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Research Article

Field Performance of Winegrape Rootstocks and Fumigation during Establishment of a Chardonnay Vineyard in Washington

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Abstract: In Washington, most winegrapes are own-rooted *Vitis vinifera*, which is susceptible to the plant-parasitic nematodes *Meloidogyne hapla* and *Xiphinema americanum*. Using resistant rootstocks to manage nematodes has not been evaluated in Washington vineyards. A long-term vineyard trial was established to evaluate the effects of soil fumigation and rootstock genotype on *M. hapla* and *X. americanum* population dynamics and vine growth during vineyard establishment (first three years) in a replant scenario. Vines in an existing *V. vinifera*

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'Chardonnay' vineyard were first treated with foliar glyphosate in fall 2014. Randomized areas within the vineyard were then either fumigated or not with drip-applied metam sodium. Following fumigation, vines were removed. In spring 2015, the vineyard was replanted to Chardonnay on the following rootstocks: 1103 Paulsen, 101-14 Millardet et de Grasset, Teleki 5C, and Harmony. Self-grafted and own-rooted Chardonnay were included. Fumigation reduced *M. hapla* soil second-stage juvenile (J2) population densities on own-rooted and self-grafted vines for only the first year after fumigation. One year after fumigation, the self-grafted and own-rooted vines had higher population densities of *M. hapla* J2 than rootstocks. All rootstocks supported measurable densities of *M. hapla* J2 but were poor hosts relative to *V. vinifera*. Fumigation effectively reduced population densities of *X. americanum* for up to 3.5 years. Fumigation also reduced early establishment pruning weights. Vines grown in fumigated areas had lower pruning weights through year 2; but rootstock was the bigger influence on pruning weights by year 3. This trial demonstrates that rootstocks have a more sustained impact on nematode re-establishment and subsequent vine health in a vineyard replant scenario than that of pre-plant fumigation.

Key words: fumigation, *Meloidogyne hapla*, nematode dosage, rootstocks*, Vitis vinifera, Xiphinema*

Introduction

Washington grapegrowers lack basic information regarding plant-parasitic nematodes upon which to make informed pre- and post-plant management decisions. As vineyards have aged, and as the maturing Washington winegrape industry begins a period of vineyard replant, plant-

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parasitic nematodes have become a greater concern for the winegrape industry. In Washington state vineyards, the nematodes of greatest importance are the northern root-knot nematode (*Meloidogyne hapla*) and dagger nematode (*Xiphinema americanum* in the broad sense). *Meloidogyne hapla* and *Xiphinema* spp. were detected in 60% of surveyed vineyards, with 20% of these over the suggested thresholds of either 100 *M. hapla* per 250 g soil or 25 *Xiphinema* spp. per 250 g soil (Zasada et al. 2012). If young vines are planted into infested soils, the vineyard is immediately at an establishment disadvantage; this could manifest as either young vine death or the failure to meet production goals for the duration of the vineyard's lifespan. This has been reported in other grape growing regions, including California and Australia (Nicol et al. 1999, Westphal et al. 2002)

In perennial crop production the most important window for nematode control is prior to establishment, and this is often achieved with pre-plant soil fumigation (Zasada et al. 2010). Soil fumigation immediately kills target nematodes and there is little residual effect. Efficacy of fumigation varies depending on soil moisture, soil type, amount of nematode-infected root material left in the ground, and whether vineyard infrastructure was left in in place (Lembright 1990). The long-term effect of fumigation on plant-parasitic nematode species like *M. hapla* and *Xiphinema* spp. has not been established in vineyards. Due to changes in regulations regarding soil fumigation, this practice will become more cumbersome. In addition, many growers are interested in participating in sustainable programs (e.g., Low Input Viticulture and Enology; LIVE) which do not allow soil fumigation. If nematodes are not controlled prior to planting, there are few effective post-plant management options available for vineyards, including no proven effective registered post-plant nematicides at the time of this publication.

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Another option available to growers for plant-parasitic nematode management is the use of resistant or tolerant grape rootstocks (Sauer 1967, McKenry et al. 2001, Ferris et al. 2012, Zasada et al. 2019). Washington state winegrape growers generally grow *Vitis vinifera* on their own roots, due to: 1) a historical lack of established phylloxera (*Daktulosphaira vitifoliae*); and 2) the threat of above-ground cold damage (Moyer et al. 2011). Because of this, there is a lack of enthusiasm for the adoption of rootstocks to manage soil-borne pests or soil-related problems, which has the compounding effect of lack of interest in evaluation of rootstocks under Washington's climate (Keller et al. 2011). However, this lack of enthusiasm has very recently changed due to vineyard survey results that indicate a more established presence of phylloxera than originally thought (Prengaman 2019). A third complication to making informed decisions on the selection of a rootstock for *M. hapla* management in Washington, is the fact that most *Meloidogyne* species-resistant rootstocks have not been tested against *M. hapla*, but rather, other *Meloidogyne* species that are problematic in other grape-growing regions (McKenry et al. 2001, McKenry and Anwar 2006, Ferris et al. 2012). Whether these rootstocks are also resistant to *M. hapla* in a vineyard setting remains to be determined. While we have evaluated the host status of rootstocks for *M. hapla* in greenhouse experiments (Zasada et al. 2019), the applicability of short-term rootstock evaluation trials (greenhouses, pot studies) to the reality of long-term vineyard establishment and production can be problematic (McKenry and Anwar 2006, McKenry et al. 2001, Ferris et al. 2012). Rootstocks that may appear resistant or tolerant to a nematode infestation in the short-term may not be in the long-term, and this might be exacerbated under field conditions.

The objectives of this research were designed to address several of the concerns related to: 1) How preplant fumigation affects *M. hapla* and *Xiphinema* spp. population densities both

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immediately after fumigation, and for several years after fumigation; 2) How the chosen rootstocks affect vine growth under Washington state's climate; and 3) How effective these rootstocks are at limiting the population growth of *M. hapla* and *Xiphinema* spp. or tolerating nematode feeding over time. The commercial vineyard established as a part of this experiment is part of a long-term (over 10 years) trial designed to measure the duration of efficacy for pre-plant fumigation, as well as long-term impacts of plant-parasitic nematode infestation on vineyard health and productivity. This paper examines the establishment phase of this vineyard, defined here as the first three growing seasons, from planting in 2015 to the first partial-cropping year in 2017.

Materials and Methods

An existing *V. vinifera* 'Chardonnay' (clone unknown) vineyard planted in 1992 in Paterson, WA (45.871876, -119.764033) was used for this experiment. It had established populations of *M. hapla* (northern root-knot nematode) and *Xiphinema* sp. (dagger nematode). The *Xiphinema* sp. found at this site belongs to the taxonomically confusing *X. americanum* species complex (Robbins 1993, Zasada et al. 2012) and has not been assigned a specific designation within this group. For the purpose of this paper, this population will be referred to as *X. americanum*. This site was slated for replant by the grower, with the intent of maintaining the existing vineyard infrastructure (e.g., retention of vineyard posts and irrigation lines). The soil at the site is a Quincy loamy sand, with a 0 to 30% slope (Web Soil Survey; https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx). On 5 Sep 2014, the existing vines were treated with a foliar glyphosate (2% solution in 702 L/ha) application as described by Moyer et al. (2017; Fig. 1B). Approximately two weeks after the foliar glyphosate application,

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the vineyard block was divided into four replicate plots of six rows each (total of 24 rows, Fig. 1A). Each of the four plots was randomly assigned a fumigation treatment to one half of the plot, where one-half of each row was fumigated, and the other half left nonfumigated. Soil fumigation consisted of metam sodium CLR 42% (sodium methyldithiocarbamate; metam sodium; Vapam HL) applied through the existing irrigation drip tubing with 1.9 L (0.5 gallon) emitters on 18 Sep 2014 at a rate of 215 L/ha delivered in 702 L/ha for 8 hrs and then flushed for 2 hrs as described by Moyer et al. (2017). After fumigation, the existing vines were removed (between 28 Oct and 18 Dec 2014), but the trellising infrastructure was retained; this allowed for the evaluation of the impact of fumigation in a replant scenario where the existing trellis system is retained. Retention of existing vineyard infrastructure in Washington state vineyard replant scenarios is common practice.

On 12 May 2015, the site was replanted in a randomized split-block design consisting of six main plot vine rootstock treatments, and fumigation (Fumigated = F; Nonfumigated = NF) as the split block treatments (Fig. 1A). The treatments were replicated four times. Vine treatments consisted of entire rows (approximately 106 vines per row) planted on one of four rootstocks or non-grafted or self-grafted *V. vinifera*. The entire experimental area was approximately 2.4 ha. Rootstocks were chosen for their resistance to *Meloidogyne* species (Sauer 1967, Chitambar and Raski 1984, Nicol et al. 1999, McKenry and Anwar 2001, McKenry and Anwar 2006, Ferris et al. 2012), as well as availability of certified stock material. All planted materials, both rootstock and scion, were either certified through the Washington State Department of Agriculture or the California Department of Food and Agriculture. The rootstocks evaluated were: ‘Millardet et de Grasset 101-14’ (101-14 Mgt), ‘Harmony’, ‘Paulsen 1103’ (1103 P), ‘Teleki 5C’ (5C), and a

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self-grafted (Chardonnay grafted to Chardonnay) control. 'Harmony' was selected over the similar rootstock 'Freedom' due to availability from the supplier. Chardonnay FPS selection 15 was the scion. A second control, consisting of non-grafted, own-rooted Chardonnay was included in the experimental design because this is the most common form of planting material in Washington state. All grafted rootstocks and self-grafted vines were bench-grafted using an omega graft. All rootstocks, aside from Harmony, were grafted in spring of 2014, greenhouse-healed in summer and fall 2014, and placed into dormancy for the 2014-2015 winter. Harmony was grafted in fall 2014, and greenhouse-healed for the winter 2014-2015, then shipped for planting without a dormancy period. All vines were planted the week of 11 May 2015. Within the NF plots, a continuous 10-vine section was inoculated with approximately 20,000 supplemental *M. hapla* eggs applied to the roots of vines in 10 ml water at planting (NF+) (Fig. 1D). This inoculated 10-vine section was designed to mimic an extreme level of nematode pressure in a replant situation. *Meloidogyne hapla* egg inoculum was produced by collecting soil from the vineyard the year prior to establishment and planting with tomato. Eggs produced on tomato roots were extracted using bleach, concentrated in water, and adjusted to the desired density. Since the NF+ treatment was limited to 10-vine sections within each rootstock replicate row, two other continuous 10-vine sections were marked off for data collection in each row as well; one in the F block, and one in the uninoculated parts of the NF block (Fig. 1C). All data was collected from these 10-vine sections. Vines were trained towards the cordon wire (1.06 m high) in 2015. In 2016, vines were trained to a single trunk with bilateral cordons. In 2017, the canopy was trained to a modified VSP (vertical shoot positioning) with catchwires at 28 cm above the cordon wire. The vines were spur-pruned in the 2017-2018 winter. This vineyard block

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is part of a commercial operation and all irrigation, fertilization, and pest management practices were managed by the grower-cooperator.

