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Greenhouse Evaluation of Rootstocks Against the Northern Root-Knot Nematode (*Meloidogyne hapla*)

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Abstract

Background and goals

The northern root-knot nematode (*Meloidogyne hapla*) is a prevalent plant-parasitic nematode in northern grapegrowing regions. This nematode induces small galls on roots that restrict water and nutrient uptake, resulting in poor vine establishment or exacerbated decline in stressed vines. Rootstocks can be a viable option to manage vine decline caused by *M. hapla* in vineyards.

Methods and key findings

Nine *Vitis* spp. rootstocks (1616C, 99R, 44-53M, 140RU, Minotaur, SO4, SW, 5BB, and 1103P) and two *Vitis vinifera* own-rooted vines (Chardonnay and Cabernet Sauvignon) were evaluated against *M. hapla* in the greenhouse. Potted vines were inoculated with 5000 *M. hapla* eggs and destructively harvested after three months. Nematode reproduction factors (final population density/initial population density) were lower on the non-*vinifera* rootstocks than on the own-rooted *V. vinifera* vines. Only the rootstock 44-53M had a significantly greater reproduction factor value than the other non-*vinifera* rootstocks.

Conclusions and significance

This greenhouse evaluation provides a baseline resistance rating against *M. hapla* for several rootstock varieties. While many rootstocks are not fully resistant to *M. hapla*, the ability of *M. hapla* to reproduce on their roots relative to *V. vinifera* roots is several times lower. Rootstocks could improve longer-term management of *M. hapla* in Washington State vineyards.

Key words: grape rootstocks, northern root-knot nematode, reproduction factor

Introduction

The majority of Washington State vineyards are planted to own-rooted *Vitis vinifera* (Prengaman 2021). As grape producers face the prospect of replanting aging vineyards, there has been increased interest in using rootstocks for vineyard reestablishment to manage various soilborne pests and abiotic stresses. One such pest is the root-knot nematode (*Meloidogyne* spp). The primary *Meloidogyne* species found in Washington State winegrape vineyards is *Meloidogyne hapla* (northern root-knot nematode; Zasada et al. 2012), and own-rooted *V. vinifera* is susceptible to this nematode (Nicol et al. 1999, Howland et al. 2015). *M. hapla* induces small galls on roots, restricting water and nutrient uptake; in new vineyards this can inhibit healthy establishment, while established vineyards experience canopy and vine decline (East et al. 2019, 2021).

The challenge for Washington State growers seeking information to inform rootstock selection is that historically, most rootstock evaluations focus on other *Meloidogyne* spp., primarily *Meloidogyne incognita* (Melakeberhan et al. 1989, McKenry and Anwar 2006, Ferris et al. 2012, Smith et al. 2017, Magunacelaya et al. 2017). While rootstock susceptibility to *M. hapla* has been screened both in the greenhouse (Zasada et al. 2018) and in a long-term field trial (East et al. 2021), these screens evaluated only a limited number of rootstock genotypes: nine *Vitis* spp. rootstocks (with *V. vinifera* Riesling as a control) in the greenhouse and only four *Vitis* spp. rootstocks (with *V. vinifera* Chardonnay as a control) in the field, respectively.

The rootstocks evaluated here expand on these prior screening efforts, adding to the information available to grapegrowers when selecting a rootstock to manage *M. hapla*. Only one rootstock in this evaluation duplicates previous efforts: Paulsen 1103 (1103P). This rootstock was included in the

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long-term field trial (East et al. 2021) and supported moderate *M. hapla* development after several years of establishment. It was included in our evaluation to better understand the relationship between nematode development during short-term studies and potential longer-term performance in the field.

The rootstocks in this evaluation were selected for horticultural properties (Christensen 2003) of interest to Washington grapegrowers: potential drought tolerance (Paulsen 1103, Ruggeri 140, Richter 99); influence on scion vigor, such as potential vigor reduction (Malegue 44-53, Courderc 1616C, Schwarzmann); and potential for cold hardiness (Oppenheim #4, Kobber 5B). In addition, Minotaur was selected for its ability to root easily and graft without issue; while bred for general *Meloidogyne* spp. resistance, Minotaur's specific response to *M. hapla* is unknown (Cousins 2011).

