Developmental Dynamics of *Meloidogyne hapla* in Washington Wine Grapes

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Abstract

*Meloidogyne hapla* is the most prevalent plant-parasitic nematode in Washington state wine grape vineyards. Understanding the developmental dynamics of *M. hapla* can improve the timing of diagnostic sampling and nematicide application. Three *Vitis vinifera* vineyards in Washington were sampled March 2015 to March 2017 to determine the developmental dynamics of *M. hapla* by measuring second-stage juveniles (J2) in soil, eggs and adult females in roots, and fine root tips. A model of *M. hapla* J2 development based on soil growing degree days using a base temperature (Tb) of 0°C (GDDsoil) and a start date of 1 March was developed. This model was validated at two additional vineyards in Washington and was robust with $R^2$ values $> 0.74$. *M. hapla* has one generation per year and overwinters primarily as the J2 infective stage. Juvenile populations declined after 1 March, reaching their lowest density in early July and reaching a maximum density over the winter. *M. hapla* egg and root tip densities reached a maximum in early August. The number of females per root tip did not vary throughout the year. A single generation with defined peaks in J2 population densities will allow for specific timing of nematicide interventions.

Root-knot nematodes (*Meloidogyne* spp.) have been attributed to various vineyard maladies, including general vine decline and replant disorders (McKenry et al. 1994; Raski et al. 1973). Washington state is the second largest producer of wine grapes (*Vitis vinifera*) in the United States (NASS 2017). Although relatively young, the Washington wine grape industry will soon be facing a period of intensive replanting, as older vineyards become less productive and alternative varieties are wanted by winemakers. Eastern Washington, where over 99% of the state’s grape acreage is planted, is arid and requires irrigation for vineyard production. Water is strictly regulated in the state, and this limits the availability of new land for farming use. Thus, as vineyards age and new plantings become increasingly limited to replant sites, poor establishment of young vines, long term loss of productivity, and increased management costs owing to nematode parasitism (Nicot et al. 1999; Raski et al. 1965) will be key factors influencing long-term vineyard health and economic viability in the region.

Root-knot nematodes are obligate endoparasites of plant roots. They hatch from eggs in the soil as motile, infective second-stage juveniles (J2). Juveniles move within the water film on the surface of soil particles until they locate a root tip. J2 invade the plant root and move through the root before locating parenchyma cells in the root cortex (Eisenback 1985). There, J2 feed and elicit the modification of plant cortical cells to form “giant cells,” which are enlarged cytoplasm-dense feeding cells. The nematodes molt through two additional juvenile stages to become adults, which are usually female. Males may form instead of females under stressful conditions (Eisenback 1985). Females will continue to feed from the giant cells and lay eggs in a gellatinous matrix outside or just inside the root surface. Aboveground symptoms of root-knot nematode infestation can resemble the symptoms of water stress, or may cause lower yield, lower vigor, and premature leaf senescence. In new plantings, where young vines do not have an established root system, nematodes may severely stunt or kill the plants (Taylor and Sasser 1978).

In Washington state, the northern root-knot nematode, *Meloidogyne hapla* (Chitwood 1949), is present in 60% of surveyed vineyards (Zasada et al. 2012). *M. hapla* is the most common root-knot nematode north of 39°N in the United States (Taylor and Buhrer 1958) and is generally found between 34 and 47°N (Eisenback et al. 1981). Most other grape-growing regions are concerned with *Meloidogyne* species other than *M. hapla*, predominantly *M. arenaria*, *M. javanica*, and *M. incognita*. *M. hapla* and *M. chitwoodi*, the two species found in Washington state, regularly survive soil temperatures below 0°C, whereas *M. incognita*, *M. javanica*, and *M. arenaria* do not survive soil temperatures below 10°C and are absent from Washington state (Van Gundy 1985). In a 3-year microplot experiment in Washington, *M. hapla* readily reproduced on *V. vinifera*, although infection did not translate into a difference in vine biomass (Howland et al. 2015). In a greenhouse study, *M. hapla* reduced shoot and root dry matter of newly planted vines by 29 and 43%, respectively, compared with vines without nematodes (Schreiner and Zasada, unpublished data). The long-term impacts of *M. hapla* parasitism on vine health and productivity are not known. The critical threshold in Washington for wine grapes proposed by Santo (unpublished data) is 100 *M. hapla* J2 per 250 g of soil. *M. hapla* J2 density in soil may change over time, so optimizing sample timing to when J2 are near maximum in soil may help give an accurate assessment of risk and better inform management decisions.

