × type treatment was tested per experiment. Soil pH and EC were measured in a 1:1 (m/m) suspension of soil and water (Thermo Scientific Orion EA940 pH meter; YSI 3200 Conductivity Meter YSI probe; YSI Incorporated). Permanganate oxidizable carbon (POXC) was measured by adding 10 mL of 0.02 M $KMNO_4$ to 1.25 g soil. Samples were well mixed for 2 min and allowed to stand in the dark for 10 min. After 10 min, a 0.25-mL aliquot of the reacted $KMNO_4$ solution was added to 24.75 mL of water and was measured by a spectrophotometer at 550 nm (Orion AquaMate 8000, Thermo Fisher Scientific Inc.). Mineralizable carbon (MinC) was measured by titration (HI932 Potentiometric Titrator, Hanna Instruments) after a 96-h incubation (Stott, 2019). Ammonium (NH_4) and nitrate (NO_3) nitrogen were measured by a flow injection analyzer (FIALab 1000, FIAlab Instruments, Inc.) after extraction in 1 M KCl (Gavlak et al., 2003). Autoclaved citrate-extractable (ACE) protein, a measurement of bioavailable soil nitrogen (N), was measured by a spectrophotometer (same as above) after autoclaving (Hurisso & Culman, 2021; Stott, 2019). Olsen P was measured by a spectrophotometer at 882 nm after extraction with 0.5 M $NaHCO_3$ and reduction with ammonium molybdate (Gavlak et al., 2003). Ammonium acetate extractable potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) and DTPA (diethylenetriamine pentaacetic acid)-sorbitol extractable zinc (Zn), manganese (Mn), copper (Cu), and iron (Fe) were measured by inductively coupled plasma-atomic emission spectroscopy (Avio 550 Max, Perkin Elmer). Percent soil organic matter (SOM) was estimated using the Sims/Haby colorimetric method and measured by a spectrophotometer (same as above) at 600 nm (Gavlak et al., 2003).

2.3 | Greenhouse experiment

Plant-parasitic nematode populations used in the experiments were obtained from cultures maintained in a greenhouse (Filialuna et al., 2022). The population of *M. hapla* was originally collected from a vineyard in Washington and maintained on tomato, and the population of *M. xenoplax* was originally collected from a vineyard in Oregon and maintained on grapevines. Two experiments were conducted, one starting on July 7, 2022 and ending on August 24, 2022

(Experiment 1), and one starting on August 11, 2022 and ending on October 4, 2022 (Experiment 2). These experiments were performed as a randomized block design: two soils (Washington, Oregon), three pH (5.4, 6.9, and 7.9), three nematodes (*M. hapla* or *M. xenoplax*, or no nematode control), four replicates (Experiment 1), or five replicates (Experiment 2), for a total of 72 plants in Experiment 1 and 90 plants in Experiment 2. In each experiment, 4- to 6-week-old Rutgers tomatoes (*Solanum lycopersicum* L.) were planted in a 0.5-L pot with 400 g of soil from one of the six different soil pH treatments and watered to 50% field capacity. Pots were inoculated with nematodes the next day, with one of two nematode treatments or a control as follows: (1) 500 *M. hapla* second-stage juveniles (J2), (2) 500 *M. xenoplax* mixed stages, and (3) water only. Nematodes were inoculated in 3 mL water applied in three holes approximately 5-cm deep around the base of the plant. Plants were watered daily and fertigated once a week with a dilute 20:20:20 N:P:K fertilizer with micronutrients (J.R. Peters). The experiment was conducted in a greenhouse under a 16 h photoperiod, with 26˚C/18˚C day/night temperatures. The experimental duration was 7 weeks, the optimal time for *M. hapla* reproduction in this system (Filialuna et al., 2022). Tomatoes were previously used as a proxy for grapevines to study the virulence of *M. hapla* and are a suitable model plant for studying the effects of soil properties on nematode reproduction given the variety and uniqueness of both grapes and grape rootstocks grown globally which limits the applicability of using any one grape variety in studies like this (Figure S2).

In the first experiment, all tomatoes in the Washington soil modified to pH 5.4 did not survive. Eastern Washington soils have an abundance of carbonates, so as a result of adding H_2SO_4, CO_2 and gypsum salts were evolved:

$$CaCO_3 + H_2SO_4 + H_2O \rightarrow CO_2 + CaSO_4 \cdot 2H_2O$$

This increased the EC of the soil in the Washington pH 5.4 soil to the point where tomato plants could not grow (measured at 9.96 mS cm^{-1}). For the second experiment, the Washington soil adjusted to pH 5.4 was irrigated post-acidification with 7 L of DI water to leach enough salt to allow for tomato growth (EC measured at or below 7.00 mS cm^{-1}).

2.4 | Data collection

At the end of the experiment, tomato plants were removed from pots and nematode, leaf, and root data were collected. Tomato leaves were removed from plants with scissors and split into two portions. One-half was kept for later analysis, and the other half was weighed, and placed in a drying oven at 70˚C for at least 2 days and then weighed to obtain dry weight. Stems were discarded. The roots were shaken free of soil. In all three nematode treatments, three seminal roots were taken from the top, middle, and bottom of the main tap root and preserved in root fixative for later root architecture analysis (see below). The remaining fine roots were cut from the taproot, then cut into 2-cm segments and mixed. One-third of these roots was weighed for fresh weight, then put into a drying oven at 70˚C for at least 2 days to obtain dry root weight. The change in wet to dry root weight was used to calculate the total dry root weight per plant. The second-third was saved for image analysis (below). In the *M. hapla* and no nematode treatments, the remaining third was used to assess egg densities. Eggs were extracted from roots with a 10% sodium hypochlorite solution and shaken for 3 min, then poured over nested 88- and 25-μm sieves with eggs retained on the latter (Hussey & Barker, 1973). *Mesocriconema xenoplax* was extracted from all 400 g soil per pot by decant sieving and sugar centrifugation (Ayoub, 1977).

2.5 | Image analysis

Seminal roots from each plant from every treatment were removed from root fixative, gently floated in a plexiglass tray in DI H_2O, separated, and scanned at 600 dpi with an Epson Perfection V850 Pro Scanner (Epson America, Inc.) (Martin et al., 2022). Briefly, images were cropped using the NumPy package in Python to remove non-roots, and then the images were converted to HSV (hue, saturation, and value) color space using the convert color function in OpenCV (Bradski & Kaehler, 2011; McKinney, 2010; Oliphant, 2007). The adjusted images were then converted to float 32 format and segmented in Python using the *K*-means clustering algorithm from OpenCV (Bradski & Kaehler, 2011). The number of clusters was set to two, and the algorithm was set to stop after 100 iterations. Binary root mask images were generated by this process and then individual objects smaller than 200 $pixels^2$ were removed from the masks to decrease noise. Masks were then hand corrected in Fiji (an image-processing package; Schindelin et al., 2012) to remove any excess background information. Hand-corrected masks were then batch processed in RhizoVision Explorer v2.0.3 (Seethepalli & York, 2020) with a pruning value of 5. Exact program parameters can be found in Table S1.