Materials and Methods

Greenhouse evaluations of *Vitis* rootstocks against *M. hapla* were repeated three times: once in 2021 in Corvallis, OR (USDA-ARS-Horticultural Crops Disease and Pest Management Research Unit) and twice in 2022 in Prosser, WA (Washington State University Irrigated Agriculture Research and Extension Center [WSU Prosser IAREC]).

Preparation of planting media

In Prosser, soil (Warden silt loam) was collected from a fallow block of land located on the WSU Prosser IAREC campus (46°26′N; 119°73′W). Prior to soil collection, surface vegetation was removed; soil was collected to ~60 cm in depth. After collection, soil was mixed 1:1 (vol:vol) with coarse sand (Sakrete, OldCastle APG Inc.) as described (Schreiner et al. 2012). The soil mix was sterilized by steaming at 100°C for 72 hrs. To confirm the efficacy of sterilization, four random soil samples (250 g) were processed after cooling through a semi-automatic elutriator and examined through an inverted light microscope to ensure no nematodes survived. In Corvallis, a 1:1 (vol:vol) mix of Willamette loam and sand was prepared. The soil mix was steam-pasteurized in batches for 90 min prior to use.

Nematode inoculum preparation

M. hapla was originally collected from an infested vineyard in Mattawa, WA. Soil was added to a pot and *Solanum lycopersicum* Rutgers (a susceptible tomato cultivar) was planted. After approximately eight weeks, plants were removed from pots and single egg masses collected and inoculated onto another set of tomato plants; these plants were used to collect eggs for inoculum. Using molecular diagnostics, the population was confirmed as *M. hapla* by the North Carolina Nematode Diagnostics Laboratory (Raleigh, NC). Eggs were extracted from roots by placing roots in a 2% sodium hypochlorite solution, shaking for three min at 3000 rpm, then passing the solution over a 25-µm sieve to collect eggs. *M. hapla* egg densities were adjusted in water to achieve a concentration of 2500 eggs/mL.

Rootstock preparation

Corvallis, OR

Washington State Department of Agriculture-certified, pre-rooted, green-growing *Vitis* rootstocks (no scion) potted in soil-free, coconut coir-based medium, were acquired from Inland Desert Nursery (Benton City, WA). An initial shipment of Paulsen 1103 (1103P), Ruggeri 140 (140RU), Kober 5BB (5BB), Courderc 1616 (1616C), Malegue 44-53 (44-53M), Oppenheim #4 (SO4), and Schwarzmann (SW) was received on 13 May 2021. Own-rooted *V. vinifera* Chardonnay (susceptible control) was received on 20 May 2021. A second group of *Vitis* rootstocks including Richter 99 (99R), Minotaur, and *V. vinifera* Cabernet Sauvignon (susceptible control) was received on 24 June 2021.

Prosser, WA

All rootstocks tested at Corvallis, OR were also evaluated in Prosser, WA. *Vitis* rootstocks and own-rooted *V. vinifera* controls were collected as dormant cuttings (January 2022) from the Foundation Block at the Clean Plant Center Northwest (WSU Prosser IAREC). Dormant canes were pruned to a total cane length of four buds prior to rooting. Vines were rooted in 19-L buckets containing a potting soil/perlite mix (SunGro), wherein the vines were buried vertically in soil with the distal end facing down (i.e., inverted). Black polyethylene sheeting was cut to size and secured over the buckets, and the buckets were placed under heat lamps and maintained at temperatures no cooler than 10°C. Soil was maintained at 25 to 50% available water capacity (Natural Resources Conservation Services 2005). When roots were ~5 cm long (1 March 2022), cuttings were transferred to individual 4-L pots with the sandy-loam soil mix described above.