Nematode sampling and processing. Soil was sampled for *M. hapla* second-stage juveniles (J2) and *X. americanum* mixed stages starting pre-fumigation in fall 2014, and continuing spring and fall from spring 2015 to spring 2018 (total of eight sampling dates). At each sampling date, 10 soil cores, 2.5-cm diameter by 45-cm deep, were collected under drip emitters in each 10-vine treatment section (Fig. 1) and combined into one composite sample. Previous work has shown that *M. hapla* in Washington drip-irrigated vineyards are concentrated under drip emitters (Howland et al. 2014) and that *X. americanum* are evenly distributed throughout a vineyard soil (East et al. 2019b). Soil core samples were processed using a semi-automatic elutriator (Seinhorst 1962) and further processed using a sugar-centrifugation technique (Jenkins 1964) to collect *M. hapla* J2 and *X. americanum*. Nematodes were enumerated using a Leica DM IL inverted microscope (Leica Microsystems, Wetzlar, Germany). Root samples were collected each fall, from 2015 to 2017, by removing a 1,000 cm^3 section of soil from under three drip emitters in each treatment plot; roots were gently shaken out of soil manually and collected. Eggs were collected from root samples using a bleach method, where roots were shaken in a 10% sodium hypochlorite solution for 3 min, then poured over stacked 88- and 25-µm sieves to separate roots and eggs (Hussey and Barker 1973). Collected eggs were counted using an inverted microscope.

Vine parameters. Dormant pruning weights were used as an assessment of vine vigor. Each vine per 10-vine data plot was pruned and pruning debris was collected and weighed on a per-vine basis. In 2015, the year of planting, vines were segregated into two categories and

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pruned accordingly on 17 Dec. These categories were: 1) 2-bud: Prune the trunk back to two buds only, to encourage root development and stronger vine growth for the following season; or 2) Training: On vines that had established well, the trunk was pruned back to 10 cm below the fruiting wire. Pruning weights in this year were assessed as the percentage of vines that were assigned to category 2, rather than by pruning weight to account for degree of pruning; in other words, when pruning back to two buds, heavier pruning weights were often recorded than from vines that were pruned back to just below the fruiting wire. If evaluated based on weight only, those vines that were pruned back to two buds would have appeared to have better growth (high pruning weights) when in fact, they did not. During the 2016 and 2017 growing seasons, all vines were trained up to and on the wire, and dormant vines were spur-pruned to three-bud spurs and pruning weight per vine recorded (vines were pruned on 14 Dec 2016 and 14 Nov 2017). In 2017, the first partial-crop was harvested on 29 and 30 August from the 10-vine subplots, and individual vine yield was recorded.

Data analysis. Nematode densities of *M. hapla* and *X. americanum* were analyzed using the standard least squares model platform in JMP (version 14.0.0, SAS Institute Inc., Cary, NC), as a split-plot with fumigation, rootstock, fumigation*rootstock and block*rootstock with fumigation and rootstock as fixed variables and block as a random variable. Egg data was log (x+1) transformed to meet assumptions of normality, and this output was analyzed as above. Where significant differences were found, mean separation was performed using Tukey's HSD test. Table outputs are included as supplemental data.

In addition, *M. hapla* J2 data from fall of 2015, 2016, and 2017 were categorized within fumigation treatments and rootstock treatments to one of three categories. These categories

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206 captured densities relative to the proposed threshold of 100 *M. hapla* J2 for management (Santo,
207 *unpublished*). The categories were defined as: Category 1 - Fewer than 50 *M. hapla* J2 per 250 g
208 soil, where a management response would not likely occur; Category 2 - 50 to 150 *M. hapla* J2
209 per 250 g soil where a management response is recommended but the degree of response may be
210 tempered by other site factors; and Category 3 – greater than 150 *M. hapla* J2 per 250 g soil
211 where a management response would be highly recommended. At each time point, in each
212 fumigation*rootstock treatment combination, the replicate average was used for category
213 placement in fall 2015, 2016 and 2017.

214 To evaluate the impact of *M. hapla* population densities on own-rooted vine growth, the
215 typical situation in Washington state vineyards, we analyzed just the self-grafted and own-rooted
216 vines. *Meloidogyne hapla* J2 enumerated from soil in fall most likely invade and impact vines in
217 the following year (East et al. 2019a). Using the pruning weights from the following year as a
218 measure of vegetative growth may be a better indicator of the impact of *M. hapla* J2 population
219 densities on vine vigor. *Meloidogyne* sp. density has been correlated with vine vigor (Ferris and
220 McKenry 1975). *Meloidogyne hapla* J2 population densities were ranked within time points, as
221 was pruning weight. Ranked *M. hapla* J2 population densities were compared with ranked
222 pruning weights in self-grafted and own-rooted vines at the end of the following year within each
223 replicate (ex. fall 2015 *M. hapla* J2 and fall 2016 pruning weights). As the data were non-
224 normally distributed, and comparisons across years with very different densities of *M. hapla* J2
225 and pruning weights were desired, ranking allowed for comparisons across years.

226 To measure the cumulative nematode pressure experienced by grapevines over multiple
227 growing seasons, nematode dosage was calculated (Noling and Ferris 1987). Cumulative

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nematode dosage is calculated similarly to the area under the disease progress curve (AUDPC) and is expressed in nematode degree-days (the nematode density measured over multiple sampling dates multiplied by the degree-days accumulated between sampling dates). *Meloidogyne hapla* J2 population densities were log (x+1) transformed to fit assumptions of normality at each sampling point, spring and fall, from spring 2015 (at planting) to spring 2018 (3 years after planting). At these time points, growing degree days were calculated using base 10ºC from soil temperatures recorded at 20 cm under the soil surface at a nearby weather station maintained by Washington State University (AgWeatherNet). The total area under the curve formed by *M. hapla* J2 population densities at each degree-day time point was the nematode dosage over that time period. Mean separation of nematode dosage was done using JMP 15.0.0 in the Standard Least Squares platform, with block as a random effect and fumigation, rootstock, and fumigation*rootstock as fixed effects. Means were separated using Tukey HSD test at the 0.05 α level.

Results

Effect of fumigation on vine vigor. There was no interaction between rootstock and fumigation in any year on pruning weights or yield; therefore, they are presented separately in Fig. 2. In 2015, after the first year of growth, direct pruning weights were not a reliable measure of vigor, as vines were pruned differently depending on how close they had grown to the fruiting wire (different pruning strategies based on vine development is a common practice in vineyard establishment). Instead, they were categorized as: 1) lower vigor vines were cut back to 2-buds or 2) higher vigor vines that had reached the fruiting wire, and so were pruned just below the fruiting wire. More vines in the non-fumigated (NF) plots were rated category 2 (higher vigor)

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than in the NF+ plots, and F plots fell in between with intermediate vigor ($p = 0.026$; Fig. 2A). Starting in 2016, pruning weights could be reliably used directly as a measure of vine vegetative vigor. In 2016, vines in the NF plots had higher pruning weights than in both the F and NF+ plots ($p = 0.002$; Fig. 2B). By 2017, there were no differences in dormant pruning weights across fumigation treatments ($p = 0.233$; Fig. 2C). Yield was first collected in 2017, 3 years post-fumigation. There was no effect of fumigation on vine yield (*data not shown,* $p = 0.653$). Average yield was 2.72 kg per vine and ranged from 2.32 kg per vine to 3.14 kg per vine.

Effect of rootstock on vine vigor. Rootstock had a significant effect on pruning weights in all three years (2015 $p = 0.004$; 2016 $p < 0.0001$; 2017 $p < 0.0001$). Harmony was the most vigorous rootstock in the first three years of dormant pruning regardless of the relative number of *M. hapla* J2 in the soil (Fig. 3). There were no differences among the self-grafted, own-rooted, 1103 P, 101-14 Mtg, and Teleki 5C in the first dormant pruning in 2015 (Fig. 3A) or second dormant pruning in 2016 (Fig. 3B). In the third year, 2017, most of the rootstocks had higher pruning weights than the self-grafted and own-rooted vines (Fig. 3C), though Teleki 5C was not significantly different from the own-rooted control. Rootstock also had a significant effect on vine yield in 2017, the first year that yield data were collected ($p = 0.003$; Fig. 4). This was a partial-cropping year, as the 3-year-old vines were still too young to crop at their full potential. Vines planted on Harmony rootstock had the highest yield in this partial-cropping year at 3.1 kg per vine, and Teleki 5C and 101-14 Mtg were the lowest, at 2.3 and 2.4 kg per vine, respectively. 1103P, self-grafted, and own-rooted vine yields were intermediate (Fig. 4). The difference from the lowest to highest average yields across rootstock treatments was 2.25 tonnes per hectare (1 ton per acre).