Root parameters measured included number of root tips, number of branch points, total root length, branching frequency, network area, average root diameter, median root diameter, maximum root diameter, root perimeter, root volume, and root surface area. Outputs were saved in comma separated values (CSV) file format.

2.6 | Data analysis

Data were analyzed using R Statistical Software (v4.1.1; R Core Team, 2021). Due to differences between experimental

repeats, *M. hapla* data were transformed to a percentage of the maximum number of eggs counted in a sample in each experimental run as follows:

$$M.\,hapla\,\text{eggs}/\text{maximum value of}\ M.\,hapla\,\text{eggs}\cdot 100 = \text{percentage of maximum}$$

This allowed for both experiments (repeats) to be analyzed together. *Mesocriconema xenoplax* data were log-transformed ($\log x + 1$) to meet assumptions of normality. All data were assessed for normality using the Shapiro–Wilk test, and for homoscedasticity of residuals using Levene's test (car package; Fox & Weisberg, 2019). The reproduction factor (Rf) for both nematode species was also calculated, with the final nematode population divided by the initial nematode population. Tomato plant data, including dry root weight and dry leaf weight, were normally distributed. Outputs from the root analysis, including total root length, number of root tips, and root volume were all log-transformed to meet assumptions of variance; average root diameter did not require this transformation. As there were unbalanced treatments, due to differences in treatment sample size between Experiment 1 and 2, as well as the loss of a treatment in Experiment 1, a Type III analysis of variance (ANOVA) was used, which is more robust to differences in sample sizes. A Type III ANOVA was conducted on both experiments as a single data set, using soil pH, type, and nematode treatments as factors with all interactions (where applicable; car package). Analysis of soil properties was limited to two samples per type · pH treatment combination due to limited modified soil volumes. Soil properties were analyzed by ANOVA. Posthoc means comparisons were performed with the Tukey honest significant difference test for all analyses at 95%.

3 | RESULTS

3.1 | Soil properties

Soil pH was altered by pH adjustment, with no differences between the soils at each pH step ($p < 0.001$; Table 1). Soil EC was also altered by pH adjustment, but only for the Washington sandy loam which was acidified using H_2SO_4 ($p < 0.05$). POXC was only altered by pH adjustment in the low-pH Washington sandy loam ($p < 0.001$). MinC was greater in the Oregon loam than the Washington sandy loam ($p < 0.05$). Ammonium N ($p < 0.05$) and nitrate N ($p < 0.001$) were generally greater in the Oregon loam compared to the Washington sandy loam, especially at high pH. ACE protein was greater at low pH than high pH ($p < 0.001$) and greater in the Oregon loam than the Washington sandy loam at each pH step ($p < 0.001$). Olsen P was unaltered in the Oregon loam with increasing pH, but was elevated by almost an order of magnitude in the Washington sandy loam with decreasing pH ($p < 0.001$). Ammonium acetate extractable K was higher in the Washington sandy loam than the Oregon loam at all pH steps ($p < 0.001$). Ammonium acetate extractable Ca was higher in the Washington sandy loam than the Oregon loam ($p < 0.001$), and increased with pH adjustment due to the addition of $Ca(OH)_2$ to the Oregon loam and the liberation of Ca from $CaCO_3$ in the Washington sandy loam during acidification with H_2SO_4 ($p < 0.05$). Ammonium acetate extractable Mg ($p < 0.01$) and Na ($p < 0.01$) were greater in the Washington sandy loam than the Oregon loam. DTPA-extractable Zn was greater at low pH than high pH in both soils ($p < 0.05$). A similar, but nonsignificant trend was observed for Mn in both soils. Neither DTPA-extractable Cu nor Fe were altered by soil pH adjustment, and no differences were measured between the two types. SOM was greater in the Oregon loam than the Washington sandy loam ($p < 0.001$).

3.2 | Nematode population densities

Soil pH ($p < 0.0001$), but not soil type ($p = 0.95$), affected *M. hapla* reproduction (Figure 1). Soils with pH values of 6.9 and 7.9 had significantly fewer *M. hapla* eggs per gram root than with pH of 5.4. Changes in *M. hapla* eggs per gram root mass were consistent across soil type, despite having different textures. Interactions between soil type and pH were not significant ($p = 0.20$). *Meloidogyne hapla* egg data were transformed to a percent of maximum in each experiment, as treatments in the October experiment had considerably more egg production in general than the August experiment. This way, data from both experiments were on a similar scale and could be combined for analysis. The reproduction factors calculated for *M. hapla* agreed with the above results; Rf values ranged from 2.1 to 6.3 in the August experiment, 10 times less than the range of 24–125 from October (Table S2). Looking at the Rfs for just October, the lowest pH (5.4) treatment in both soils had the highest Rf, with an Rf of 68 compared to an Rf of 24 and 26 in Oregon soil, and 125 compared to 73 and 78 for Washington soil.

Mesocriconema xenoplax population growth did not occur under these experimental conditions, with average Rf values of 0.77 and 0.09 in the two runs of the experiment. Accordingly, final population densities did not vary with soil pH ($p = 0.99$), soil type ($p = 0.44$), or their interaction (Figure 2). When experimental repeats were considered separately, soil type did not influence *M. xenoplax* density, although the response to pH varied. At the lowest pH (5.4), both experiments had similar *M. xenoplax* densities, however, nematode density increased with increasing pH in the August experiment, but declined in the October experiment. As there

TABLE 1 Soil testing results from pH-adjusted Washington sandy loam and Oregon loam soils at pre-planting. Washington 7.9 and Oregon 5.4 were unadjusted; Washington 6.9 and 5.4 were acidified, and Oregon 6.9 and 7.9 were alkalized prior to testing.

Treatment		Carbon, protein, and macronutrients (range, $n = 2$)							
Type	Adjusted pH	Soil organic matter (%)	POXC (mg kg^{-1})	MinC (mg kg^{-1})	nitrate N (mg kg^{-1})	ACE protein (mg kg^{-1})	ammonium N (mg kg^{-1})	Olsen P (mg kg^{-1})	K (mg kg^{-1})
Oregon	5.4	2.9 ± 0.2a	177 ± 29AB	16.3 ± 7.7a	3.9 ± 0.1A	5.33 ± 0.39A	8.6 ± 0.3AB	6 ± 3B	65 ± 3a
Oregon	6.9	2.9 ± 0.1a	354 ± 126AB	21.1 ± 11.3a	1.4 ± 0 C	3.01 ± 0.14B	24.4 ± 1.2 AB	4 ± 1B	65 ± 2a
Oregon	7.9	2.7 ± 0.2a	368 ± 112AB	28.3 ± 15.2a	2.3 ± 0.2B	1.33 ± 0.02CD	31.2 ± 0.4 A	8 ± 4B	63 ± 1a
Washington	5.4	0.3 ± 0b	616 ± 209A	7.3 ± 2.7b	0.2 ± 0.1E	3.45 ± 0.58B	13.5 ± 9.7AB	56 ± 3A	85 ± 3b
Washington	6.9	0.3 ± 0.1b	64 ± 56B	8 ± 5.8b	0.2 ± 0.1E	1.45 ± 0.13C	4.7 ± 4.4B	64 ± 2A	76 ± 1b
Washington	7.9	0.3 ± 0.1b	67 ± 41B	10.5 ± 6.5b	0.7 ± 0D	0 ± 0 D	6 ± 6.7B	6 ± 2B	77 ± 4b
	Site	***	NS	*	***	***	*	***	***
	pH	NS	NS	NS	***	***	NS	***	NS
	Site × pH	NS	**	NS	***	NS	*	***	NS