Experimental set-up

Corvallis, OR

Due to the green-potted vines arriving in separate shipments, two evaluations were conducted in Corvallis, OR. Prior to both evaluations, the vines were rinsed of their existing potting medium and transferred to 4-L pots containing the sandy-loam mix in preparation for nematode inoculation. There were five replicate vines of each rootstock arranged in a randomized design in a greenhouse under long-day conditions (16 hrs light) with 26/18°C day/night temperature cycling. *M. hapla* inoculations occurred seven days after vines were transplanted into pots (inoculations occurred 4 June and 22 July 2021). A total of 5000 eggs (2 mL egg solution) were pipetted directly into the vine root zone via 1-cm-deep depressions made in the soil around the vine. Inoculated vines were maintained in a greenhouse for 12 weeks under the conditions mentioned above. Vines were watered by hand when soil was dry and fertilized every other week with a 20-20-20 N-P-K water-soluble fertilizer prepared per manufacturer instructions (J.R. Peters).

Prosser, WA

Evaluations were conducted twice in Prosser; while occurring at the same time, they were spatially separated (separate benches at different locations in the greenhouse). There were five replicate pots of each rootstock in each of the two blocks of the experiment (n = 10) and rootstocks were arranged in a randomized design on a greenhouse bench. Rooted cuttings were planted into pots on 1 March 2022. Inoculation occurred as described above, 134 days later on 14 July 2022, after vines had at least five unfolded leaves and an established root system. Vines were inoculated as described above. Inoculated vines were maintained in a greenhouse for 12 weeks under natural light for an average of 13.6 hrs light and 32/18°C day/night temperatures. Vines were watered by hand when soil was dry to the touch. Miracle-Gro Water-Soluble All-Purpose Plant Food (Scotts Company LLC) was applied every other week following manufacturer instructions.

Nematode extraction

Vines were destructively harvested 12 weeks after M. *hapla* inoculation. After vines were removed from pots, the roots were pruned from each vine and soil was rinsed from roots. Roots from each vine were individually immersed in a 10% sodium hypochlorite solution and shaken for three minutes at 3000 rpm to extract eggs. The solution was then poured over stacked 88- and 25-µm sieves to separate and collect roots and eggs (Hussey and Barker 1973). Eggs were backwashed from the 25-µm sieve into 50-mL centrifuge tubes and dyed with 0.35% acid fuchsin (Byrd et al. 1972). Eggs were stored at 4°C until enumeration. A 1-mL aliquot of egg suspension was pipetted onto a 1-mL nematode counting slide and eggs were counted under a Leica DM IL inverted microscope (Leica Microsystems). After nematode extraction, roots were retained, wrapped in paper towels, dried at 70°C for five days, and weighed.

Statistical analyses

The data were expressed as M. *hapla* eggs/plant (pot), M. *hapla* eggs/g root, and reproduction factor (R_f = final egg density/initial egg density of M. *hapla* eggs) (Windham and Williams 1987). An $R_f > 1$ indicates that a nematode was able to complete their full life cycle on the host, while an $R_f = 0$ indicates they could not (no reproduction). This is generally interpreted as susceptible ($R_f > 1$) and resistant ($R_f = 0$); however, the R_f does not factor in the phenotype response of the host (i.e., tolerance to nematode feeding were $R_f > 1$, but the plant showed no symptoms of feeding). While not encapsulating the entire host status of the rootstock, R_f value does give a useful metric for growers and academics in determining and comparing the response of rootstocks to M. *hapla* parasitism.

Normality of data was assessed using Shapiro-Wilk W Test and was found to be not normally distributed (p = 0.0002, 0.0004, and 0.0004, respectively, for eggs/plant, eggs/g root, and R_f). Dry root weights, eggs/g root, and R_f values were then analyzed using a general linear mixed model to account for random effects and non-normal data. The restricted maximum likelihood method was used for all analysis, where replicates were random effects, and rootstock and experimental repeat was a fixed effect. Means separation and significant differences were compared post-hoc using Tukey's honest significant difference (significance at $\alpha < 0.05$). The experimental repeats at Prosser, WA were not significantly different from each other ($p = 0.23$) and data for those experiments were pooled. Statistical analysis was conducted using JMP software (16.0.0 SAS Institute, Inc.).

Results and Discussion

As expected, the V. *vinifera* controls Chardonnay and Cabernet Sauvignon had R_f values greater than 1, indicating susceptibility, and had significantly greater R_f values than all non-*vinifera* rootstocks (Tables 1 to 4). There were very few differences among the non-*vinifera* rootstocks. This aligns with a previous greenhouse experiment that used a different Pacific Northwest M. *hapla* population (Zasada et al. 2018), where own-rooted V. *vinifera* Riesling supported several orders of magnitude greater reproduction of M. *hapla* than other non-*vinifera* rootstocks, as defined by their R_f.