Current diagnostic sample timing and nematicide application timing in grapes are based primarily on information from California, where the major tropical species *M. incognita*, *M. javanica*, and *M. arenaria* are the primary concern. These species and the temperate *M. hapla* differ in their activity at different temperatures, including reproduction, life cycle, and overwintering capability of life stages (Daulton and Nusbun 1961; Lyons et al. 1975; Melakeberhan et al. 1989; Thomason 1962; Vrain et al. 1978); therefore, it is not possible to directly draw management concepts (such as application timing) from these species to *M. hapla*. In the Pacific Northwest, the other temperate species is *M. chitwoodi*, which is an economically important parasite of potato (Ingham et al. 2018). This nematode has been shown to have three or more generation cycles per season.

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Vitis vinifera study. Sites included (i) a 30-year-old own-rooted vines. The life stage of M. hapla state vineyards is important to inform selection of sample times explored. (Wallace 1966). The developmental biology of M. hapla in Washington vineyards is unknown. The objectives of this study were (i) to characterize the life cycle of M. hapla during the vineyard growing season in eastern Washington, and (ii) to use that information to develop a model that would improve the timing of nematicide application for M. hapla management in northern temperate viticulture regions.

Materials and Methods

Experimental design and vineyard sampling. Three commercial vineyards, each with M. hapla, were selected for inclusion in the study. Sites included (i) a 30-year-old own-rooted Vitis vinifera ‘Riesling’ vineyard located near Mattawa, WA, that was sampled for model development in both 2015 and 2016 (Mattawa); (ii) a 15-year-old V. vinifera ‘Cabernet Sauvignon’ vineyard in Alderdale, WA, that was sampled in 2015 and used for model validation (Alderdale); and (iii) a 36-year-old V. vinifera ‘Riesling’ vineyard in Prosser, WA, that was sampled in 2016 and also used for model validation (Prosser). Within each vineyard, five 150-vine sampling plots were established. At each sampling date, 10 vines within each plot were sampled from 10 15-vine sections. Each individual vine was sampled at most four times over 2 years of data collection. One soil core per vine, 2.5 cm diameter by 45 cm deep, containing soil and roots, was collected from underneath the vine roots, where the majority of M. hapla are known to be concentrated (Howland et al. 2014). The 10 soil cores per plot were combined into a single composite sample, with five composite samples collected per site at each sampling date. Samples were collected weekly during the growing season (April to September) and monthly from October to March, for a total of 150 samples from each site per year. Vine phenology was noted at each sampling date. Sampling began in March 2015 and ended in March 2017.

M. hapla J2 and egg extraction and enumeration. A 250-g subsample of soil containing roots was processed to extract M. hapla J2 and roots from soil using a semiautomated elutriator (Seinhorst, 1962). Roots were captured on a 500-μm sieve and M. hapla J2 on a 37-μm sieve. The contents collected on the 37-μm sieve were backwashed into a 50-ml tube and the resulting liquid cleared of soil particles and debris using a centrifugation-flotation technique (Jenkins, 1964). Extracted M. hapla J2 were counted from a 1-ml aliquot of the cleared sample under a Leica DM IL inverted microscope (Leica Microsystems, Wetzlar, Germany). The remaining soil in the sample was processed using a semiautomated elutriator to recover all root material in the sample. M. hapla eggs were collected by removing eggs masses adhering to roots retained from the 500-μm sieve. Roots were gently washed on the sieve to remove debris, and large roots (>2 mm in diameter) were removed from the sample using tweezers. The remaining fine roots (<2 mm in diameter) were removed from the sieve, blotted dry, and weighed. Root samples were then placed into a 650-ml screw-top container containing a 10% hypochlorite solution and shaken for 3 min to extract eggs from egg masses (Hussey and Barker, 1973). The solution was then poured over stacked 88- and 25-μm sieves to catch roots and eggs, respectively. Fine roots were removed from the 88-μm sieve and stored in a fixative solution (10% acetic acid, 50% ethanol) for subsequent processing (see below). The 25-μm sieve containing eggs was backwashed into a 50-ml tube and dried with 0.35% acid fuchsin (Byrd et al., 1972) to facilitate counting. Eggs were counted from a 1-ml aliquot of the dyed solution under a Leica DM IL inverted microscope. A separate 50-g subsample of soil was also retained and dried in a soil oven at 70°C for 7 days to determine the gravimetric water content.