Treatment		Chemistry and micronutrients (mean ± standard error)									
Type	Adjusted pH	pH (actual)	EC (mS cm^{-1})	Ca (mg kg^{-1})	Mg (mg kg^{-1})	Na (mg kg^{-1})	Zn (mg kg^{-1})	Mn (mg kg^{-1})	Cu (mg kg^{-1})	Fe (mg kg^{-1})	B (mg kg^{-1})
Oregon	5.4	5.3 ± 0.1a	0.208 ± 0B	490 ± 10B	73 ± 0a	16.1 ± 2.3a	1.3 ± 0.4a	8 ± 2.1	0.2 ± 0.1	12 ± 3	0.05 ± 0.02
Oregon	6.9	6.8 ± 0.1b	0.338 ± 0B	1710 ± 30B	24 ± 0a	16.1 ± 0a	0.1 ± 0.1b	2.2 ± 0.2	0.3 ± 0.1	16 ± 9	0.06 ± 0
Oregon	7.9	7.8 ± 0.1c	1.118 ± 0.026B	2980 ± 20B	24 ± 0a	11.5 ± 0a	0 ± 0b	2.2 ± 0.1	0.4 ± 0.1	7 ± 2	0.03 ± 0.01
Washington	5.4	5.6 ± 0.1a	8.242 ± 1.716A	11,180 ± 1380A	617 ± 339b	34.5 ± 16b	0.5 ± 0.2a	49.7 ± 24.5	0.4 ± 0.1	32 ± 9	0.05 ± 0.03
Washington	6.9	7 ± 0.3b	6.851 ± 0.169A	8020 ± 600A	569 ± 36b	39.1 ± 2.3b	0.3 ± 0.1b	1.4 ± 0	0.3 ± 0.1	9 ± 2	0.01 ± 0
Washington	7.9	7.8 ± 0.5c	1.053 ± 0.273B	3750 ± 110B	405 ± 18b	39.1 ± 2.3b	0.2 ± 0.1b	1.6 ± 0.1	0.2 ± 0	2 ± 0	0.07 ± 0.01
	Site	NS	***	***	**	**	NS	NS	NS	NS	NS
	pH	***	*	*	NS	NS	*	NS	NS	NS	NS
	Site × pH	NS	**	**	NS	NS	NS	NS	NS	NS	NS

Note: Results from a sample from each of the first and second experiments (August and October) were combined ($n = 2$); analyzed with ANOVA and Tukey's honest significance test. Uppercase letters denote significant differences between type · pH treatments, except in circumstances where type · pH was not significant, where lowercase letters denote differences in type (% soil organic matter, MinC, K, Mg, and Na) or pH treatment (pH and Zn).
Abbreviations: ACE, autoclaved-citrate extractable; ANOVA, analysis of variance; EC, electrical conductivity; MinC, mineralizable carbon; NS, nonsignificant; POXC, permanganate oxidizable carbon.
*, **, and *** denote significance at the 0.05, 0.01, and 0.001 probability levels, respectively.

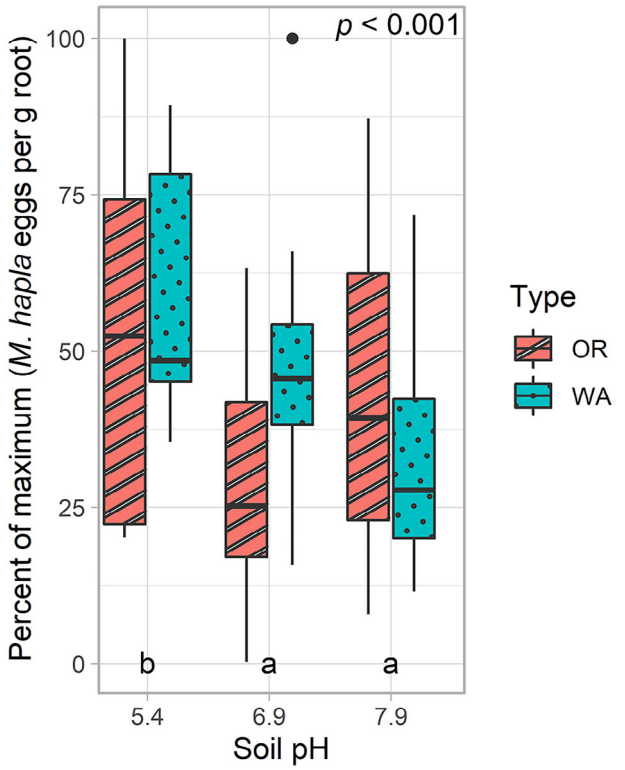

FIGURE 1 Normalized mean number of *Meloidogyne hapla* eggs per gram tomato root for each combination of soil pH (5.4, 6.9, and 7.9) and soil type (coarser-textured Washington [WA] sandy loam = teal dots and finer-textured Oregon [OR] loam = coral stripe). Data were adjusted to a percent-of-maximum value within an experimental repeat, then examined with analysis of variance (ANOVA). Different lowercase letters and *p*-value ($p \leq 0.01$) denote significant differences among soil pH treatment only; the interaction of pH × soil is shown for visual purposes and is not significant.

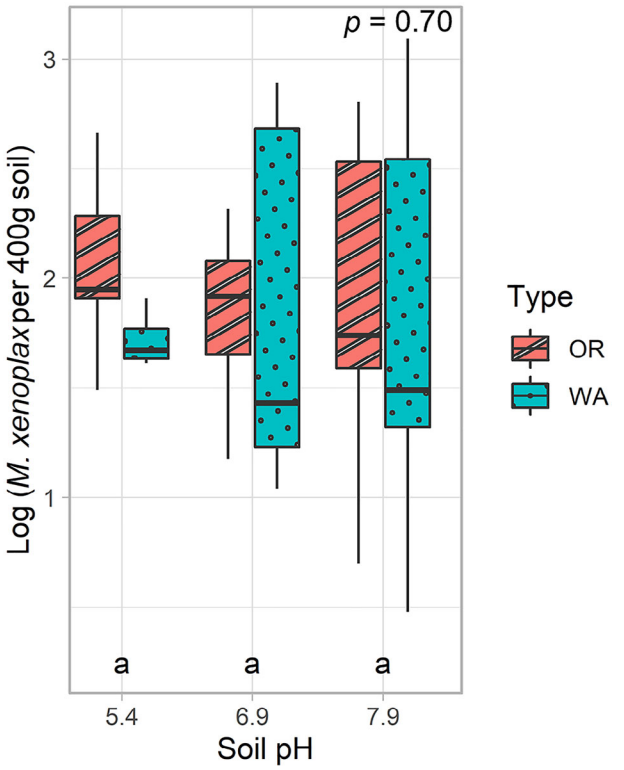

FIGURE 2 Mean number of *Mesocriconema xenoplax* eggs per 400 g soil for each combination of soil pH (5.4, 6.9, and 7.9) and soil type (coarser-textured Washington sandy loam = teal dots and finer-textured Oregon loam = coral stripe). Data were log transformed to meet the assumptions of normality of residuals and homoscedasticity for analysis of variance (ANOVA). Same lowercase letters ($\alpha = 0.05$) denote nonsignificant differences between soil pH treatments (*p*-value = 0.99); the *p*-value and interaction of pH × soil is shown for visual purposes and is also not significant ($p = 0.70$).