The same study also highlighted that while non-*vinifera* rootstocks have lower R_f values than V. *vinifera*, those non-*vinifera* rootstocks were not resistant to M. *hapla*. We saw this in our study as well: 44-53M had an $R_f > 1$. Similarly, SO4 had an $R_f > 1$ at the evaluation in Corvallis (Table 1), but the R_f was <1 during evaluations at Prosser (Table 3). This indicates that while SO4 is a poorer host for M. *hapla* than own-rooted *vinifera* varieties, it might still support nematode reproduction. Practically, while 44-53M and SO4 supported reproduction of M. *hapla*, the rate at which M. *hapla* would build up on these rootstocks could be significantly slower than on V. *vinifera*. Even with greater reproduction rates, the onset of visible decline induced by M. *hapla* can take several years in own-rooted V. *vinifera* (East et al. 2021). The other rootstocks tested, 5BB, SW, 1103P, 140RU, and 1616C, had $R_f < 1$, indicating that they are poor hosts for M. *hapla* and would likely perform well in a field setting.

Because R_f is a calculated value, it can be difficult to translate to field performance. Another way to consider rootstock susceptibility is to compare its R_f to that of a known variety that is susceptible and expresses an agronomically negative phenotype as a result. This comparison is summarized in Table 5, where the R_f is expressed as a percentage relative to the susceptible control used in that experiment. In this study, all the evaluated rootstock species hosted between 0.00 and 27.41% of the M. *hapla* relative to the susceptible control. Also included in Table 5 are the results of previous M. *hapla* ratings (Zasada et al. 2018) and a comparison of how those rootstocks would be rated on a scale of susceptible, moderately susceptible, moderately resistant, and resistant, as summarized previously for other plant nematode species (Ferris et al. 2012).

Table 1 Reproduction of *Meloidogyne hapla* on *Vitis* rootstocks and on own-rooted *Vitis vinifera* Chardonnay in Corvallis, OR.

Rootstock	Average *M. hapla* eggs/plant (pot)	Average root dry weight (g)	Average *M. hapla* eggs/g of root	R_f[a]
Chardonnay	673,280 a[b]	9.8 ab	69,773 a	134.7 a
44-53M	179,520 b	9.0 ab	21,911 b	34.7 b
SO4	12,920 b	10.5 a	1181 b	2.5 b
5BB	480 b	6.9 b	80 b	0.1 b
SW	0 b	9.2 ab	0 b	0.0 b
1103P	0 b	7.9 ab	0 b	0.0 b
140RU	0 b	8.2 ab	0 b	0.0 b
1616C	0 b	10.8 a	0 b	0.0 b
p values	<0.0001	0.0063	<0.0001	<0.0001

[a]R_f, reproduction factor values calculated as final population density/initial population density (5000 eggs).
[b]Different letters within a column denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's honest significant difference.

Table 2 Reproduction of *Meloidogyne hapla* on *Vitis* rootstocks and on own-rooted *Vitis vinifera* Cabernet Sauvignon in Corvallis, OR.

Rootstock	Average *M. hapla* eggs/plant (pot)	Average root dry weight (g)	Average *M. hapla* eggs/g of root	R_f[a]
Cabernet Sauvignon	6480 a[b]	9.8 ab	518.3 a	1.3 a
Minotaur	0 b	9.0 a	0 b	0.0 b
99R	320 b	10.5 b	29 b	0.08 b
p values	0.0001	0.026	<0.0001	<0.0001

[a]R_f, reproduction factor values calculated as final population density/initial population density (5000 eggs).
[b]Different letters within a column denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's honest significant difference.

Table 3 Reproduction of *Meloidogyne hapla* on *Vitis* rootstocks and on own-rooted *Vitis vinifera* Chardonnay in Prosser, WA.