Fine root analysis and M. hapla female density determination. Preserved root samples containing small woody and fine feeder roots were placed on a 500-μm sieve and rinsed with water to remove root fixative. Roots were then spread across a large (15-cm diameter) Petri dish and examined under a stereoscope, and the fine roots with an intact cortex were cut from older roots as needed and transferred to a small (10-cm diameter) Petri dish with tweezers. The number of fine root tips in each sample was counted under a stereoscope. After counting root tips, the roots were further processed to stain females inside roots with acid fuchsin according to the method of Byrd et al. (1983). Destained roots containing females were spread across a large Petri dish, and females now stained red inside roots were counted under a stereomicroscope.

Collection of environmental data. Environmental data using weather stations closest to the sites was downloaded from AgWeatherNet (https://weather.wsu.edu; “Alderdale” at 1.3 km from Alderdale site; “McClure” at 22.6 km from Mattawa site, and “WSU Prosser” at 1.8 km from Prosser site). AgWeatherNet is a weather network maintained by Washington State University. The weather stations are equipped with Model 107 temperature probes (Campbell Scientific, Logan, UT) installed above ground (1 m) and 20.5 cm below the soil surface. They are also equipped with a rain sensor (Rain Gauge Tipping Bucket TR-5251; Texas Electronics, Dallas, TX). Data were collected in 15-min intervals, and daily averages were used in the development of the model (see below). These include average daily soil temperature, average daily air temperature, and average daily precipitation.

M. hapla developmental model construction. To develop the model, only data from the Mattawa site from 2015 and 2016 was used. The 2015 Alderdale and 2016 Prosser site data were used for validation; that is, to assess if the model developed from a single site (Mattawa) performed well at other vineyard sites (Alderdale and Prosser). Raw counts of M. hapla J2 per 250 g of soil were standardized to J2 per 250 g of dry soil by multiplying by the ratio of (mass of wet soil) to (mass of dry soil) for each sample. The five composite samples per collection date from each site were used to calculate the average J2 per 250 g of dry soil. To reduce variability in the data from the weekly sampling strategies, sampling dates were condensed by averaging weekly samples over 2-week periods. Samples that were collected on a monthly timescale were not condensed. The average number of J2 per 250 g of dry soil was then converted to a percentage of maximum density (percent max) per year, by dividing the density at each sampling time by the greatest average density in that year. This allowed for between-site and between-year comparisons of M. hapla population dynamics.

Model development used the percent max J2 as the dependent variable. Soil growing degree days (GDDsoil) was used as the independent variable, and this was calculated using the following degree-day equation:

$$GDD_{soil} = \sum_{i=1}^{n} (T_i - T_0)$$

where $T_i = \text{daily average soil temperature in degrees Celsius}$, $T_0 = \text{base temperature (multiple bases used, described below)}$, and $n = \text{1 day, accumulated from a start date, which was selected as 1 March}$. The base temperature was used for all instances where $T_i - T_0 > 0$. The case where $T_i - T_0 \leq 0$, the value 0 was used. $GDD_{soil}$ was calculated using $T_0$ of 0, 5, and 10°C. The minimum temperature for M. hapla development is likely between 8 and 10°C (Lahtinen et al. 1988; Tyler 1933). A final $T_0$ of 0°C was chosen based on data fitting described below and to more accurately capture potential development in a Washington temperate (cold-winter) climate.

Data sets were modeled in two parts: one modeling the decline in M. hapla J2 densities during the first half of the vine growing cycle and the second modeling the increase in M. hapla J2 densities in the
second half of the vine growing cycle. The transition point between the two curves of 1,800 GDD\text{soil} was chosen to be just before the lowest M. hapla J2 density. Data specific to each curve were transformed to improve model fit using a ln(y) function for each base temperature (T\text{b}) of 0, 5, and 10°C using the Fit Special function in Bivariate fit (Fit Y by X) platform in JMP 13.0.0 (SAS Institute, Cary, NC). Predicted values were calculated from each function of the form ln(y) = β + β1 · x, where y is percent max J2 and x is accumulated GDD\text{soil}. Linear regression of predicted values versus observed values was used to assess model fit, and R² and root mean squared error (RMSE) values were used to determine the best-fit model.

