Host Status of *Rubus* Species and Hybrids for the Root Lesion Nematode, *Pratylenchus penetrans*

Inga A. Zasada¹

USDA-ARS Horticultural Crops Research Unit, 3420 NW Orchard Avenue, Corvallis, OR 97330

Patrick P. Moore

Washington State University–Puyallup, 2606 West Pioneer, Puyallup, WA 98371

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Abstract. The root lesion nematode, *Pratylenchus penetrans*, is a production-limiting pest in red raspberry, *Rubus idaeus*. Genetic resistance, as a tool to manage *P. penetrans* in raspberries, would reduce the impact of this nematode on raspberry productivity as well as reduce the need for pre- and/or post-plant chemical treatments to keep populations in control. The host status of 11 *Rubus* species (*R. coreanus*, *R. crataegifolius*, *R. innominatus*, *R. leucodermis*, *R. niveus*, *R. parviflorus*, *R. parvifolius*, *R. pungens*, *R. spectabilis*, *R. sumatranus*, and *R. odoratus*) for *P. penetrans* was evaluated in greenhouse studies. Additionally, hybrids of *R. cockburnianus*, *R. lasiostylus*, *R. niveus*, *R. phoenicolasia*, and *R. sumatranus* with *R. idaeus* ‘Meeker’ or ‘Tulameen’ were evaluated. The industry standard *R. idaeus* ‘Meeker’ was included in all trials as the control. Across trials, *R. niveus* and *R. leucodermis* were identified as poor hosts for *P. penetrans*. In addition, when another selection of *R. niveus* was evaluated in the final year of this study, it was also a poor host for *P. penetrans*. Among the remaining *Rubus* species materials tested, there were no consistent differences in host status for *P. penetrans*. It appears that *R. niveus* and *R. leucodermis* might be sources of resistance for *P. penetrans*. However, a hybrid between *R. niveus* and *R. idaeus* ‘Tulameen’ did not consistently support fewer *P. penetrans* than the ‘Meeker’ control. These results indicate that more research is needed to learn about the inheritance of the putative resistance.

Plant–parasitic nematodes were first reported in *Rubus* species in North America in the 1930s, when *Pratylenchus* species were associated with declining red raspberries (*Rubus idaeus* L.) (McElroy, 1992). Of the plant–parasitic nematodes associated with raspberry, *Pratylenchus penetrans*, the root lesion nematode, is the most economically important (McElroy, 1991). Feeding on roots by *Pratylenchus penetrans* (Cobb) Filipjev and Schuurmans Stekhoven can reduce the capacity of the plant to uptake nutrients and water. *Pratylenchus penetrans* was shown to cause 24% mortality of ‘Willamette’ red raspberry plants after 2 years (McElroy, 1977). In other studies, soil fumigation to control *P. penetrans* before planting red

raspberry dramatically increased yields (Seipp, 1986; Trudgill, 1986), and in one study, there was a 98% increase in yield of fumigated plots compared with non-fumigated plots containing *P. penetrans* in the first year of production (Bélair, 1991). Rate of decline will depend on the cultivar, but significant yield loss can occur when this nematode is left unchecked and population densities increase on raspberry plants.

Since the 1940s, growers have been able to manage plant–parasitic nematodes in raspberry by pre-plant soil fumigants and/or post-plant treatment with fenamiphos. In recent years, increased understanding of the negative environmental and health impacts of these compounds has led to restrictions or termination of their legal use. The registration for fenamiphos was cancelled in the United States [U.S. Environmental Protection Agency (EPA), 2008] and methyl bromide use in all U.S. commodities is in the process of being phased out. In addition, broadcast fumigation will become more burdensome with new EPA reregistration eligibility decisions (U.S. EPA, 2013); raspberry growers currently rely on a combination of 1,3-dichloropropene and chloropicrin for pre-plant fumigation. As a result, the raspberry industry is at a point in time when new, long-term, and economically viable