was no consistent effect of soil pH on *M. xenoplax*, and in fact opposite effects between the two experiments, they were combined.

3.3 | Plant metrics

Dry leaf weight was affected by soil type ($p < 0.001$), pH ($p < 0.001$), and the interactive effect of soil and pH ($p < 0.001$) (Figure 3). Generally, Oregon loam had lower dry leaf weight than Washington sandy loam, especially at pH 7.9, at which Oregon loam had the lowest leaf dry weight. Only at pH 6.9, the leaf dry weight between the two soils was similar. Nematode treatment did not have a significant effect on dry leaf weight.

The treatment effects on dry root weight were more complicated than dry leaf weight. There was an interaction between both pH and soil type ($p < 0.001$) and between pH and nematode treatment ($p = 0.016$) on dry root weight. The magnitude of the effect of pH and soil type was greater than the magnitude of the effect from nematodes and pH based on *F*-statistic values. At the highest soil pH, tomatoes in the Washington sandy loam had much greater root mass than those in Oregon loam ($p < 0.001$) (Figure 4a,b). At pH 7.9, tomatoes with *M. hapla* had greater root weight than those with *M. xenoplax*, while the noninoculated control was not different from either ($p = 0.016$) (Figure 4a,b). There were no differences among dry root weights between pH 5.4 and pH 6.9, regardless of treatment.

3.4 | Root morphology

Root length was affected by nematode treatment ($p = 0.014$), but not by pH ($p = 0.14$), soil type ($p = 0.67$), or any interaction combination between pH, soil type, and nematode treatments. *Mesocriconema xenoplax* had a negative effect on root length compared to *M. hapla*, but neither differed from

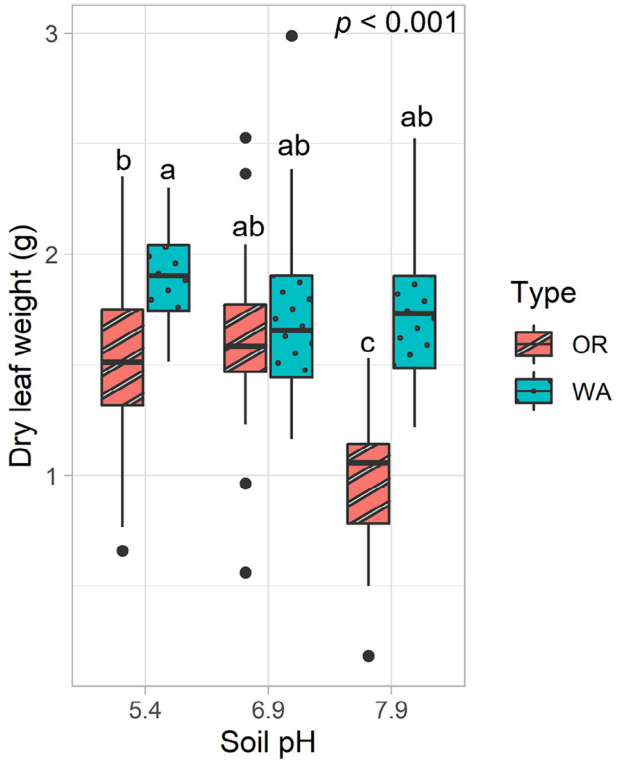

FIGURE 3 Interactive effect of pH (5.4, 6.9, and 7.9) and soil type (coarser-textured Washington sandy loam = teal dots and finer-textured Oregon loam = coral stripe) on tomato dry leaf mass. Data met the assumptions of normality and homoscedasticity for analysis of variance (ANOVA). Different lowercase letters ($\alpha = 0.05$) denote significant differences within the distinct comparisons.

the noninoculated control. (Figure 5a). The number of root tips was affected by nematode treatment ($p = 0.004$) and pH ($p = 0.008$), but not soil type ($p = 0.88$). Similar to root length, treatment with *M. xenoplax* decreased root tip number compared to *M. hapla* but neither differed from the noninoculated control. (Figure 5b). Root tip number was greater at pH 6.9 and 7.9 than at pH 5.4 (not shown). Root volume was affected by soil type ($p = 0.002$), and nematode treatment ($p = 0.046$), but not pH ($p = 0.95$). Root volume was greater in plants with *M. hapla* compared to *M. xenoplax* (Figure 5c), but neither differed from the noninoculated control. Root volume across treatments was greater in plants grown in the Oregon loam compared to the Washington sandy loam (Figure 5d).

Both soil type ($p < 0.001$) and pH ($p < 0.001$) had a significant effect on root diameter, while inoculation with nematodes did not ($p = 0.42$). Root diameter was greater across soil types at pH 5.4 compared to pH 6.9 or 7.9 (Figure 6a). Average root diameter was greater in the Oregon loam compared to the Washington sandy loam (Figure 6b).

4 | DISCUSSION

4.1 | Nematode response to soil pH and soil type

Meloidogyne hapla reproduction was greater in the lowest soil pH (5.4) than at either higher soil pH, regardless of soil type. This is contrary to previous studies with other species of *Meloidogyne*, in which *M. javanica* was limited in movement for invasion by soil pore size, but soil pH had little to no effect on *M. javanica* movement (Wallace, 1966). Highly alkaline soils may reduce the ability of *M. javanica* to parasitize plants. In a study in which soil pH was increased to near 11.0 with an N source, *M. javanica* juveniles were immobilized at that pH (Oka et al., 2006), though this is an extreme example and a pH unlikely to occur in vineyards. Based on our results, *M. hapla* appears to be better suited to reproduce in more acidic soils, like those in western Oregon. Yet *M. hapla* is more common in higher pH Washington soils. One reason for this may be the widespread use of rootstocks in Oregon, and the use of own-rooted vines in Washington, which are more susceptible to *M. hapla*. Many common grape rootstocks, including those used in Oregon, have some resistance to *M. hapla*, but few rootstocks have resistance to ring nematode (Forge et al., 2020; Schreiner et al., 2012; Zasada, Howland et al., 2019).