The models for both curves were then validated using data from the Alderdale and Prosser sites. These sites represented different cultivars of wine grape (Cabernet Sauvignon and Riesling), different years (2015 and 2016), and different areas of Washington State (Alderdale and Prosser). Linear regression of predicted values versus observed values was used to assess model fit. All statistical evaluations were done using JMP 13.0.0.

Results

Developmental dynamics of M. hapla in a Washington wine grape vineyard. In the Mattawa vineyard in 2015 and 2016, M. hapla appeared to complete a single generation per year. Seasonal trends were similar in both years for M. hapla J2 (Fig. 1A) and eggs (Fig. 1B). M. hapla J2 population densities were highest in early March before vine bud break (Fig. 1A). Densities of M. hapla J2 then declined from a high at 0 GDD\text{soil} (T\text{b} of 0°C, starting 1 March) to their lowest point at 2,379 GDD\text{soil} in 2015 (18 July) and 1,895 GDD\text{soil} in 2016 (3 July). This coincided phenologically with lag-phase (EL 35, extended BBCH scale; Lorenz et al. 1995) of berry development in both years. The BBCH scale is used to identify phenological stages of plant development; EL (Eichhorn-Lorenz) is an extension of that scale specifically designed for grapevine. Densities of M. hapla J2 then increased, reaching a maximum at 4,881 GDD\text{soil} (14 January) in 2015 and 4,291 GDD\text{soil} (26 October) in 2016 (Fig. 1A). Accumulation of GDD\text{soil} continued to a total of 5,029 GDD\text{soil} in 2015 and 4,744 GDD\text{soil} in 2016.

M. hapla egg densities reached a maximum at 3,069 GDD\text{soil} in 2015 (14 August) and 2,871 GDD\text{soil} in 2016 (12 August; Fig. 1B). The peak in egg production at 2,800 to 3,100 GDD\text{soil} (mid-August) began approximately when M. hapla J2 were at minimum density and was followed closely by the increase in M. hapla J2 density. The pattern of root tip density closely followed that of M. hapla egg density (Fig. 1C), with maximums at 2,739 GDD\text{soil} in 2015 (18 July) and 2,871 GDD\text{soil} in 2016 (12 August). When assessed on a per root tip basis, densities of adult females per root remained relatively unchanged over time, around 0.5 females per root tip (Fig. 1D).

M. hapla developmental model. The life cycle of M. hapla was best modeled as two separate curves. Curve 1 (spring decline curve), which accounted for the early-season decline in M. hapla J2 density, was best described using T\text{b} of 0°C for calculating GDD\text{soil}, as noted by a fit with the highest R² (0.86) and lowest RMSE (0.22), compared with the models using T\text{b} of 5°C (R² = 0.85, RMSE = 0.22) or 10°C (R² = 0.82, RMSE = 0.25). Curve 2 (fall increase curve), which modeled the late-season increase in M. hapla J2 density, was the opposite, because calculating GDD\text{soil} using T\text{b} of 0°C was less effective at describing M. hapla J2 densities over accumulated time/temperature (R² = 0.73, RMSE= 0.39) than 5°C (R² = 0.73, RMSE= 0.39) or 10°C (R² = 0.75, RMSE = 0.37) for the fall increase in J2 density. We chose to use 0°C as our T\text{b} for GDD\text{soil} calculations for model simplification because it was a better numeric fit for the early-season decline, despite being not as good a fit for the fall increase in M. hapla J2 as using 10°C (Fig. 2). Winter soil temperatures in the major grape growing regions of Washington state are often lower than 10°C but rarely drop below 0°C; all the subsequent GDD\text{soil} were calculated from T\text{b} of 0°C. The equation for curve 1 (spring decline) is

\[
\ln(y) = 4.3871599 - 0.0010693x \quad \text{for all GDD}_{\text{soil}} \text{ of 0 to 1,800},
\]

and the equation for curve 2 (fall increase) is

\[
\ln(y) = 1.5767586 + 0.000611x \quad \text{for all GDD}_{\text{soil}} \text{ > 1,800},
\]

where y is the percent max of M. hapla J2 and x is the accumulated GDD\text{soil} at T\text{b} of 0°C.