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Effect of fumigation and rootstock on *Meloidogyne hapla*. There were no differences in *M. hapla* J2 population densities in soil between plots in fall 2014 prior to establishing the experiment, with an average of 69 *M. hapla* J2 per 250 g soil (Table 1). In spring 2015 (6 months after fumigation / preplant), there was a fumigation effect ($p = 0.002$); fumigated plots had zero *M. hapla* J2 compared to non-fumigated plots, which had on average 28 *M. hapla* J2 per 250 g soil. There was no rootstock effect in spring 2015; this was expected as vines were not planted until after the spring 2015 sampling. However, at all time periods after spring 2015, the self-grafted and own-rooted vines had higher *M. hapla* J2 population densities than the rootstocks (Table 1). In fall 2015 (1 year after fumigation / six months after planting), fumigation, rootstock, and fumigation*rootstock were all significant. Looking closer at the variables, the differences in *M. hapla* J2 population densities within both the susceptible own-rooted and self-grafted Chardonnay treatments were mostly due to fumigation, as the differences in initial nematode density as a result of soil fumigation were amplified as the nematode reproduced. Conversely, there was little difference in *M. hapla* density among F, NF, and NF+ within the rootstock treatments ($p = 0.0001$) but a large difference between rootstocks and the controls. When all data were considered together, fumigation, rootstock, and fumigation*rootstock were all significant.

By spring 2016 (1.5 yrs post-fumigation / 1 year after planting) the effect of fumigation on *M. hapla* J2 population densities was lost ($p = 0.072$), and only rootstock had a significant effect. In spring 2016, 1 year after planting, Harmony and Teleki 5C had fewer *M. hapla* J2 than the own-rooted control ($p = 0.005$), and other two rootstocks were no different from either the self-grafted or own-rooted vines. In fall 2016, Harmony, Teleki 5C, 1103 P, and 101-14 Mtg

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vines all supported fewer *M. hapla* J2 ($p = 0.001$) and eggs ($p < 0.0001$) (Fig. 5A) than the self-grafted and own-rooted controls. Although the effect of fumigation treatment on *M. hapla* J2 population densities was not significant in fall 2016, it was a factor for *M. hapla* egg densities per g root ($p = 0.0001$), with NF+ having more eggs than NF and F treatments (Fig. 5B).

In spring 2017, Teleki 5C and 1103 P rootstocks supported fewer *M. hapla* J2 than own-rooted and self-grafted vines ($p < 0.0001$) (Table 1). In fall 2017, Harmony, Teleki 5C, 1103 P, and 101-14 Mtg vines all supported fewer *M. hapla* J2 than the own-rooted control ($p < 0.0001$), but only Teleki 5C and Harmony had fewer *M. hapla* eggs than own-rooted and self-grafted vines ($p < 0.0001$) (Fig. 5C). There was no effect of fumigation on *M. hapla* egg densities, though NF+ had higher densities of *M. hapla* eggs than F or NF treatments ($p = 0.003$) (Fig. 5D). By spring 2018 (3.5 yrs post-fumigation / 3 yrs post-planting), all plots had measurable population densities of *M. hapla* J2, though nematode density differed by rootstock alone ($p < 0.0001$) (Table 1). Teleki 5C had the fewest *M. hapla* J2, and the own-rooted control the most, with little difference among the other treatments ($p < 0.0001$) (Table 1). In general *M. hapla* population densities slowly increased over time in all treatments.

Nematode density category. The trends described above and in Table 1 for *M. hapla* J2 population dynamics over time were better visualized by categorically describing *M. hapla* J2 (Fig. 6). In own-rooted and self-grafted Chardonnay vines, only the F treatment in the first year (fall 2015) resulted in the lowest density of *M. hapla* (Category 1; < 50 *M. hapla* J2 per 250 g soil); NF and NF+ treatments either had moderate to high population densities (Category 2, 50 to 150 *M. hapla* J2 per 250 g soil; Category 3, > 150 *M. hapla* J2 per 250 g soil). By fall of 2016 and 2017, *M. hapla* population densities on both treatments with *V. vinifera* roots were in

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Category 3, regardless of fumigation treatment. Conversely, *M. hapla* population densities never exceeded Category 1 in Teleki 5C vines. For 101-14 Mgt and 1103P rootstocks, *M. hapla* population densities eventually reached Categories 2 and 3, but not until fall of 2017. Harmony rootstock in fumigated plots had *M. hapla* densities in Category 1 through fall 2017. In NF+ plots, Harmony did support higher *M. hapla* population densities, with densities increasing from Category 2 in fall of 2015 to Category 3 in fall of 2017. Overall, *M. hapla* population densities increased in all the rootstock treatments over the first three years of establishment, just at a slower rate than in the own-rooted and self-grafted controls.

Ranked pruning weights in own-rooted vines relative to *M. hapla* population densities. Given that the more common practice in Washington state is to grow *V. vinifera* on its own roots, we evaluated whether there was a relationship between *M. hapla* J2 population density and vine vigor (measured as pruning weight) using linear regression and ranked variables. There was a similar negative trend between ranked *M. hapla* population densities and ranked pruning weights in both of the full vegetative growth cycles considered (cycle 1: influence of *M. hapla* J2 population densities in fall 2015 on subsequent vine growth in 2016, recorded as fall 2016 pruning weights; and cycle 2: influence of *M. hapla* J2 population densities in fall of 2016 on subsequent vine growth, recorded as fall 2017 pruning weights). Pruning weights of own-rooted vines decreased as *M. hapla* J2 population densities increased (cycle 1: $R^2 = 0.34$, $p = 0.003$; cycle 2: $R^2 = 0.30$ $p = 0.006$) (Fig. 7). The regression lines for both sets of years are nearly parallel, with very similar trends. This is evidence for there being a negative relationship between *M. hapla* population density and vine growth in the subsequent year.

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Nematode dosage. Nematode dosage quantifies the accumulated impact of nematode pressure over time (Noling and Ferris 1987). In the statistical model, both fumigation and rootstock were significant at all time points after planting ($p \leq 0.0001$), and there was no significance to the interaction between the two ($p > 0.5$). By fall 2016, after 2 growing seasons, both the self-grafted and own-rooted vines had a higher cumulative nematode dosage than the vines on rootstocks (Fig. 8A), and the gap between the self-grafted and own-rooted vines, and rootstocks, increased through spring 2018. The initial nematode density variation caused by fumigation treatments persisted through spring 2018 ($p < 0.0001$) (Fig. 8B).

Effect of fumigation and rootstock on *X. americanum* population densities. There was no difference in *X. americanum* population densities between plots prior to establishing the experiment ($p = 0.53$) (Table 2), and the average initial density of *X. americanum* was 214 individuals per 250 g soil. Fumigation was the only significant parameter in the model; there was no difference in *X. americanum* population densities between the rootstocks and own-rooted and self-grafted vines. All rootstocks, regardless of parentage, were able to support the development of the *X. americanum* at this site. Population densities of *X. americanum* varied from season to season in the non-fumigated plots, but these were not related to the rootstock genotype ($p > 0.21$). Fumigation significantly reduced *X. americanum* population densities to near zero from spring 2015 through spring 2018. In fumigated plots, *X. americanum* still had not reached pre-fumigation densities by spring 2018.

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Discussion

Over the lifetime of a vineyard, a slow decline in individual vines and vineyard productivity as a result of plant-parasitic nematode parasitism can significantly reduce farm profits (Raski 1986). In most cases, the bulk of nematode management is focused on pre-plant soil fumigation. This is the case in Washington vineyards where highly-susceptible own-rooted *V. vinifera* is almost exclusively planted (Howland et al. 2015). Our experiment is one of the first investigations (Moyer et al. 2017) on the long-term effectiveness of pre-plant nematode management tools such as fumigation and rootstocks in Washington vineyards. The winegrape industry in the state is relatively young, and to this point has been able to plant new vineyards on non-vineyard soils; however, a period of vineyard replanting is approaching and with it, the need for information on managing a potential replant disorder due to plant-parasitic nematodes.

The effects of fumigation and rootstock were complicated with respect to *M. hapla* management. Fumigation reduced *M. hapla* compared to the nonfumigated treatment for the first six months after fumigation. However, by one-year post-fumigation, there was no difference in *M. hapla* J2 population densities between fumigated and nonfumigated plots, and only the plots inoculated with extra *M. hapla* eggs (NF+) had higher population densities. Even with the added *M. hapla*, there was no difference among any treatments in *M. hapla* J2 population densities by 1.5 years after fumigation. These results indicate that pre-plant soil fumigation is likely not a long-term solution for the management of *M. hapla* in scenarios where the trellis infrastructure is retained and the fumigant is applied through the existing driplines. The juvenile and adult female life stages of this sedentary endoparasitic nematode's life cycle are embedded within vine roots which are relatively impervious to fumigants at commercial application rates (McKenry et al.

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1977), thus preventing their ability to provide complete control of *Meloidogyne* spp. In addition, the effectiveness of fumigation relies on product distribution throughout the soil profile. This distribution is affected by soil type, temperature, product solubility, and application rate (Ajwa and Trout 2004). *Meloidogyne hapla* is generally concentrated under drip emitters in Washington vineyards, where most fine roots are located (Howland et al. 2014), and therefore would likely be concentrated in this area if vines are replanted into the same spot. In addition, the retained trellis system may have a 'shadowing' effect, where pockets of soil around the in-ground posts may remain untreated. Altogether, in a situation where the existing vineyard infrastructure is maintained in a replant scenario, any *M. hapla* that are missed by fumigation will likely be in the vicinity of any newly planted vines, increasing the likelihood of reinfestation. Even though fumigation was not effective long-term against *M. hapla*, we cannot discount the short-term benefits that this practice might provide; however, these benefits are hard to measure.