Both soils had nearly the same silt content (30% in Washington to 28% in Oregon), but the Oregon loam had 10 times more clay than the Washington sandy loam. Both soils are representative of common vineyard soils in Washington and Oregon, with the Jory soil series at one point being the most widely planted soil series at 29% of vineyards in the Willamette Valley in Oregon, and the Warden soil series being part of the dominant soil association on Red Mountain, a prominent Washington viticultural area (Burns, 2011; Meinert & Busacca, 2002). While there were other properties that differed between the Oregon and Washington soils (Table 1), the Washington sandy loam was more coarsely textured, and based on previous literature (Wallace, 1966), should be better suited for nematode movement. However, there was no difference in *M. hapla* reproduction due to soil type. It may be that between the sieving, pH mixing, and planting phases of the experiment, that the soils lost some structure normally present in the natural environment. In addition, pot experiments do not accurately reproduce the structural and hydrological regimes of field soils. This could result in smaller pore spaces than the texture would imply, especially in the Washington sandy loam. Other studies have examined differences between muck, clay, and sandy soils with respect to *M. incognita* reproduction on soybean, and generally the more sandy soils supported higher nematode reproduction than soils with more clay

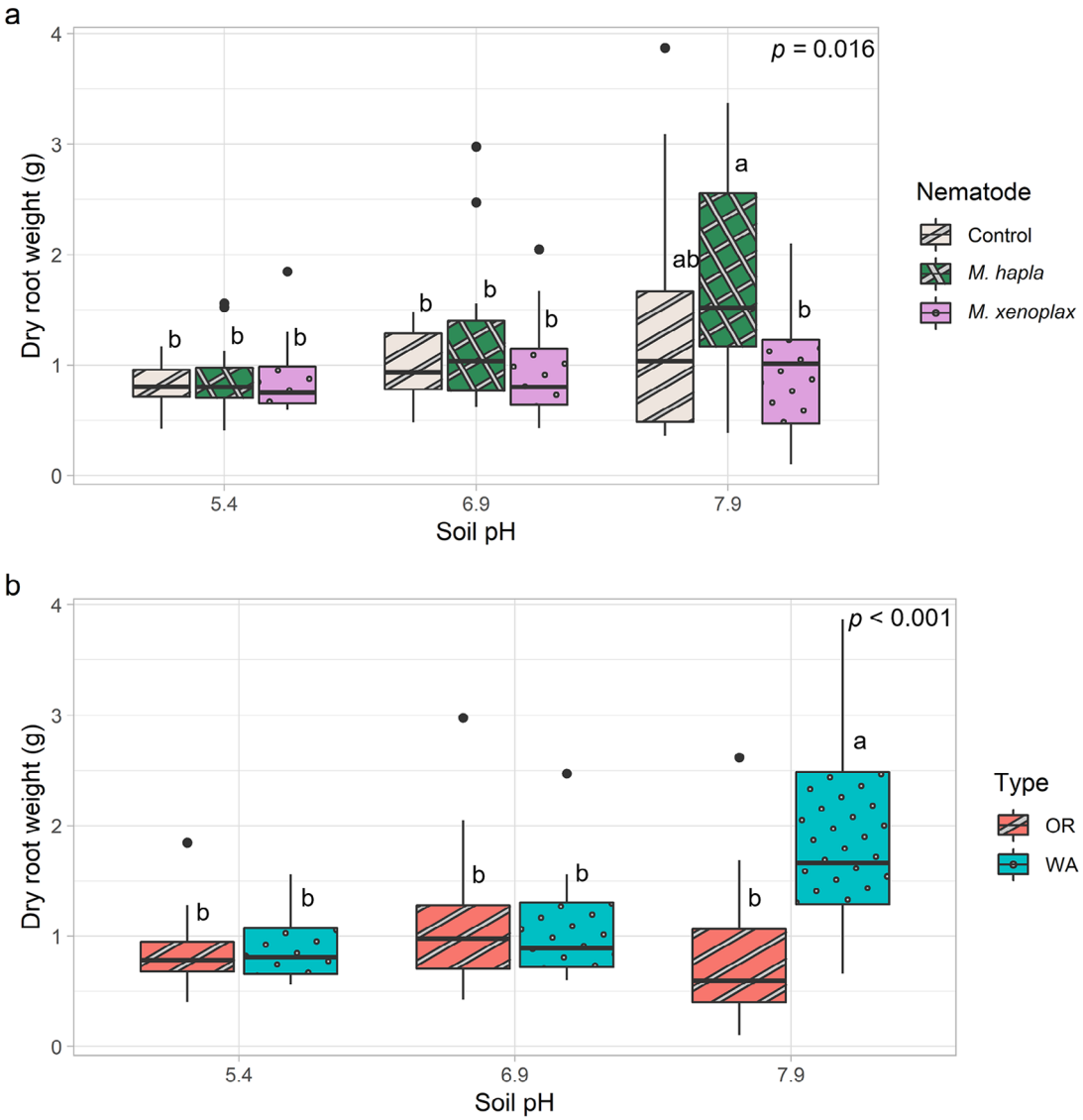

FIGURE 4 Tomato dry root mass separated (a) by interaction between nematode treatment (control = tan stripe, *M. hapla* = dark green crosshatch, and *M. xenoplax* = pink dots) and pH, and (b) by interaction between soil type (coarser-textured Washington sandy loam = teal and finer-textured Oregon loam = coral) and pH. Data met the assumptions of normality and homoscedasticity for analysis of variance (ANOVA). Different lowercase letters ($\alpha = 0.05$) denote significant differences within the distinct comparisons.

content (Windham & Barker, 1986). It is possible that the soils used in this study were too similar in texture to see significant differences in reproduction in either nematode species, though the difference in clay percentage was substantial.

Mesocriconema xenoplax population densities were not affected by either soil pH or texture in this greenhouse study. Overall, the number of *M. xenoplax* declined during these experiments relative to initial inoculum, with Rf values well below 1.0 for all but two combinations of soil and pH in the first run of the experiment. This lack of reproduction, which may not have been directly related to soil properties, negated our ability to detect effects of pH or soil type. While we do have good information on the length of time for *Meloidogyne* species reproduction in greenhouses, commonly greenhouse studies with *Mesocriconema xenoplax* run anywhere from 15 to 26 weeks (Wenefrida et al., 1998; Schreiner & Pinkerton, 2008; Nyczepir et al., 2009). However, in laboratory studies, the life cycle of *M. xenoplax* takes 25–34 days (Seshadri, 1965), meaning the length of this experiment should be sufficient for reproduction. Tomato is also not as good a host for *M. xenoplax* as it is for *M. hapla* (Seshadri, 1965). This might explain why the reproductive factor for *M. xenoplax* was ≤1. Given that *M. xenoplax* is an ectoparasite and occupies the soil for the entirety of its life cycle, we anticipated that there might be more influence of soil pH or texture on *M. xenoplax*. In orchard and vineyard soils of the Okanogan valley of British Columbia, Canada, *Mesocriconema* spp. were found to be positively correlated with percent sand (Forge