Inclusion of accumulated precipitation did not improve the model (data not shown). Because these are irrigated vineyards in an area with a yearly precipitation of 30 cm that falls predominately between October and April (WSU AgWeatherNet), the amount of soil water...
Discussion

Both the egg and J2 life stages of *M. hapla* had single annual peaks in eastern Washington wine grape vineyards, indicating that this nematode likely undergoes a single generation per year in this region. *M. hapla* J2 densities declined in the spring to a low in summer and then increased again to a maximum in the late fall to early winter. Although there is some constant egg and female presence over the winter, the major overwintering stage of *M. hapla* appears to be the J2 stage. *M. hapla* egg densities increased to a peak in early August and declined quickly as the new generation of J2 began to hatch in late summer to early fall. The density of root tips peaked at about the same time as egg densities. The number of females per root tip remained relatively constant across the year; it follows that with increased root tip production that overall number of females per vine was maximal at the same time as root tips were. The peak in root tips may serve to align *M. hapla* development because (i) there are more fine roots available for invasion and subsequent female development, and (ii) there may be an increase in egg production owing to increased carbon supply to fine roots. This may explain why there is a definitive peak in egg production and a subsequent peak in J2. We cannot definitively say when the point of greatest J2 root invasion is occurring; further research would address this question.

The pattern of root tip growth observed here (coinciding with the peak in *M. hapla* egg density in midsummer) contrasts with the commonly reported pattern of grapevine root development in which root development peaks at two times per growing season: once around bloom (spring) and again in the fall (Mullins et al. 1992). Other studies, however, that have reported similar results (Bauerle et al. 2008; Eissenstat et al. 2006), in which a single peak of root growth occurred in midsummer. Those studies were conducted on irrigated 'Merlot' on rootstocks in Oakville, CA, which has a similar hot and dry growing season. Schreiner et al. (2007) also observed a single peak in fine root length density in an own-rooted Cabernet Sauvignon vineyard under regulated deficit irrigation in Paterson, WA. Because fine roots are the primary means to take up water and nutrients, if they are compromised by nematodes, a reduction in vine vigor over time would be expected. The method of root collection used here, however, only

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Table 1. Linear regression statistics for predicted vs. observed percent maximum *Meloidogyne hapla* second-stage juveniles for curve 1 (GDD$_{soil}$ < 1,800) and curve 2 (GDD$_{soil}$ > 1,800) for the Prosser and Alderdale, WA, vineyard validation sites$^a$

<table>
<thead>
<tr>
<th>Location, curve</th>
<th>N</th>
<th>$R^2$</th>
<th>RMSE</th>
<th>Parameter</th>
<th>Parameter estimate</th>
<th>SE</th>
<th>$P$ value</th>
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</thead>
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<tr>
<td>Spring decline; GDD$_{soil}$ &lt; 1,800</td>
<td>7</td>
<td>0.83</td>
<td>15.5</td>
<td>Intercept</td>
<td>−14.8</td>
<td>13.7</td>
<td>0.33</td>
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<td>Fall increase; GDD$_{soil}$ &gt; 1,800</td>
<td>12</td>
<td>0.74</td>
<td>12.1</td>
<td>Intercept</td>
<td>15.4</td>
<td>7.2</td>
<td>0.058</td>
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<tr>
<td>Alderdale, WA</td>
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<tr>
<td>Spring decline; GDD$_{soil}$ &lt; 1,800</td>
<td>4</td>
<td>0.44</td>
<td>11.9</td>
<td>Intercept</td>
<td>15.8</td>
<td>18.8</td>
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<tr>
<td>Fall increase; GDD$_{soil}$ &gt; 1,800</td>
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<td>12.0</td>
<td>Intercept</td>
<td>22.6</td>
<td>6.2</td>
<td>0.0038</td>
</tr>
</tbody>
</table>

$^a$GDD$_{soil}$ = soil growing degree days at 20.5 cm depth; $N$ = sample size; $R^2 = R$-squared value; RMSE = root mean squared error; and SE = standard error of the parameter estimate.
captured fine roots in the wetted zone of drip irrigation and may not reflect potential root growth that occurred deeper in the soil profile. Our sampling method was specifically designed for the collection of roots for *Meloidogyne hapla* egg extraction and was not optimized for fully assessing entire root systems or their temporal dynamics.