P. penetrans management strategies must be developed.

A key component of any integrated nematode management program is resistance. Having resistance as a tool to manage *P. penetrans* in raspberries would reduce the impact of this nematode on raspberry productivity as well as reduce the need for pre- and/or post-plant chemical treatments to keep this nematode in control. Although there are red raspberry breeding programs actively developing cultivars resistant to *Phytophthora rubi* and Raspberry Bushy Dwarf Virus, none are currently attempting to identify sources of resistance to *P. penetrans*, a significant production constraint to raspberry (Bélair, 1991; McElroy, 1977). Efforts have been made to evaluate raspberry cultivars for their reactions to *P. penetrans* (Bristow et al., 1980; Vrain and Daubeny, 1986). *Rubus idaeus* ‘Newburgh’, ‘Chilcotin’, ‘Skeena’, and ‘Canby’ were susceptible to *P. penetrans*, whereas the other tested cultivars, including ‘Latham’ and ‘Matsqui’, had varying levels of resistance to *P. penetrans* (Bristow et al., 1980). Vrain and Daubeny (1986) also screened several commercially available raspberry cultivars for their reaction to *P. penetrans*; ‘Nootka’ was the most resistant and ‘Glen Clova’ and ‘Chilcotin’ were the most susceptible; ‘Meeker’, ‘Skeena’, ‘Willamette’, and ‘Haida’ were intermediate in reaction. The most resistant material screened in this study was not from a *R. idaeus* cultivar, but rather from a Japanese accession of *R. crataegifolius*. These results indicate that resistance might be more readily identified in *Rubus* species other than raspberry.

The long-term goal of this research program is to identify a source of resistance in *Rubus* species to *P. penetrans* that can be incorporated into a red raspberry cultivar of commercial quality. The objective of the experiment described here was to determine the host status of *Rubus* species and hybrids to *P. penetrans*.

Materials and Methods

Accessions of *Rubus* species were obtained by the Washington State University breeding program and used in crossability studies in 1996 and 1997 (Moore and Trole, 1999). The hybrids were planted in the field and evaluated for fertility, and only the most fertile hybrids were retained in the breeding program. Species and hybrids that were still available plus additional *Rubus* species accessions were evaluated for host status for *P. penetrans* in 2010–12 (Table 1). Generally, there was only a single genotype representing a species or hybrid. *Rubus idaeus* ‘Meeker’ was included as a control in each trial (Table 1). During each year of the study, tissue culture plants (clones) of *Rubus* species and hybrids were initiated from surface-sterilized shoots at Washington State University, Puyallup Research & Extension Center, Puyallup, WA. The tissue culture plants were placed on rooting media and then rooted in a greenhouse. Approximately 3 months after

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¹To whom reprint requests should be addressed; e-mail inga.zasada@ars.usda.gov.

Table 1. Sources and lineages of *Rubus* species and hybrids evaluated for host status to *Pratylenchus penetrans*.

Entry	Source
<i>R. coreanus</i>	PI 618519
<i>R. crataegifolius</i>	Jogkal ²
<i>R. idaeus</i>	Meeker ³
<i>R. innominatus</i>	PI 553646
<i>R. leucodermis</i>	Holden Village, WA—collected in 2005 by P. Moore
<i>R. niveus</i>	PI 606461
<i>R. niveus</i> (WSU [*] 2263)	(PI 618524 × OP ^W) × OP
<i>R. parviflorus</i>	Puyallup, WA—collected in 1970 by B. Barritt
<i>R. parvifolius</i>	Carbondale, IL—collected in 1973 by J.W. Hall
<i>R. pungens</i>	PI 553849
<i>R. spectabilis</i>	Puyallup, WA—collected in 1970 by B. Barritt
<i>R. sumatranus</i>	PI 618429
<i>R. odoratus</i>	Cunningham Falls, MD—collected in 1960 by R. Converse
WSU 1414	<i>R. sumatranus</i> (PI 618429) × Meeker
WSU 1415	<i>R. sumatranus</i> (PI 618429) × Meeker
WSU 1474	Tulameen × <i>R. lasiostylus</i> (PI 553670)
WSU 1475	Tulameen × <i>R. phoenicolasius</i> (PI 553835)
WSU 1479	Tulameen × <i>R. cockburnianus</i> (PI 618443)
WSU 1673	<i>R. niveus</i> (PI 606461) × Tulameen

¹Hong et al. (1971); Vrain and Daubeney (1986).