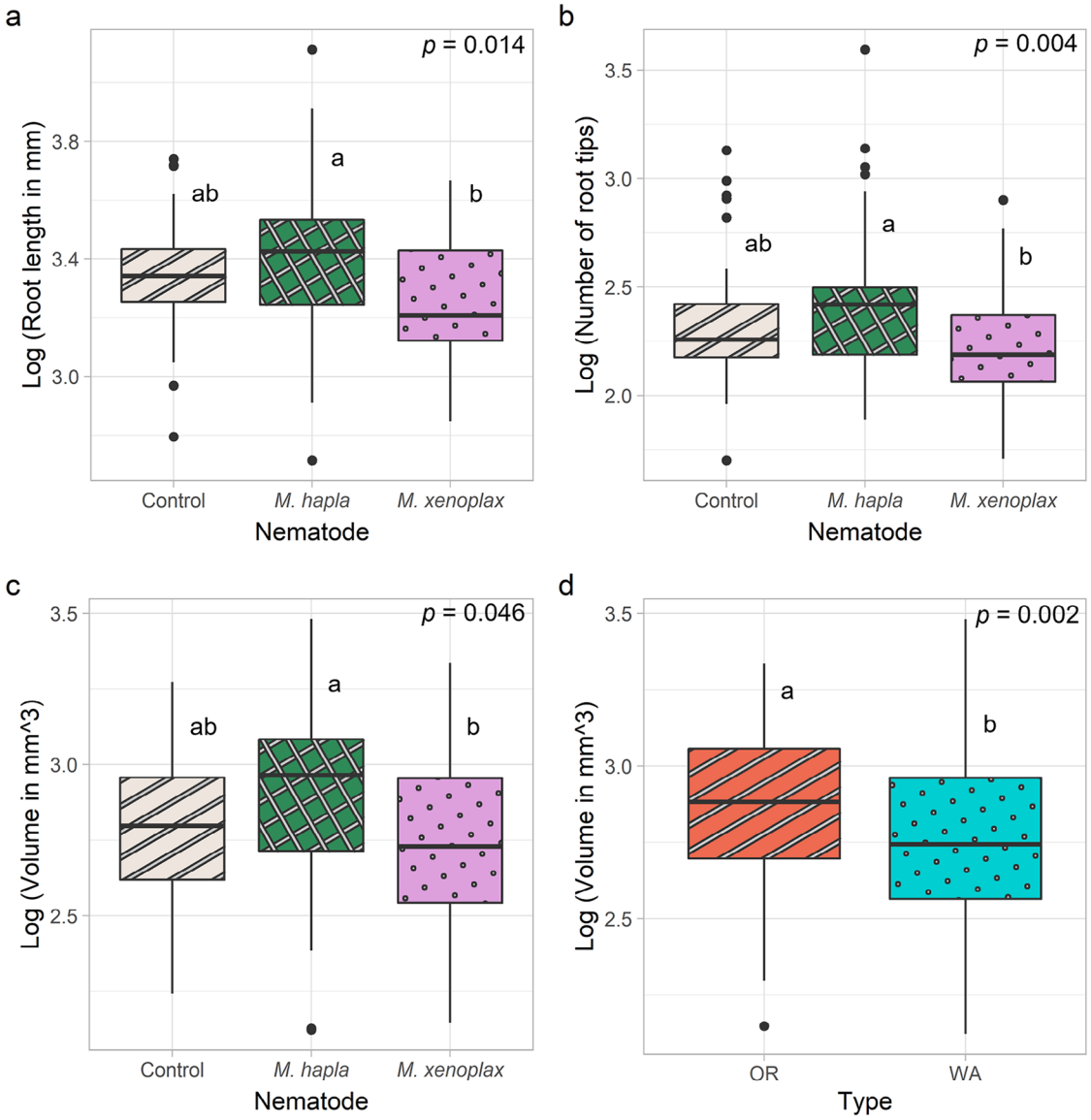

FIGURE 5 Tomato (a) root length (mm) separated by main effect nematode treatment (control = tan, *M. hapla* = dark green crosshatch, and *M. xenoplax* = pink dots); (b) number of root tips separated by main effect nematode treatment (control = tan, *M. hapla* = dark green crosshatch, and *M. xenoplax* = pink dots); (c) volume (mm^3) separated by main effect nematode treatment (control = tan, *M. hapla* = dark green crosshatch, and *M. xenoplax* = pink dots); and (d) volume (mm^3) separated by main effect soil type at each pH (coarser-textured Washington sandy loam = teal dots and finer-textured Oregon loam = coral stripe). Root metrics required log transformation to meet the assumptions of normality or homoscedasticity for analysis of variance (ANOVA). Different lowercase letters ($\alpha = 0.05$) denote significant differences between main effect means.

et al., 2021). Additionally, *M. xenoplax is* an important pest in peach trees grown in acid soils, especially those below pH 6.0, in the Southeastern United States (Reilly et al., 1985). Given their prevalence as the major nematode pest of wine grapes in western Oregon, a region with acidic soils (Doerge & Gardner, 1985), it is surprising that there was no effect of pH on *M. xenoplax* population densities. These results, however, do suggest that another aspect of the grape production system contributes to the relative success of these two plant-parasitic nematode species in the different regions, rather than a direct impact of soil texture or pH. More work to assess a greater range of soil textures in the future would verify this. As stated above, the use of rootstocks in one system versus the other may be a driver of the differential prevalence of these plant-parasitic nematodes in the two regions.

Another potential contributor to the prevalence of specific nematodes in specific regions is cropping history. *Mesocriconema xenoplax* population densities above a damage threshold of 125 per 250 g soil were greater in vineyards that were previously orchards planted to *Prunus* (sweet cherry and relatives) than other cropping types (grass, pasture, and native vegetation) histories in a survey of Oregon vineyards