The pattern of *Meloidogyne hapla* development reported here closely mimics that of *Meloidogyne chitwoodi* on potato in eastern Washington (Pinkerton et al. 1991), in that there is a low density of J2 in midsummer and an increase in the fall. *Meloidogyne chitwoodi* J2 densities were lowest from June to August and highest in September and October. Based on the infection of potato tubers, the authors interpreted the fall increase of *Meloidogyne chitwoodi* J2 on potato as arising from multiple generations. However, their data could also be interpreted as a single generation with multiple cohorts of J2 that invaded potato roots in two to three different waves. Both *Meloidogyne hapla* and *M. chitwoodi* are temperate species and must persist through subfreezing winters. Most *Meloidogyne* species found in warmer grape-growing regions can complete their life cycle within 30 days at soil temperatures typical for their regions (McKenry and Anwar 2006), resulting in potentially 12 generations and overlapping cohorts per year under optimal environmental conditions. In this situation, repeated nematicide applications would be required because an abundance of J2 would be present owing to multiple generations. This appears not to be the case for *Meloidogyne hapla* in eastern Washington vineyards. Indeed, this study indicates that more specific timing for treatment (and fewer annual treatments overall) may be possible to improve *Meloidogyne hapla* management.

Our data show that *Meloidogyne hapla* overwinters primarily as J2, which are then present to infect new root tips in the spring. This is in contrast to *M. incognita* and *M. arenaria*, for which eggs were more likely to survive low soil temperatures than were J2 (Jeger and Starr 1985). Mature females of *M. incognita* were also found to overwinter and produce eggs the resulting spring at budbreak in a California vineyard, whereas J2 did not survive the winter (Melakberhan et al. 1989). We found mature female *Meloidogyne hapla* in roots in winter; however, because egg numbers were low from fall to spring, these females appeared not to produce new eggs during this time. This means that *Meloidogyne hapla* J2 must persist in the soil for up to 6 months before infecting roots. *M. naasi*, another temperate species, is known to undergo a diapause in eggs that is broken by chilling (Van Gundy 1985), and retardation in hatching of *M. incognita* J2 from eggs has been described as dormancy (de Guiran 1979). There could be an environment-specific root host cue, such as increases in soil temperatures, that metabolises produced by grapevine roots as they come out of dormancy, that affects the activity of *Meloidogyne hapla* J2 in spring. Metabolic root activity of grapes resumes in spring, around when soil temperatures approach 7°C (Alllewelt 1965). All sites reached soil temperatures above 7°C by 7 March in both years. Further research on whether overwintering *Meloidogyne hapla* J2 exhibit signs of dormancy would also provide an indication of factors that trigger J2 to come out of dormancy. Such knowledge could help identify management practices that might enhance overwinter mortality.

The life cycle model developed here was able to capture most (44 to 86%) of the variation in the maximum *Meloidogyne hapla* J2 density across multiple years and sites using only GDD<sub>soil</sub> as the independent variable. Knowing that nematodes progress through their life stages based on heat units, using GDD<sub>soil</sub> rather than calendar date was chosen to model J2 densities. This also allows for the model to be useful in areas with varying site temperatures. Plotting J2 against GDD<sub>soil</sub> based on heat units, using GDD<sub>soil</sub> rather than calendar date was chosen to be the most suitable life stage of *Meloidogyne hapla*. A degree-day model based on the study from Pinkerton et al. (1991) has been developed and is used to inform management decisions for fumigation and nematicide applications in potato for *Meloidogyne chitwoodi* in the Pacific Northwest (Ingham et al. 2018). The model presented here for *Meloidogyne hapla* could be used to improve timing of sampling to determine if population densities are above a critical threshold, and to improve nematicide timing in wine grapes in Washington state. If nematodes are to be used for *Meloidogyne hapla* control, based on this model, the best timing is likely in fall. At this time, J2 densities in soil are increasing but have not yet reached a maximum. Further research is necessary to support any conclusions of nematicide timing.

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**Literature Cited**