One-year post-fumigation (6 months post-planting), the differences in *M. hapla* densities transitioned from being a result of fumigation to a result of rootstock choice. All the non-*vinifera* rootstocks evaluated here eventually supported measurable densities of *M. hapla* by the end of the establishment period. This demonstrates that while these rootstocks are not resistant to *M. hapla,* they are likely less-than-optimal hosts and may support a smaller density of this nematode while not displaying a typical decline in vigor or yield. These results are similar to what was found by Zasada et al. (2019), in a glasshouse study using an *M. hapla* population from eastern Washington. In this experiment, *M. hapla* had a reproduction factor of less than 1 on Harmony and 101-14, indicating that these are poor hosts for *M. hapla*. The own-rooted *V. vinifera* Riesling control, on the other hand, had a reproductive factor of 20.7, indicating that it was an

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excellent host for *M. hapla*. Though these rootstocks were poor hosts for *M. hapla* in the short-term glasshouse experiment, in the field they were less-than-optimal hosts, as *M. hapla* reproduced on these rootstocks, though far less than on *vinifera* roots. Of the evaluated rootstocks, Teleki 5C may be the poorest host for *M. hapla*, as this rootstock was associated with reduced eggs per gram root and did not support a nematode density after three years of the experiment that would trigger a management action (Fig. 6). Reductions in *M. arenaria* egg densities have been seen previously in Teleki 5C and were associated with poor development of giant cells in vine roots (Anwar and McKenry 2002). We chose the other rootstocks in this study, 1103 P, 5C, 101-14 Mgt, and Harmony because some have demonstrated resistance to at least one *Meloidogyne* species, including *M. arenaria, M. javanica,* and *M. incognita* (Sauer 1967, Chitambar and Raski 1984, Nicol et al. 1999, McKenry and Anwar 2001, McKenry and Anwar 2006, Ferris et al. 2012). Some resistance-breaking pathotypes of *M. incognita* and *M. arenaria* can reproduce on Harmony, but not on other rootstocks, including 101-14 Mgt (Ferris et al. 2012). Resistance to one species of nematode within a genus does not always extrapolate to other species within that genus or even populations within a species (Cain et al. 1989), and few grape rootstocks have been specifically tested against *M. hapla*.

We utilized three different approaches to data analysis to further explore the effect of *M. hapla* on vine productivity and ability to colonize newly planted vines. It is difficult in perennial systems to ascribe the specific impacts of nematode parasitism on overall vine vigor. Unlike in annual systems, there is the compounding of plant age, nematode population changes, and other stresses over the year that make it difficult to measure. One way of accounting for multiple years of nematode pressure may be to sum the cumulative nematode dosage experienced by the vine

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over time. Plant diseases are often quantified as the disease intensity over time by calculating the area under disease progress curve (AUDPC). Similarly, Noling and Ferris (1987) used female *Meloidogyne* population densities as a measure of nematode dosage, and growing degree days as thermal time. We have used the same premise, with *M. hapla* J2 population densities as the nematode intensity at each sampling time point (Fig. 8). The difference in cumulative nematode dosage from the initial fumigation treatments persisted through spring 2018, which contrasts with the results from the discrete analysis of population densities at each timepoint (Table 1), where fumigation no longer influenced *M. hapla* densities starting in spring 2016. Though there was no difference between *M. hapla* population densities due to fumigation within the sampling points after spring 2016 , the lasting effects from there having been a difference in the first year (2015) are better captured using the cumulative nematode dosage and might be more appropriate for a perennial system. Looking at just rootstock (Fig. 8A), all rootstocks experienced far lower nematode dosage starting fall 2016, more consistently than the individual sampling date analysis, and the difference in dosage increased over time. It is also interesting to note that the nematode dosage increased mostly from spring to fall, and very little in the off-season, from fall to spring.

Secondly, while looking at absolute nematode numbers is useful for statistical analysis, it can be difficult to visualize and interpret for growers and other end-users. A more realistic way of looking at the data is to assign ranges of nematode densities into categories. We chose to use categories around the presumed action threshold of 100 *M. hapla* J2 per 250 g soil (Santo, *unpublished data*) (Fig. 5). The graphic easily displays both the changes in nematode density due to fumigation and rootstock and shows the changes over time. We used only fall data, because that was the most consistent in terms of timing and when growers most commonly sample for

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nematodes. Interpretations are the same as above, where own rooted and self-grafted vines were above the threshold in the highest category immediately if not fumigated, unlike most rootstocks evaluated. When fumigated, the effects only lasted through fall 2015 in the own-rooted and self-grafted vines, then the *M. hapla* population densities were above the threshold by the next year. Teleki 5C, which was the least-suitable host for *M. hapla,* remained in the lowest population density category through the entire establishment period, below the management threshold.

The third approach was to examine the influence of *M. hapla* on the susceptible own-rooted Chardonnay vines. We altered the initial *M. hapla* nematode population densities using soil fumigation or through the addition of *M. hapla* eggs at planting. This was intended to measure both the impact of fumigation on *M. hapla* population dynamics as well as on vine vigor over time. However, in this process, we obtained a wide range of *M. hapla* population densities in the Chardonnay vines grown on their own roots. This gave us an opportunity to see whether there was a relationship between *M. hapla* population densities and vine vigor. We did find an overall decrease in pruning weights when vines had higher ranked densities of *M. hapla* in the fall of the previous year. This was consistent over two cycles of fall *M. hapla* J2 densities and the next year's pruning weight, demonstrating reduced vine vigor with increased *M. hapla* J2 population densities in soil. Since these values are ranked, it is difficult to define a specific nematode density that results in a reduction in pruning weights; this examination was mainly to identify whether there was a pattern of vigor reduction. The R^2 values for these regressions were not particularly high (0.34, 0.29), but high variability in vine vigor is often common in the early stages of vineyard establishment, regardless of vine health status.

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The other plant-parasitic nematode widely distributed in this vineyard, *X. americanum*, was controlled by fumigation with metam sodium; fumigated plots had almost zero *X. americanum* through spring of 2018, 3.5 yrs post-fumigation. *Xiphinema americanum* is often found deep in the soil in Washington (Howland et al. 2014; East et al. 2019b) and this nematode has a long life cycle of one year or more (Malek 1969). Based upon its biology, it would likely take multiple years for this nematode to recolonize the upper 45 cm of soil where sampling occurred. *Xiphinema americanum* can feed along roots and are likely able to feed on roots that are deeper in the soil, so they may not have incentive to return to the upper profile (Cohn 1970). From a management perspective, fumigation was effective, but the rootstocks evaluated in this experiment would not be effective against *X. americanum*. All the rootstocks evaluated supported high population densities of the *X. americanum* as are found in Washington state, which is consistent with previous research with *X. americanum* in California (McKenry et al. 2004; Ferris et al. 2012).

From a vine vigor perspective, Teleki 5C was consistently the least vigorous of the rootstocks and Harmony the most vigorous, as determined by dormant pruning weights and yield from the cropping year. Both 1103 P and 101-14 Mtg had intermediate vigor, which does contrast to previous findings in the region (Keller et al. 2012). This matches the vigor categories from California where Harmony and 1103 P are medium to high vigor, 101-14 Mtg is medium vigor, and Teleki 5C is low to medium vigor (Bettiga 2003), in both reproductive (yield) and vegetative (pruning weight) growth. Some of Harmony's vigor in the first year may be attributed to the fact that it was a green graft that had not gone through a dormancy period, unlike the rest of the grafted rootstocks; however, Harmony is known as a high-vigor rootstock and was

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consistently the most vigorous rootstock in all years. Even in the presence of *M. hapla*, lower vigor rootstocks, like 1103 P and Teleki 5C, maintained vegetative growth in the presence of *M. hapla*, whereas it appeared that the own-rooted and self-grafted vines could not, exacerbated by the loss of the fumigation effect. This relative vigor decline in the own-rooted and self-grafted vines across all soil treatments, especially in year 3 (2017) is likely attributable to *M. hapla* as it was present in all plots. The high nematode dosage experienced by own-rooted vines compared to rootstocks (Fig. 8), as well as the relationship between higher *M. hapla* population density and lower vine vigor the following year (Fig. 7) support this hypothesis.

Growth stimulation can also occur in the presence of nematode feeding (Seinhorst 1965), which may explain why vines grown in non-fumigated plots had greater pruning weights than vines in fumigated plots in 2015. This stimulation occurs during light feeding and is overcome under heavy nematode pressure. This effect was weaker in 2016, and no effect was seen in 2017. It is likely that the vigor response seen by year three was mostly a result of nematode feeding, as *M. hapla* population densities in the own-rooted controls were far higher than those in the rootstocks. This could be due to both *X. americanum* and *M. hapla* parasitism. McKenry and Anwar (2006) found that *X. americanum* parasitism stimulated growth in 11 of the 16 rootstock cultivars evaluated, and that parasitism by *M. javanica* stimulated growth of Harmony. Growth stimulation may contribute to the tolerance of some rootstocks to nematode parasitism. An additional potential explanation for reduced pruning weights in fumigated plots as compared to non-fumigated may be that fumigation kills not only nematodes in soil, but mycorrhizal fungi which form symbioses with grapevines. Stunting in some vineyards has been found to be a result of poor colonization with mycorrhizae (Menge et al. 1983), and metam sodium has been found to

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kill mycorrhizal fungi (Davis et al. 1996). This study underlines the importance of understanding which nematode species are present in a vineyard facing replant, as the efficacy of these management techniques (fumigation and rootstocks) are species dependent.