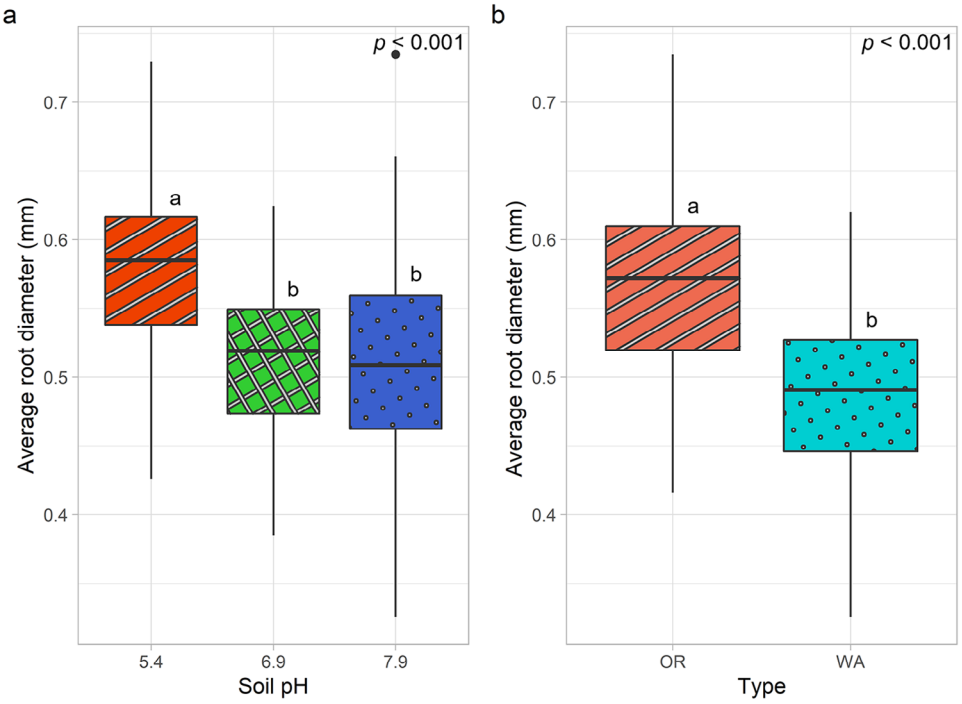

FIGURE 6 Tomato root diameter (mm) separated (a) by pH (pH 5.4 = red stripe, pH 6.9 = green crosshatch, and pH 7.9 = blue dots) and (b) by soil type (coarser-textured Washington sandy loam = teal dots and finer-textured Oregon loam = coral stripe). Data met the assumptions of normality and homoscedasticity for analysis of variance (ANOVA). Different lowercase letters ($\alpha = 0.05$) denote significant differences amongst (a) soil pH and (b) between soil type.

(Pinkerton et al., 1999). In eastern British Columbia, a viticultural area north of and with similar edaphic conditions to eastern Washington, *M. xenoplax* is more prevalent in vineyards than *M. hapla* (Forge et al., 2021). Growing space in the Okanagan valley is limited, and many vineyards were planted in areas that were previously orchards or *Vitis labrusca* L. (juice grape) vineyards (Bowen et al., 2005). *Vitis labrusca* is a better host to *M. xenoplax* than *M. hapla* (Bird & Ramsdell, 1985). *Mesocriconema xenoplax* was also regularly found in British Columbia cherry orchards, while *M. hapla* was rarely found (Forge et al., 2021). In contrast to Oregon and British Columbia, most Washington vineyards planted between 2007 and 2022 were planted into non-orchard soils, including alfalfa (an excellent host for *M. hapla*), pasture, winter wheat, fallow, and shrubland (NASS, 2022). It may be that the cropping histories of these growing regions contribute to which nematode species are more prevalent in vineyards; those planted after orchards might be more likely to have already been colonized by *M. xenoplax* than those planted to non-orchard soils. Examination of nematode populations in vineyards in Washington planted on previous orchard sites and Oregon vineyards planted into non-orchard sites will help reveal the extent that cropping history plays on which of these nematodes tend to dominate.

4.2 | Soil property response to pH change

Addition of H_2SO_4 to the Washington sandy loam and $Ca(OH)_2$ to the Oregon loam effectively altered soil pH and EC. Significantly more H_2SO_4 than $Ca(OH)_2$ on a molar mass basis was required to alter the pH of the Washington sandy loam than the Oregon loam (Table 1). This is most likely due to the pH buffering capacity of the carbonates in the Washington sandy loam (Figure S1) (Pearson & Adams, 1984). Complete dissolution of carbonates is required before soil pH can be permanently decreased, and when H_2SO_4 is used, soluble $CaSO_4$ is formed (De Vries et al., 1989; Pearson & Adams, 1984). The higher molar rate of acid used also made the EC of H_2SO_4 -treated Washington soil greater than the $Ca(OH)_2$-treated Oregon soil (Table 1). In fact, the EC of the H_2SO_4 treated Washington sandy loam was so high at pH 5.4, that it caused the tomato plants to die in the August experiment. Tomatoes are known to be intolerant of excessive EC; for the subsequent experiment, the soil was leached with water and soluble salts were removed, enabling satisfactory plant growth at the lowest pH (del Amor et al., 2001). Increased EC associated with compost application was previously reported to be suppressive to *Meloidogyne* spp., though it's unclear if EC had an effect on *M. hapla* in this study (Oka, 2010).

SOM was highest in the Oregon loam and was unaffected by the pH change. The Oregon loam had more organic matter than the Washington sandy loam because that region receives greater rainfall, enabling significant plant growth, which leads to greater organic matter accumulation over time. The Washington sandy loam was taken from a semiarid, water-limited environment which limits the potential for SOM accumulation. POXC is typically almost linearly associated with SOM, but in this study, it was only altered by pH adjustment in the Washington sandy loam at pH 5.4, which might have been due to the liberation of organic matter entombed in carbonates during the acidification process. Soil POXC content was previously negatively correlated to plant parasitic nematode populations across a variety of crops, including corn, soybeans, and forage crops in Ohio (Martin et al., 2022). MinC and ACE protein were both greater in Oregon loam than the Washington sandy loam because of the greater organic matter content of the Oregon loam. A linear relationship between SOM content, MinC, and ACE protein is well established in the literature (Mann et al., 2019; Rippner et al., 2021). However, MinC was not pH dependent while ACE protein increased significantly in both soils as pH decreased. Both MinC and ACE protein were previously measured to be positively correlated with plant parasitic nematode populations in corn, soybeans, and forage crops in Ohio (Martin et al., 2022). The relationship between ammonium-N and nitrate-N with type and pH was complex, but generally the Oregon soil had greater concentrations of both, likely driven by greater SOM content (Huang et al., 2021). The stoichiometry of SOM means that it contains significant amounts of soil organic N which could have been mineralized by soil microorganisms during the incubation period for pH adjustment (Zechmeister-Boltenstern et al., 2015).

4.3 | Leaf biomass

Dry leaf biomass was not influenced by pH in the Washington sandy loam, but decreased at the highest pH treatment in the Oregon loam. Soil pH between 6.0 and 7.0 is considered agronomically optimal; below these values, aluminum (Al) and Mn, soluble in acid soils, can negatively affect plant growth, while at higher pH, micronutrient (Zn) solubility and mobility can be limited (Barrow & Hartemink, 2023; Hartemink & Barrow, 2023; Sainju et al., 2003; Worley, 1976). These generalizations may explain the current results given the interactive effects of soil pH and type (texture); Zn was limited in the high-pH treatments in both soil types, and was especially low (though not statistically different to Washington) in the high-pH Oregon soil, where no Zn was detectable (Table 1). Dry leaf biomass was also consistently greater in the Washington sandy loam compared to the Oregon loam, particularly at high pH. Other investigators previously found tomato biomass to be positively influenced by coarse-textured soils like sandy loams due to reduced soil compaction during irrigation events in sandy soils compared to more clayey soils (Zucco et al., 2015). Dry leaf mass was greater in plants taken down in August (Experiment 1) compared to October (Experiment 2), which could be due to differences in the number of daylight hours or temperature differences at northern latitudes between the two months (Adams, 2001; Adams et al., 2008).