Rootstock	Average *M. hapla* eggs/plant (pot)	Average root dry weight (g)	Average *M. hapla* eggs/g of root	R_f[a]
Chardonnay	87,312 a[b]	6.5	14,070 a	17.5 a
44-53M	7968 b	7.5	1073 b	1.6 b
SO4	696 b	7.3	99 b	0.1 b
5BB	0 b	6.0	0 b	0.0 b
SW	64 b	6.9	11 b	0.01 b
1103P	0 b	6.5	0 b	0.0 b
140RU	1304 b	6.2	205 b	0.3 b
1616C	32 b	6.1	5 b	0.006 b
p values	<0.0001	1.39	<0.0001	<0.0001

[a]R_f, reproduction factor values calculated as final population density/initial population density (5000 eggs).
[b]Different letters within a column denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's honest significant difference.

Table 4 Reproduction of *Meloidogyne hapla* on *Vitis* rootstocks and on own-rooted *Vitis vinifera* Cabernet Sauvignon in Prosser, WA.

Rootstock	Average *M. hapla* eggs/plant (pot)	Average root dry weight (g)	Average *M. hapla* eggs/g of root	R_f[a]
Cabernet Sauvignon	73,992 a[b]	8.8 a	8145 a	14.8 a
Minotaur	40 b	8.1 a	6 b	0.008 b
99R	40 b	6.3 b	6 b	0.008 b
p values	0.0033	0.003	0.0006	0.003

[a]R_f, reproduction factor values calculated as final population density/initial population density (5000 eggs).
[b]Different letters within a column denote significant differences among treatment means at $\alpha = 0.05$ using Tukey's honest significant difference.

In other winegrape-growing regions of the world, different *Meloidogyne* spp. than *M. hapla* are the primary concern for long-term vine root health (Gutiérrez-Gutiérrez et al. 2011). Several evaluations describe rootstock resistance and tolerance to *Meloidogyne* spp. parasitism. Adding to those studies, we found that 44-53M was able to host *M. hapla* development, but at a level that would be rated as "moderately resistant" (Table 5). Other studies rated 44-53M as susceptible to *Meloidogyne arenaria* pathotype Harmony A and *M. incognita* pathotype Harmony C (both virulent on Harmony rootstock) (Ferris et al. 2012). We found that SO4 could host *M. hapla* (Table 5), but at a level that was resistant relative to our *V. vinifera* control. Other studies have found SO4 to be susceptible to *M. arenaria*, *M. incognita*, and *Meloidogyne javanica*, with R_f values of 2.3, 2.3 and 1.7, respectively (Gutiérrez-Gutiérrez et al. 2011), while the R_f of *Meloidogyne ethiopica* on SO4 was 0.03 (Magunacelaya et al. 2017). We rated 5BB as resistant to *M. hapla*, consistent with its ratings against *M. arenaria* pathotype Harmony A, *M. incognita* pathotype Harmony C (Ferris et al. 2012), and *M. ethiopica* (Magunacelaya et al. 2017). We also rated SW as resistant to *M. hapla*, but its performance against other nematode *Meloidogyne* species is highly variable, as it is susceptible to *M. incognita*, *M. arenaria*, and the mixed *Meloidogyne* spp. population, and moderately resistant to *M. javanica* (McKenry et al. 2001). 1103P was resistant to *M. hapla* in this study, but when evaluated against *M. arenaria*, *M. incognita*, and *M. javanica*, it was rated as susceptible with R_f values of 2.4, 7.1, and 4.5, respectively (Gutiérrez-Gutiérrez et al. 2011). The same study also demonstrated that 140RU was susceptible to the same three *Meloidogyne* species, with R_f values of 2.5, 7.3, and 5.3, respectively, but when evaluated against *M. hapla* in this study, it had an average R_f of 0.15 and was classified as resistant (Table 5). 1616C was found to be partially resistant to *M. incognita* (Walker et al. 1994), and was also classified as resistant against *M. hapla* in this study (Table 5).