Conclusion

Plant-parasitic nematode management is an important part in the process of vineyard replanting. Fumigation was not an effective long-term strategy for suppressing *M. hapla*. Soil population densities of this nematode recovered 1.5 years post-fumigation and exceeded pre-fumigation levels, as well as the proposed threshold for management, by 2 years post-fumigation in plots containing own-rooted and self-grafted vines. Increased *M. hapla* J2 population densities in the fall of a year were correlated with lower pruning weights in the following year in own-rooted and self-grafted Chardonnay vines. All non-*vinifera* rootstocks had increased vigor over the own-rooted and self-grafted vines by year 3 of establishment, and generally supported lower *M. hapla* population densities compared to *V. vinifera* vines. However, by year 3, all treatments regardless of rootstock genotype had measurable *M. hapla* population densities. Therefore, it appears that none of these non-*vinifera* rootstocks is fully resistant to *M. hapla,* but rather, are better classified as partially resistant to feeding (i.e., poor hosts). Fumigation was an effective tactic for management of *X. americanum* which was only detectable in fumigated soil 3.5 years post-fumigation. None of the rootstocks evaluated (1103 P, 101-14 Mgt, Teleki 5C, and Harmony) was resistant to *X. americanum*, as expected. As Washington growers move forward into an era of replant, adoption of rootstocks for *M. hapla* management is a potentially viable

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option, whereas fumigation may provide only short-term protection from *M. hapla* but is a suitable management strategy for the long-term suppression of *X. americanum*.

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Table 1 Average *Meloidogyne hapla* second-stage juvenile (J2) soil densities (per 250 g soil) at fall and spring sampling dates from fall 2014 to spring 2018. Fumigation occurred on 18 Sep 2014 and planting on 12 May 2015. Fumigation treatments were fumigated (F), non-fumigated (NF), and non-fumigated inoculated (NF+) with approximately 20,000 additional *M. hapla* eggs applied at planting. All rootstocks were grafted with *V. vinifera* Chardonnay FPS selection 15 as the scion. Different letters denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's HSD.

		Timing of Sampling															
		Fall 2014		Spring 2015		Fall 2015		Spring 2016		Fall 2016		Spring 2017		Fall 2017		Spring 2018	
Rootstock	Fumigation	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Own-rooted	F	41	25	0	0	25	23	45	33	225	154	248	165	240	49	413	218
	NF	83	33	48	35	169	39	180	162	199	93	375	249	210	128	180	107
	NF+	83	33	48	35	338	89	210	82	844	667	143	52	220	106	218	149
Self-grafted	F	15	7	0	0	17	8	15	17	281	167	98	57	675	246	713	284
	NF	85	68	45	29	136	85	135	114	461	258	570	338	555	222	780	406
	NF+	85	68	45	29	281	51	165	107	1058	431	405	210	600	147	514	240
Harmony	F	146	29	0	0	0	0	0	0	0	0	0	0	0	0	30	24
	NF	123	111	28	27	8	10	0	0	150	173	8	9	15	17	98	91
	NF+	123	111	28	27	58	23	0	0	56	65	90	14	320	214	225	88
101-14 Mtg	F	124	45	0	0	41	30	15	17	0	0	60	69	68	30	218	152
	NF	60	35	17	10	4	5	75	66	0	0	98	82	330	236	75	46
	NF+	60	35	17	10	25	12	45	17	11	13	30	35	195	71	195	54
5C	F	25	10	0	0	4	5	45	52	0	0	0	0	20	20	8	9
	NF	18	20	21	5	12	9	0	0	15	17	0	0	0	0	30	35
	NF+	18	20	21	5	21	12	0	0	34	39	30	35	30	20	68	9
1103P	F	121	103	0	0	0	0	30	35	0	0	0	0	60	69	53	50
	NF	43	38	7	5	8	6	0	0	0	0	0	0	0	0	53	30
	NF+	43	38	7	5	41	29	75	44	11	13	30	35	180	185	128	59

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Table 2 Average *Xiphinema americanum* population densities (per 250 g soil) at fall and spring sampling dates from fall 2014 to spring 2018. Fumigation occurred on 18 Sep 2014, and planting on 12 May 2015. Fumigation treatments were fumigated (F) and non-fumigated (NF). Rootstocks were Teleki 5C (5C), 101-14 Millardet et de Grasset (101-14 Mtg), Paulsen 1103 (1103 P), Harmony, self-grafted *Vitis vinifera* Chardonnay (self-grafted), and own-rooted non-grafted Chardonnay (own-rooted). All rootstocks were grafted with *V. vinifera* Chardonnay FPS selection 15 as the scion.

		Timing of Sampling															
		Fall 2014		Spring 2015		Fall 2015		Spring 2016		Fall 2016		Spring 2017		Fall 2017		Spring 2018	
Rootstock	Fumigation	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Own-rooted	F	253	69	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NF	149	7	62	26	37	9	0	0	240	123	23	17	75	66	90	49
Self-grafted	F	145	58	0	0	0	0	0	0	0	0	0	0	0	0	8	9
	NF	155	79	86	67	37	16	0	0	41	28	68	55	90	45	98	62
Harmony	F	303	125	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NF	204	78	69	43	25	17	0	0	131	79	83	22	90	66	203	157
101-14 Mtg	F	138	76	0	0	0	0	0	0	0	0	0	0	0	0	8	9
	NF	239	57	24	8	33	26	15	17	50	5	90	49	30	35	113	54
5C	F	203	122	0	0	0	0	0	0	2	2	8	9	0	0	0	0
	NF	299	38	21	14	12	5	30	20	45	52	83	38	240	102	225	67
1103P	F	331	245	0	0	0	0	0	0	0	0	0	0	0	0	15	17
	NF	144	42	52	34	37	16	60	40	105	84	83	54	20	20	68	26

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Rep	Rootstock	Row	Treatments		
A	Harmony	1	NF+	NF	F
	Own-Rooted	2	NF+	NF	F
1	101-14 Mtg	3	NF+	NF	F
	Teleki 5C	4	NF+	NF	F
	Self-Grafted	5	NF+	NF	F
	1103 P	6	NF+	NF	F
	Teleki 5C	7	F	NF	NF+
	1103 P	8	F	NF	NF+
2	Harmony	9	F	NF	NF+
	101-14 Mtg	10	F	NF	NF+
	Self-Grafted	11	F	NF	NF+
	Own-Rooted	12	F	NF	NF+
	Self-Grafted	13	F	NF	NF+
	1103 P	14	F	NF	NF+
3	Teleki 5C	15	F	NF	NF+
	Own-Rooted	16	F	NF	NF+
	Harmony	17	F	NF	NF+
	101-14 Mtg	18	F	NF	NF+
	Own-Rooted	19	NF+	NF	F
	Harmony	20	NF+	NF	F
4	Self-Grafted	21	NF+	NF	F
	101-14 Mtg	22	NF+	NF	F
	1103 P	23	NF+	NF	F
	Teleki 5C	24	NF+	NF	F

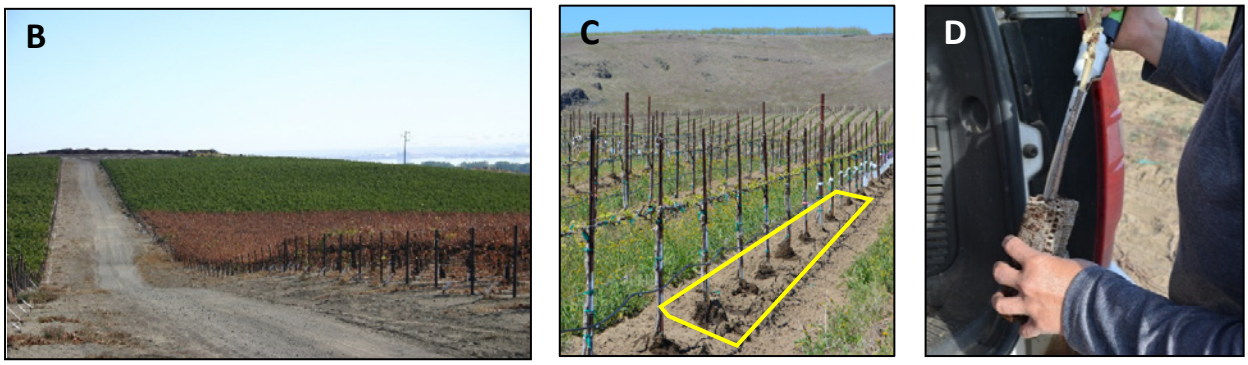

Figure 1 (**A**) Vineyard experimental diagram, where a rootstock consists of an entire vineyard row, and where half of that row was either fumigated (dark gray) or not fumigated (light grey). Within each vineyard row, three, 10-vine sections were designated for data collection: F (blue) in the fumigated half; NF (yellow), in the non-fumigated half of the row; and NF+ (orange), where additional *M. hapla* eggs were added to vine roots at planting in the non-fumigated half of the row. Fumigation occurred on 18 Sep 2014 and planting and additional nematode inoculation occurred on 12 May 2015. (**B**) Foliar glyphosate was applied to kill the existing vines in fall 2014 prior to being removed and replanting. (**C**) Vineyard rows with NF (yellow) 10-vine section highlighted as an example. (**D**) In the NF+ plots, vines were inoculated with *M. hapla* eggs prior to planting.