²Fernández-Fernández et al. (2011).

³WSU = Washington State University raspberry breeding program, Puyallup, WA.

^WOP = open-pollinated.

rooting, the tissue culture plants were transported to USDA-ARS Horticultural Crops Research Unit, Corvallis, OR, where they were transplanted into 3.7-L pots containing a steam-pasteurized 1:2 sand:loam mix. Plants were allowed to establish in pots for ≈1 month before inoculation with *P. penetrans*. During this time period plants were fertilized with 20N–8.8P–16.6K (J.R. Peters, Allentown, PA) twice a week and were grown in a greenhouse under long-day conditions (16-h photoperiod) with 26/18 °C day/night temperatures.

The *P. penetrans* population used in this experiment was obtained from a raspberry field in Lynden, WA, and maintained on raspberry and mint (*Mentha piperita*) in the greenhouse. Inoculum was obtained by extracting *P. penetrans* from roots under intermittent mist for 48 h (Ingham, 1994). At inoculation, ≈1800 (2010) or 2500 (2011 and 2012) mixed-stage individuals of *P. penetrans* were inoculated into the root zone in 1-mL aliquots placed in five 2.5-cm deep holes made around the base of the plant. The holes were filled after inoculation. Each *Rubus* species or hybrid was replicated eight times in each of three trials and plants were arranged in a randomized block design. The experimental duration after nematode inoculation was ≈4 months, during which time the plants were pruned and staked to manage growth and fertilized and grown in a similar environment as described previously.

At termination, the above-ground portion of the plant was removed and discarded. The contents of the pot were emptied onto a tray where the roots were shaken free of soil and a 50-g soil sample was collected and placed on a Baermann funnel and nematodes were extracted for 5 d (Ingham, 1994). Roots were washed free of soil and *P. penetrans* was extracted from the root system emanating from the original root ball by intermittent mist for 1 week (Ingham, 1994). The roots

were then placed in a 70 °C oven for 1 week before determining dry weight. In 2010, the entire root system, including the original root ball, was weighed, whereas in 2011 and 2012, the original root ball was removed and only roots emanating from the original root ball were weighed. *Pratylenchus penetrans* recovered from soil and roots was enumerated using a dissecting microscope at 40× magnification and is expressed as number of *P. penetrans* per gram dry root and total number (soil plus root) of *P. penetrans* recovered per pot. In addition, reproduction factor (RF = final total *P. penetrans* population density/initial *P. penetrans* population inoculation density) values were calculated.

Root weight and nematode data were $\log_{10}(x + 1)$ transformed before analysis to control for heteroscedasticity; non-transformed data are shown. Trials were analyzed separately. Data were then analyzed for effects of block and plant type using a mixed linear model analysis of variance (ANOVA) with block as a random factor and plant type as a fixed factor. Means were separated using Tukey's least significant differences ($P < 0.05$) (JMP 9.1; SAS Institute, Cary, NC).

Results and Discussion

We evaluated a diverse set of *Rubus* species in an attempt to identify a source of resistance to *P. penetrans*, which could potentially be introgressed into a commercially acceptable raspberry cultivar. There was a clone × trial interaction in the ANOVA, and therefore trials are presented separately (Table 2); however, similar trends were observed across trials. In all trials, *R. niveus* and *R. leucodermis* consistently supported the fewest total *P. penetrans* and *P. penetrans*/gram root. The RF values for these species indicate that both are poor hosts for *P. penetrans* ($1 > RF > 0$; Ferris et al., 1993). In 2010, *R. sumatranus* and *R. odoratus*