4.4 | Root mass and morphology

The effects of the experimental variables on dry root mass and root morphology were complicated with respect to nematode treatment, soil type, pH, and the interaction between pH and soil type. While the soil pH optimum for tomato plant growth is between pH 6.0 and 7.0, root dry mass was greatest in the Washington sandy loam at pH 7.9 (Worley, 1976). *Mesocriconema xenoplax* reduced most measured root parameters, but only when compared to *M. hapla*, including root length, root tip number, and root volumes across pH treatments (Figure 5a–c), and root weight at pH 7.9 (Figure 4a), the last of which is most attributable to increases in root weight when infected with *M. hapla* than a reduction from *M. xenoplax*. These negative effects may be due to how *M. xenoplax* interacts with the plant where they modify a single cortical cell to facilitate solute transport to the parasitized cell (Hussey et al., 1992; Westcott, 1992). Fine root production and starch concentration in susceptible grape varieties is commonly decreased under *M. xenoplax* parasitism (Schreiner & Pinkerton, 2008; Schreiner et al., 2012).

Somewhat surprisingly, *M. hapla* infection was not associated with increased root length, tip number, or volume compared to the control plants, only when compared to *M. xenoplax* (Figure 5a–c). Infection by *M. hapla* is characterized by the formation of galls in plant roots, and has been noted to cause excessive root branching (Mojtahedi et al., 1988; Santo et al., 1988; Williamson & Hussey, 1996). In this study, galls were visible to the naked eye. In the Washington sandy loam at high pH, galling and root branching was so severe that it required additional root processing to obtain images that could be analyzed. *Meloidogyne hapla* infection both increased root volume and dry root biomass compared to *M. xenoplax* infection likely due to differences in parasitism between the two nematode groups, *M. hapla* being an endoparasite and *M. xenoplax* being an ectoparasite (Ciancio & Grasso, 1998; Williamson & Hussey, 1996).

Root diameter was also influenced by soil pH value and soil type. Average root diameter across pH treatments and soil types was greatest at pH 5.4 compared to the higher pH treatments. This could be due to slight Al toxicity at this soil pH. Plants may exhibit symptoms of Al toxicity in soils with

pH below 5.8 caused by changes in Al speciation at this pH (Eduah et al., 2022; Lofton et al., 2010; Pearson & Adams, 1984). Exposure to Al^{3+} is reported to lead to thicker fine roots in some plant species, presumably due to lower rate of root extension (Bojórquez-Quintal et al., 2017; Pearson & Adams, 1984). Plants grown in the Oregon loam also had greater root volumes and diameters than plants grown in the Washington sandy loam. The Oregon loam had greater clay content than the Washington sandy loam. Root thickening caused by increasing clay content was observed previously and is thought to be an adaptation to mechanical impedance (Bengough et al., 2006).

5 | CONCLUSIONS

In this study, *M. hapla* and *M. xenoplax* population densities were not affected by the soil type of two common viticultural soils from eastern Washington and western Oregon, and *M. hapla* only was minorly affected by soil pH. This might indicate that observed differences in abundance of *M. hapla* and *M. xenoplax* between the two regions are not due to differences in soil texture or pH. Artificially varied soil pH, as in this study, also had unintended consequences like increasing soil salinity. In the future, sourcing naturally occurring variable pH soils from Washington and Oregon might provide more realistic treatments and better represent what nematodes encounter in the field. This study was designed to be short term, lasting only 7 weeks, but the lifespan of a vineyard is far longer than that. Over many nematode generations, perhaps the effects of soil pH or type would accumulate on a nematode population and reflect the differences between regions in abundance.

AUTHOR CONTRIBUTIONS

Katherine E. East: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing—original draft; writing—review and editing. **Inga A. Zasada**: Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing—review and editing. **Jungmin Lee**: Conceptualization; funding acquisition; methodology; project administration; resources; validation; writing—review and editing. **R. Paul Schreiner**: Conceptualization; funding acquisition; methodology; project administration; resources; writing—review and editing. **Devin A. Rippner**: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Research Impact Statement

Please use layperson language when completing this form. This document will be read by members of Congress and it is important to be specific with details. Congress must understand the value of your work.

1. **Project Title**: The effect of soil parameters on plant-parasitic nematodes of wine grapes in Washington and Oregon

2. **Principle Investigator & Cooperator(s)**: Katherine East and Devin Rippner

3. **Research Objectives & Procedures**:
   Objective 1. Determine soil parameters that affect Meloidogyne hapla (Northern root-knot nematode) invasion and success in vineyards. Wine and Juice Grape Viticulture

   Objective 2. Determine the effect of soil pH and texture on M. hapla and Mesocriconema xenoplax (ring nematode) invasion and success. Wine and Juice Grape

   Objective 3. Develop a protocol for using machine-learning to count M. hapla eggs.

4. **Total $ Funding through NCSFR**: $10,768

5. **Describe the Economic Impact and Benefits**. Vineyard establishment is the largest one-time cost for vineyard owners, ranging between 10,000 and $85,000+ an acre. Young vine success is crucial to vineyard profitability; however young vines are most susceptible to soil born parasites like plant parasitic nematodes. Our results show Permanganate oxidizable carbon, an easily measured soil health metric, is associated with resistance to plant parasitic nematode parasitism. Increasing permanganate oxidizable carbon in young vineyards is could potentially decrease plant parasitic nematode success, saving growers thousands of dollars per acre.

6. **Describe the Environmental Impact and Benefits**. Our results have the potential to decrease soil fumigation through the identification of soil properties that are intrinsic to decreased plant parasitic nematode success.

7. **Describe Other Impact and Benefits**. Please include whether they are actual or potential.

8. **Concluding statement**. Our research is valuable because we are connecting soil health metrics to plant health which is very rarely done. We found that an easily measured soil health metric, permanganate oxidizable carbon, was positively associated with plant resistance to nematode parasitism. These results open a path for investigating the use of winery waste for ameliorating nematode parasitism in vineyards; a win-win for grape growers and the environment.

NCSFR Completed Research Form

This form is used to gather project information to complete the conference proceedings document. Please do not change any of the formatting.

Project Title:
The effect of soil parameters on plant-parasitic nematodes of wine grapes in Washington and Oregon

Authors:
Katherine East and Devin Rippner

Institution:
(USDA-ARS Horticultural Crops Production and Genetic Improvement Research Unit (worksite), Prosser, WA

Abstract/ Summary:
Plant parasitic nematodes are costly pests that cause global crop loss of over $100 billion dollars. Previously it was thought that the large populations of ring nematode in Oregon and Northern root-knot nematode in Washington vineyards were caused by differences in soil characteristics. We found that soil texture had no influence on both nematodes' population growth. We found that Northern root-knot nematodes that live inside of the roots thrived in acidic (low pH) soil than alkaline (high pH) soil. Soil pH had no effect on ring nematodes that live outside of the roots. We also generated a computer model to automate nematode egg counting. These results will help generate parasitism risk maps, help wine grape growers make better vineyard planting decisions, and increase the speed with which scientists can identify plant parasitic nematode eggs.