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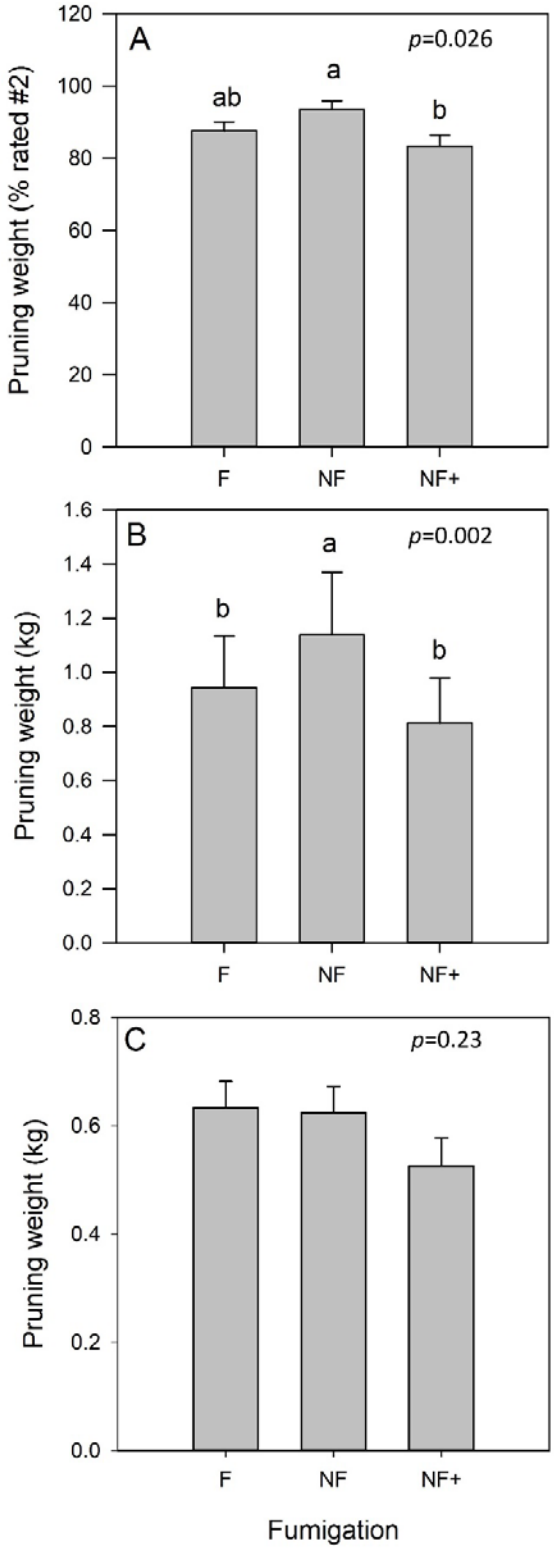

Figure 2 Dormant vine pruning weights by fumigation (soil) treatment in fall of (**A**) 2015 , (**B**) 2016 and (**C**) 2017. Fumigation treatments were: fumigated (F), non-fumigated (NF), and non-fumigated inoculated (NF+) where approximately 20,000 additional *Meloidogyne hapla* eggs were added to the vines at planting. Rootstock treatments were combined within fumigation treatments because there was no rootstock*fumigation interaction. Fumigation occurred on 18 Sep 2014. Planting occurred on 12 May 2015. Error bars are standard error (n = 4). Different letters denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's HSD.

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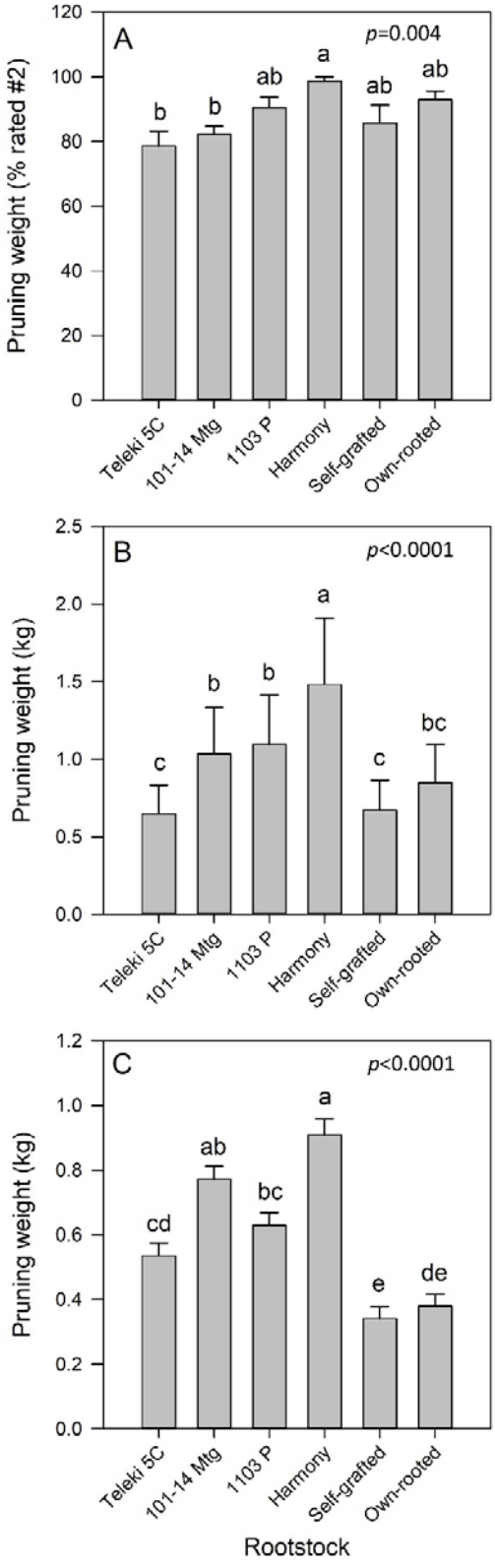

Figure 3 Dormant vine pruning weights by rootstock treatment in (**A**) 2015, (**B**) 2016, and (**C**) 2017. Rootstocks were: Teleki 5C, 101-14 Millardet et de Grasset (101-14 Mtg), Paulsen 1103 (1103 P), Harmony, self-grafted *Vitis vinifera* 'Chardonnay' (self-grafted), and own-rooted non-grafted Chardonnay (own-rooted). All rootstocks were grafted with *V. vinifera* 'Chardonnay' FPS selection 15 as the scion. Fumigation treatments were combined within rootstock treatments as there was no rootstock*fumigation interaction. Within a graph, different letters denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's HSD. Error bars are standard error (n = 4). Fumigation occurred on 18 Sep 2014 and planting occurred on 12 May 2015.

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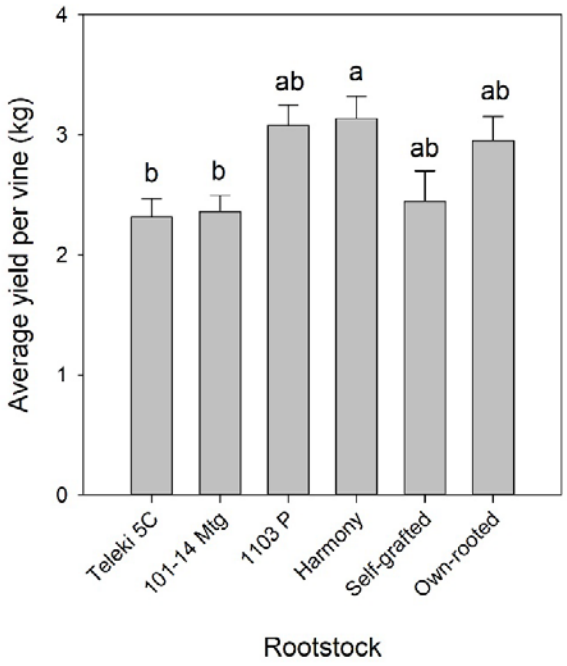

Figure 4 First partial harvest in 2017 with average yield per vine by rootstock treatment (p = 0.003). Rootstocks were: Teleki 5C, 101-14 Millardet et de Grasset (101-14 Mtg), Paulsen 1103 (1103 P), Harmony, self-grafted *Vitis vinifera* 'Chardonnay' (self-grafted), and own-rooted non-grafted Chardonnay (own-rooted). All rootstocks were grafted with *V. vinifera* Chardonnay FPS selection 15 as the scion. Fumigation treatments were combined within rootstock treatments as there was no rootstock*fumigation interaction. Within a graph, different letters denote significant differences among treatment means at α = 0.05 using Tukey's HSD. Error bars are standard error (n = 4). Fumigation occurred on 18 Sep 2014 and planting occurred on 12 May 2015.

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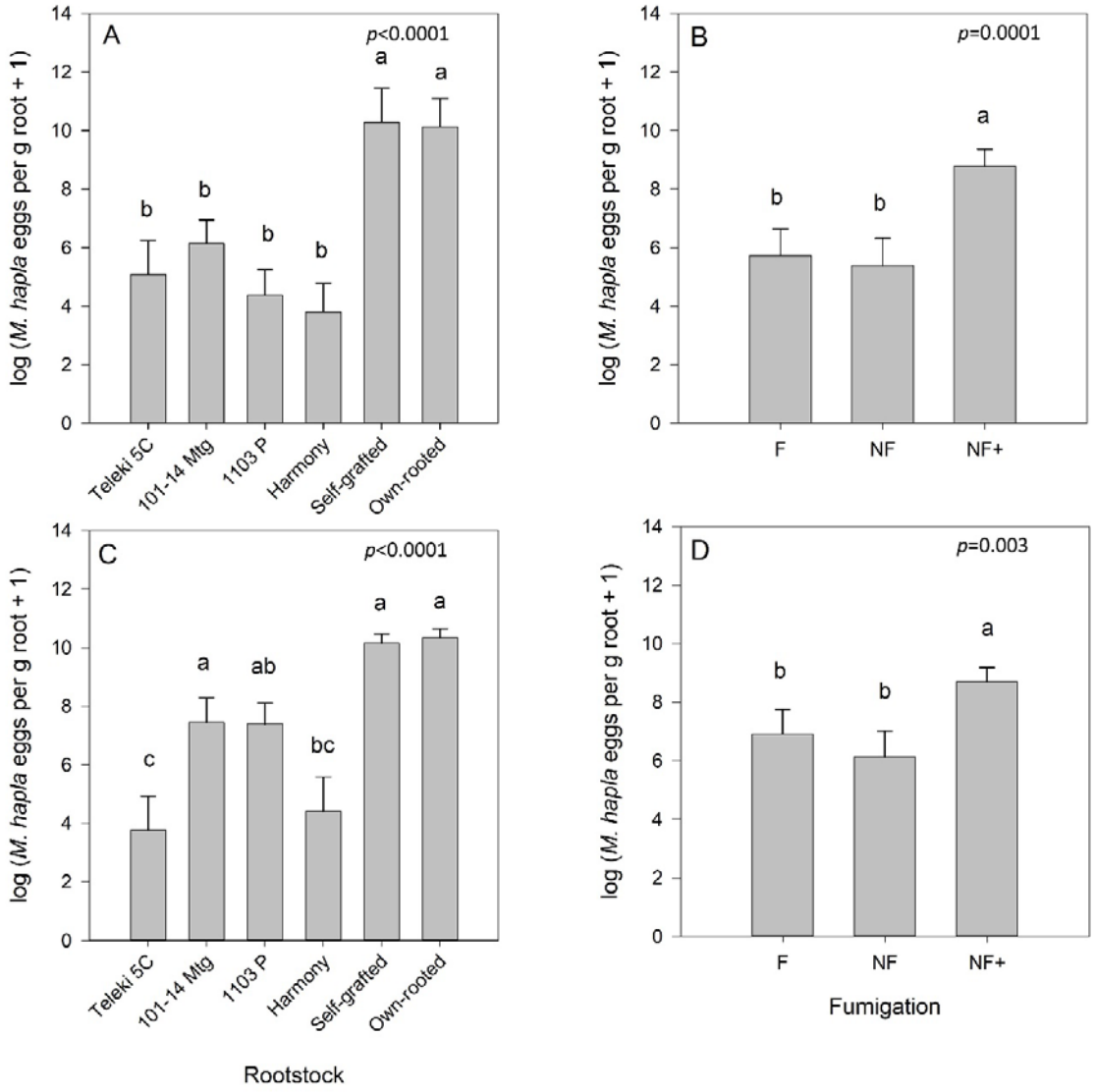