supported similarly low *P. penetrans* population densities as *R. niveus* and *R. leucodermis*. All of these species supported lower population densities of *P. penetrans* than *R. idaeus* 'Meeker', the most commonly planted cultivar in Washington (Peerbolt Crop Management, 2013). When RF values were considered, only *R. innominatus* and *R. parviflorus* would be considered good hosts ($10 > RF > 1$ = good host) for *P. penetrans* in 2010 (Table 2). In 2011, *R. sumatranus* had similarly low *P. penetrans*/gram root as *R. niveus* and *R. leucodermis*; however, total *P. penetrans* was similar to those found in *R. idaeus* 'Meeker'. For *R. odoratus*, completely opposite results were observed in 2011 compared with 2010 with *R. odoratus* supporting the second highest total *P. penetrans* population densities of any *Rubus* species and considered a good host for *P. penetrans*. In 2012, the same *R. leucodermis* selection evaluated in 2010 and 2011 continued to be resistant to *P. penetrans*. In addition, another selection of *R. niveus*, WSU 2263, was a similarly poor host for *P. penetrans* as *R. niveus* PI 606461.

In 2010 and 2011, we evaluated the same selection of *R. crataegifolius*, 'Jogkal' (Hong et al., 1971) that Vrain and Daubeney (1986) evaluated for resistance to *P. penetrans*. Our finding regarding the host status of *R. crataegifolius* 'Jogkal' to *P. penetrans* was inconsistent across trials (Table 2). Vrain and Daubeney (1986) screened two *R. crataegifolius* selections, one from Japan and the other 'Jogkal' from Korea (Hong et al., 1971), both of which supported few *P. penetrans* with RF values less than 0.2. These combined results indicate that *R. crataegifolius* may be a useful source of resistance to *P. penetrans*.

There were few consistent trends in root weight, which would explain the ability of a *Rubus* species to serve as a good or poor host. In 2010, the average dry root weight across *Rubus* species was 9.33 (± 0.25) g. The *Rubus* species with the largest root systems were *R. odoratus*, *R. leucodermis*, *R. sumatranus*, and *R. idaeus* 'Meeker' with dry root weights ranging from 11.17 (± 0.43) g to 14.74 (± 0.9) g. *Rubus niveus* had the smallest root system, 7.03 (± 0.35) g, but was only different from the aforementioned species as well as *R. innominatus*. In 2011, the average dry root weight across *Rubus* species was 8.25 (± 0.44) g. Similar to 2010, *R. odoratus* had one of the largest root systems, 19.99 (± 2.12) g, which was not different from *R. innominatus* and *R. coreanus*. *Rubus parvifolius* had the smallest roots system, 3.56 (± 0.46) g, which was not different from the dry root weights of *R. niveus*, *R. spectabilis*, and *R. pungens*.

In addition to the *Rubus* species material, we evaluated a number of *Rubus* hybrids in 2011 and 2012 (Tables 1 and 2). The average dry root weights across hybrids were 6.18 (± 0.35) g and 4.08 (± 0.21) g in 2011 and 2012, respectively. The *R. phoenicolasius* (WSU 1475) and *R. cockburnianus* (WSU 1479) hybrids did not differ from *R. idaeus* 'Meeker' in population densities of *P. penetrans* in roots and total number in either trial.

Table 2. Host status of *Rubus* species and hybrids to *Pratylenchus penetrans* (Pp).