The greenhouse evaluations presented here were conducted following the same procedures in two locations: Prosser, WA and Corvallis, OR. Even with a consistent approach, there were variations in microclimate among the inoculated vines and the inoculum "batches" were different. In addition, there were subtle differences in the soils used at each location. Soil type plays an important role in nematode development, as nematodes are very sensitive to their surrounding environment (Martin and Sprunger 2023). These differences between the trials resulted in differences in R_f values within a rootstock between the two locations. However, the R_f differences relative to the susceptible control remained the same. This between-experiment variability is common, due to the diversity in genetics and environmental responsiveness seen between nematode species (Ferris and McKenry 1975, McSorley 2003, McKenry and Anwar 2006, Bogale et al. 2020). This inherent variability does not mean that greenhouse evaluations are not useful tools. Greenhouse evaluations can

Table 5 Summary of reproduction factor (R_f) of *Meloidogyne hapla* on *Vitis* rootstocks and on own-rooted *Vitis vinifera*. Table consists of data from this paper and from Zasada et al. (2018).

Rootstock	Average R_f [a]	R_f relative to a *V. vinifera* control (%)[b]	Resistance rating[c]	Reference
Chardonnay	**76.10**	-		**Current paper**
44-53M	18.15	27.41%	MR	Current paper
SO4	1.3	1.53%	R	Current paper
5BB	0.05	0.095%	R	Current paper
SW	0.005	0.013%	R	Current paper
1103P	0	0.00%	R	Current paper
140RU	0.15	0.24%	R	Current paper
1616C	0.003	0.005%	R	Current paper
Cabernet Sauvignon	**4331.65**	-		**Current paper**
Minotaur	3.0	0.05%	R	Current paper
99R	17.5	0.55%	R	Current paper
Riesling	**20.7**	-		**Zasada et al. 2018**
Salt Creek	0.0	0.094%	R	Zasada et al. 2018
Freedom	0.0	0.08%	R	Zasada et al. 2018
Harmony	0.0	0.05%	R	Zasada et al. 2018
St. George	0.0	0.0004%	R	Zasada et al. 2018
Riparia Gloire	0.6	0.02%	R	Zasada et al. 2018
101-14 MGT	0.6	0.02%	R	Zasada et al. 2018
3309C	0.0	0.0006%	R	Zasada et al. 2018
110R	0.0	0.0008%	R	Zasada et al. 2018
420A	0.0	0.0006%	R	Zasada et al. 2018

[a] R_f values calculated as final population density/initial population density.
[b] Bold text indicates the *V. vinifera* cultivar used as a susceptible control to calculate R_f percentages. Rootstocks compared to each susceptible control are listed below them.
[c] Resistance scale as described in Table 6 of Ferris et al. (2012).

be used to evaluate multiple genotypes relatively quickly. An important element for all greenhouse nematode evaluations is the inclusion of a highly susceptible control for comparison.

However, greenhouse evaluations do have one major limitation: they may not always be indicative of how well rootstocks perform under field conditions. The ability for nematodes to feed on grapevine roots, the usual measure in greenhouse studies, may not indicate that the vine will display reduced growth in response to that feeding (McKenry and Anwar 2006). For example, in this study, 1103P had an R_f of 0, indicating it was resistant. This rootstock supported *M. hapla* reproduction in the field over a number of years (East et al. 2021), but this development was still significantly lower than what was seen on field-grown Chardonnay. The scion on 1103P in that trial also did not display any decline symptoms as a result of *M. hapla* feeding.

In short-term greenhouse studies, simple metrics such as reproduction factor and number of eggs per gram of root are useful data points, but they cannot always capture whether a rootstock might impart a tolerant phenotype to its scion. Fundamentally, while a calculation such as R_f can be useful and has defined thresholds for easy classification, it still must be considered in the context of a known susceptible control to understand the long-term implications for rootstock adoption for *M. hapla* management. This highlights the importance of complementing short-term greenhouse screens with longer-term field trials when evaluating rootstock performance.

Conclusion

We evaluated nine commercially available *Vitis* spp. rootstocks in the greenhouse for their ability to host *M. hapla*. All non-*vinifera* rootstocks were poorer hosts for *M. hapla* than *V. vinifera*. The rootstock 44-53M could host *M. hapla*, although at a rate that was 27% that of the susceptible *V. vinifera* control. SO4 supported *M. hapla* reproduction in one of two experiments. While greenhouse evaluations are useful tools to quickly assess potential host status, field evaluations of *Vitis* spp. rootstocks should be conducted to better understand vine performance and ability to host *M. hapla* in vineyards over longer periods of time.

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