Figure 5 *Meloidogyne hapla* egg population densities (per g root) in (**A**) fall 2016 by rootstock, (**B**) fall 2016 by fumigation, (**C**) fall 2017 by rootstock, and (**D**) fall 2017 by fumigation. There was no interaction between rootstocks and fumigation, so they are presented separately. Rootstocks were: Teleki 5C, 101-14 Millardet et de Grasset (101-14 Mtg), Paulsen 1103 (1103 P), Harmony, self-grafted *Vitis vinifera* 'Chardonnay' (self-grafted), and own-rooted non-grafted Chardonnay (own-rooted). All rootstocks were grafted with *V. vinifera* Chardonnay FPS selection 15 as the scion. Fumigation treatments were: fumigated with metam sodium (F), non-fumigated (NF), and non-fumigated inoculated with approximately 20,000 additional *M. hapla* eggs applied at planting (NF+). Fumigation occurred on 18 Sep 2014 and planting and additional nematode inoculation (NF+) occurred on 12 May 2015. Error bars are standard error (n = 4). Different letters denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's HSD.

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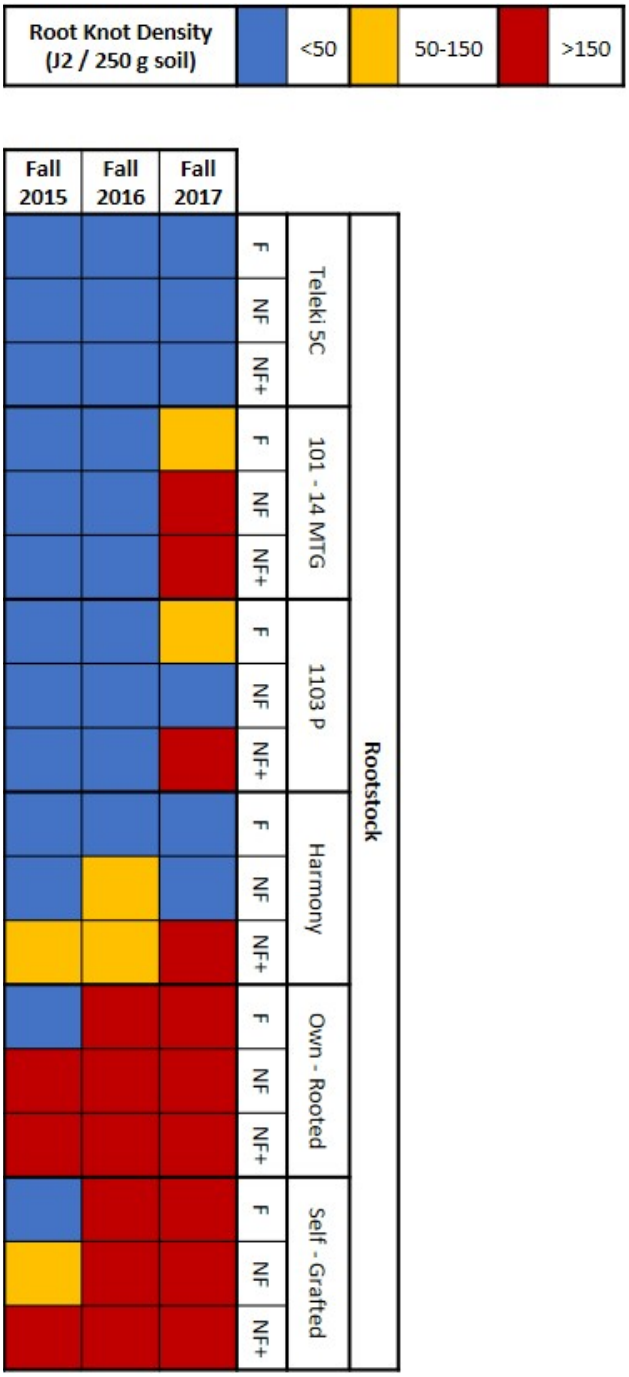

Figure 6 Categorical diagram of *Meloidogyne hapla* management risk over time. Rootstock and fumigation combination *M. hapla* second-stage juveniles (J2) density categories: 1) less than 50 *M. hapla* J2 per 250 g soil (blue; below management threshold), 2) 50 to 150 *M. hapla* J2 per 250 g soil (yellow; around proposed management threshold), and 3) more than 150 *M. hapla* J2 per 250 g soil (red; above management threshold)) in fall of 2015, 2016 and 2017. Fumigation treatments were: fumigated (F), non-fumigated (NF), and non-fumigated inoculated with approximately 20,000 additional *M. hapla* eggs at planting (NF+). Rootstocks were: Teleki 5C, 101-14 Millardet et de Grasset (101-14 Mtg), Paulsen 1103 (1103 P), Harmony, self-grafted *Vitis vinifera* 'Chardonnay' (self-grafted), and own-rooted non-grafted *V. vinifera* Chardonnay (own-rooted). Each data point within a treatment combination is the average of n = 4. Fumigation occurred on 18 Sep 2014 and planting and additional nematode inoculation occurred on 12 May 2015.

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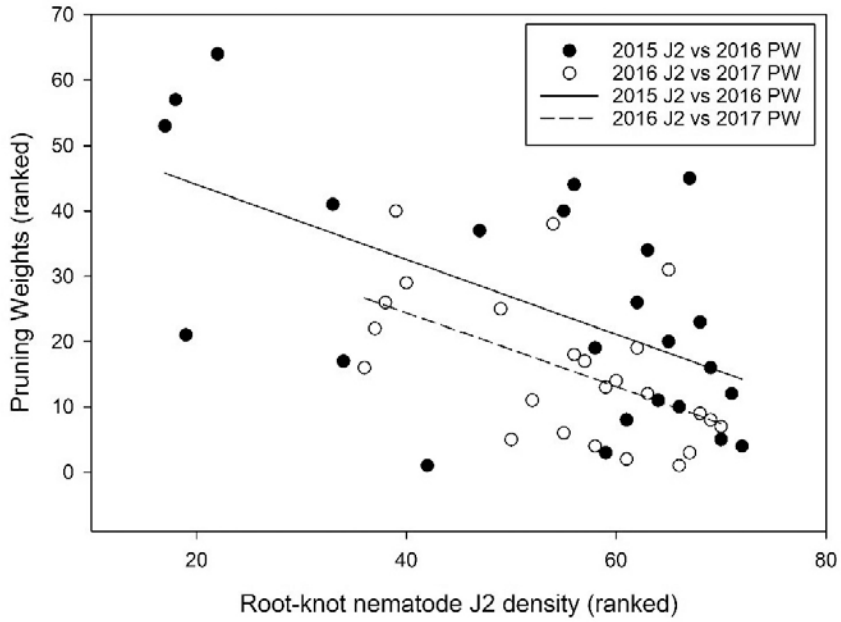

Figure 7 Higher nematode population densities in the previous growing season negatively impact vine vingor (pruning weights; PW) the following season. Linear regression comparision between ranked pruning weights (PW) of vines on susceptible *Vitis vinifera* 'Chardonnay' roots and the previous years' ranked *Meloidogyne hapla* second-stage juveniles (J2) population densities for two growing season cycles: fall 2015 *M. hapla* J2 densities compared to fall 2016 pruning weights (black circles), and fall 2016 *M. hapla* J2 densities compared to fall 2017 pruning weights (white circles). 2015-2016 regression (solid line): $y = 67.3 – 0.5846x$, $R^2 = 0.34$, $p = 0.003$. 2016-2017 regression (dashed line): $y = 63.7 – 0.5259x$, $R^2 = 0.29$, $p = 0.006$.

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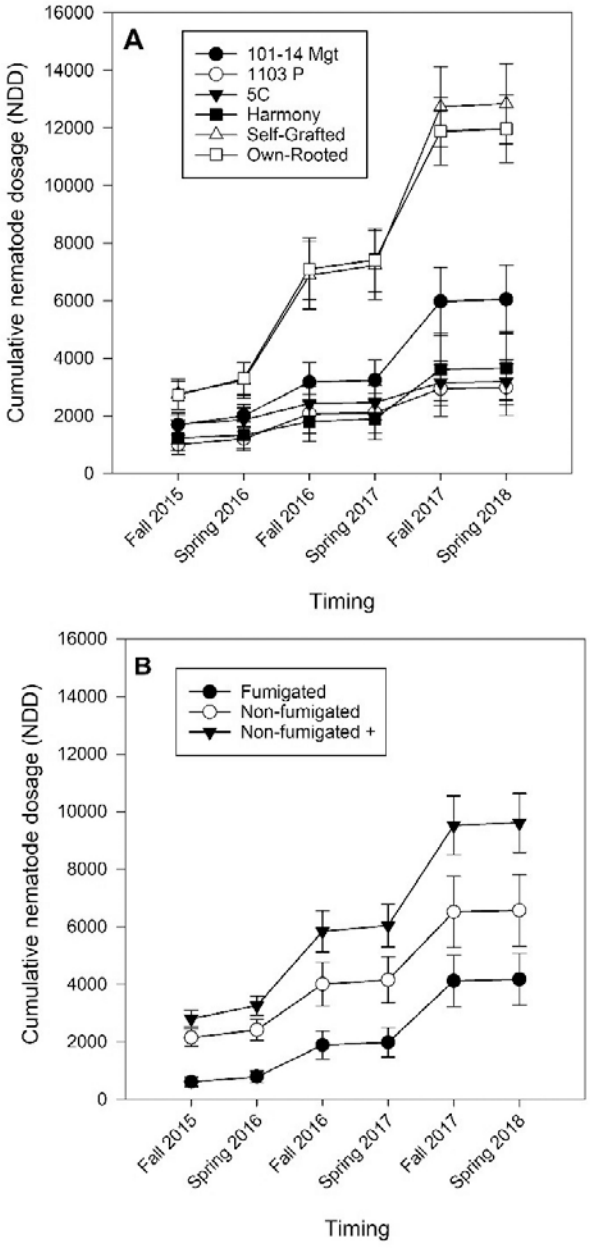

Figure 8 Cumulative *Meloidogyne hapla* second-stage juvenile (J2) dosage (in nematode degree days; Noling and Ferris 1987) at sampling timepoints post-planting (Spring 2015). Nematode dosage due to rootstock is far lower on rootstocks than the susceptible *V. vinifera* controls (**A**), and dosage due to fumigation persists across all three years (**B**). Each error bar is constructed using 1 standard error from the mean. Fumigation occurred on 18 Sep 2014 and planting and additional nematode inoculation occurred on 12 May 2015. Error bars are standard error (n = 4). Nematode dosage is a measure of cumulative nematode pressure experienced over time, which is especially important in a perennial system. Rootstocks were: Teleki 5C, 101-14 Millardet et de Grasset (101-14 Mtg), Paulsen 1103 (1103 P), Harmony, self-grafted *Vitis vinifera* 'Chardonnay' (self-grafted), and own-rooted non-grafted Chardonnay (own-rooted). All rootstocks were grafted with *V. vinifera* Chardonnay FPS selection 15 as the scion. Fumigation treatments were: fumigated with metam sodium (F), non-fumigated (NF), and non-fumigated inoculated (NF+) with approximately 20,000 additional *M. hapla* eggs applied at planting. Fumigation occurred on 18 Sep 2014 and planting occurred on 12 May 2015.

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Supplemental Table 1 Standard least squares output for *Meloidogyne hapla* second-stage juvenile (J2) population density as a split plot with fumigation, rootstock, fumigation*rootstock as fixed variables and block*rootstock with block as a random variable (Block is the replicate blocks). Fumigation occurred on 18 Sep 2014 and planting on 12 May 2015.

Sample	Source	Nparm	DF	DFDen	F Ratio	Prob > F
Fall 2014	Fumigation	1	1	18	0.1626	0.6915
	Rootstock	5	5	18	1.5052	0.2375
	Rootstock*Fumigation	5	5	18	0.8412	0.5379
	Rootstock*Block	15	15	18	1.2724	0.3099
Spring 2015	Fumigation	1	1	18	12.7795	0.0022
	Rootstock	5	5	18	0.7232	0.6147
	Rootstock*Fumigation	5	5	18	0.7232	0.6147
	Rootstock*Block	15	15	18	0.7937	0.6712
Fall 2015	Fumigation	2	2	36	20.4491	<.0001
	Rootstock	5	5	36	17.3952	<.0001
	Rootstock*Fumigation	10	10	36	5.1259	0.0001
	Rootstock*Block	15	15	36	0.8593	0.6108
Spring 2016	Fumigation	2	2	36	2.2299	0.1222
	Rootstock	5	5	36	4.0267	0.0053
	Rootstock*Fumigation	10	10	36	1.0107	0.4535
	Rootstock*Block	15	15	36	1.8364	0.0677
Fall 2016	Fumigation	2	2	34.67	2.8347	0.0724
	Rootstock	5	5	34.78	5.2372	0.0011
	Rootstock*Fumigation	10	10	34.63	1.0013	0.4615
	Rootstock*Block	15	15	34.46	0.7481	0.7209
Spring 2017	Fumigation	2	2	36	2.1011	0.1371
	Rootstock	5	5	36	7.9843	<.0001
	Rootstock*Fumigation	10	10	36	1.4052	0.2174
	Rootstock*Block	15	15	36	1.5859	0.1272
Fall 2017	Fumigation	2	2	32.86	0.9691	0.39
	Rootstock	5	5	32.86	10.9297	<.0001
	Rootstock*Fumigation	10	10	32.85	0.8738	0.5658
	Rootstock*Block	15	15	32.81	1.0761	0.4128
Spring 2018	Fumigation	2	2	36	0.232	0.7941
	Rootstock	5	5	36	18.951	<.0001
	Rootstock*Fumigation	10	10	36	1.1884	0.3305
	Rootstock*Block	15	15	36	4.0282	0.0003

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Supplemental Table 2 Standard least squares output for *Xiphinema americanum* soil population density as a split plot with fumigation, rootstock, fumigation*rootstock as fixed variables and block*rootstock with block as a random variable (Block is the replicate blocks). Fumigation occurred on 18 Sep 2014 and planting on 12 May 2015.

Sample	Source	Nparm	DF	DFDen	F Ratio	Prob > F
Fall 2014	Fumigation	1	1	18	0.3979	0.5361
	Rootstock	5	5	18	0.4798	0.7867
	Rootstock*Fumigation	5	5	18	0.9998	0.4458
	Rootstock*Block	15	15	18	1.3234	0.2827
Spring 2015	Fumigation	1	1	18	15.4851	0.001
	Rootstock	5	5	18	0.6234	0.684
	Rootstock*Fumigation	5	5	18	0.6234	0.684
	Rootstock*Block	15	15	18	1.0422	0.4612
Fall 2015	Fumigation	1	1	18	28.4006	<.0001
	Rootstock	5	5	18	0.5017	0.771
	Rootstock*Fumigation	5	5	18	0.5017	0.771
	Rootstock*Block	15	15	18	1.0519	0.4538
Spring 2016	Fumigation	1	1	18	7.3846	0.0141
	Rootstock	5	5	18	1.5692	0.219
	Rootstock*Fumigation	5	5	18	1.5692	0.219
	Rootstock*Block	15	15	18	1.1385	0.3921
Fall 2016	Fumigation	1	1	17.82	11.7116	0.0031
	Rootstock	5	5	17.55	1.6173	0.2073
	Rootstock*Fumigation	5	5	17.55	1.6323	0.2034
	Rootstock*Block	15	15	16.64	1.1077	0.4173
Spring 2017	Fumigation	1	1	18	21.7778	0.0002
	Rootstock	5	5	18	0.4944	0.7762
	Rootstock*Fumigation	5	5	18	0.4444	0.8117
	Rootstock*Block	15	15	18	0.95	0.5347
Fall 2017	Fumigation	1	1	18	21.7778	0.0002
	Rootstock	5	5	18	0.4944	0.7762
	Rootstock*Fumigation	5	5	18	0.4444	0.8117
	Rootstock*Block	15	15	18	0.95	0.5347
Spring 2018	Fumigation	1	1	18	19.3383	0.0003
	Rootstock	5	5	18	0.7346	0.6071
	Rootstock*Fumigation	5	5	18	0.9546	0.4707
	Rootstock*Block	15	15	18	0.9755	0.5137

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Supplemental Table 3 Standard least squares output for vine parameters: pruning ratings (fall 2015), pruning weights (fall 2016, fall 2017), and harvest yield (fall 2017) as a split plot with fumigation, rootstock, fumigation*rootstock and block*rootstock as fixed variables and block as a random variable (Block is the replicate blocks). Fumigation occurred on 18 Sep 2014 and planting on 12 May 2015.

Sample	Source	Nparm	DF	DFDen	F Ratio	Prob > F
Fall 2015 Pruning rating	Fumigation	2	2	36	4.0376	0.0262
	Rootstock	5	5	36	4.3004	0.0036
	Rootstock*Fumigation	10	10	36	0.833	0.6005
	Rootstock*Block	15	15	36	0.8425	0.6276
Fall 2016 Pruning weight	Fumigation	2	2	36	7.7365	0.0016
	Rootstock	5	5	36	14.8264	<.0001
	Rootstock*Fumigation	10	10	36	0.5494	0.843
	Rootstock*Block	15	15	36	1.2533	0.2804
Fall 2017 Pruning weight	Fumigation	2	2	36	1.5156	0.2334
	Rootstock	5	5	36	34.6333	<.0001
	Rootstock*Plot	10	10	36	1.1659	0.3446
	Rootstock*Block	15	15	36	0.8573	0.6129
Fall 2017 Harvest	Fumigation	2	2	36	0.4312	0.6531
	Rootstock	5	5	36	4.502	0.0027
	Rootstock*Fumigation	10	10	36	0.4887	0.8862
	Rootstock*Block	15	15	36	1.5417	0.1419