Selection ^a	2010				2011				2012			
	No. Pp/gram dry root	Total no. Pp (root + soil)	RF	No. Pp/gram dry root	Total no. Pp (root + soil)	RF	No. Pp/gram dry root	Total # Pp (root + soil)	No. Pp/gram dry root	Total # Pp (root + soil)	RF	RF
<i>R. idaeus</i>	55 a-d ^b	1,590 a-d	0.9 b-d	221 a-d	1,381 b-f	0.6 b-f	1,202 a	5,177 bc	1,202 a	5,177 bc	0.6 b-f	2.1 bc
<i>R. coreanus</i>	37 b-e	729 c-e	0.4 cd	128 c-f	1,772 a-e	0.7 b-e					0.7 b-e	
<i>R. crataegifolius</i>	30 de	801 c-e	0.5 cd	449 ab	2,951 abc	1.2 ab					1.2 ab	
<i>R. inominatus</i>	184 a	6,483 a	3.6 a	209 a-d	3,818 a	1.5 a					1.5 a	
<i>R. leucodermis</i>	7 ef	170 f	0.1 d	31 hi	236 i	0.1 gh	50 e	417 e	50 e	417 e	0.1 gh	0.2 e
<i>R. niveus</i> (PI 606461)	3 f	176 ef	0.1 d	16 i	80 j	0.1 h	97 bc	1,004 d	97 bc	1,004 d	0.1 h	0.4 e
<i>R. niveus</i> (WSU 2263)							125 de	749 de	125 de	749 de		0.3 e
<i>R. parviflorus</i>	167 a	2,993 ab	1.7 ab	298 ab	1,498 bcd	0.6 c-h					0.6 c-h	
<i>R. parvifolius</i>	23 c-e	1,466 b-d	0.8 b-d	61 f-h	610 f-i	0.2 e-h					0.2 e-h	
<i>R. pungens</i>	112 ab	1,722 abcd	1.0 b-d	336 a-c	1,176 c-f	0.5 c-g					0.5 c-g	
<i>R. spectabilis</i>	65 a-d	1,501 abc	0.8 b-d	624 a	2,841 a-c	1.1 ab					1.1 ab	
<i>R. sumatranus</i>	6 ef	203 ef	0.1 d	69 e-h	666 e-h	0.3 d-h					0.3 d-h	
<i>R. odoratus</i>	11 ef	345 de	0.2 d	200 b-e	3,639 ab	1.5 a					1.5 a	
WSU 1414							1,075 a	9,271 ab	1,075 a	9,271 ab		3.7 ab
WSU 1415							539 b	3,140 c	539 b	3,140 c		1.3 d
WSU 1474	69 a-d	1,309 b-d	0.7 b-d	41 g-i	307 hi	0.1 gh	382 bc	5,879 ab	382 bc	5,879 ab		2.4 bc
WSU 1475	93 a-c	2,500 a-c	1.4 bc	381 ab	2,168 a-d	0.9 a-c					0.9 a-c	
WSU 1479	53 a-d	2,797 a-c	1.6 bc	190 b-e	1,099 c-f	0.4 c-g					0.4 c-g	
WSU 1673				75 fgh	337 g-i	0.1 g-h	2,697 a	13,399 a	2,697 a	13,399 a		5.4 a

^aDescriptions of selections can be found in Table 1.^bData were $\log_{10}(x + 1)$ transformed before analysis; non-transformed data are shown. Means within a column followed by the same letter are not significantly different according to Tukey's least significant differences at $P < 0.05$ ($n = 8$).

The *R. lasiostylus* (WSU 1474) and *R. sumatranus* (WSU 1414 and 1415) hybrids supported fewer *P. penetrans* than *R. idaeus* 'Meeker' in 2011 but high populations in 2012. WSU 1673, a selection from the cross of *R. niveus* × *R. idaeus* 'Tulameen', supported few *P. penetrans* in 2011 but very high densities in 2012. These combined results indicate that more research is needed to learn about the inheritance of the putative resistance.

The variability we observed across trials in final population densities of *P. penetrans* compared with initial population densities that have been reported by others. In our study, RF values for *P. penetrans* on 'Meeker' were $0.9 (\pm 0.2)$, $0.6 (\pm 0.1)$, and $2.1 (\pm 0.2)$ in 2010, 2011, and 2012, respectively. When Vrain and Daubeny (1986) considered the host status of *R. idaeus* 'Willamette' to *P. penetrans* in greenhouse trials across years, RF values were 2.3, 0.82, and 0.86. The host status of 'Meeker' to *P. penetrans* also varied across experimental venues with RF values of 1.7 and 0.20 in greenhouse and in microplots experiments (Vrain and Daubeny, 1986) and 1.3 in another greenhouse trial (Bristow et al., 1980). This observed variability across trials could be the result of a difference in environmental conditions and methodologies used in the experiments. *Pratylenchus penetrans* reproduces over a wide range of temperatures with a generation (egg to egg) requiring 46, 38, 28, 26, and 22 d at 17, 20, 30, 25, and 27 °C, respectively, under controlled conditions (Mizukubo and Adachi, 1997). The duration of three different experiments evaluating host status of *Rubus* species materials to *P. penetrans* was ≈ 100 d (Vrain and Daubeny, 1986), 110 d (Bristow et al., 1980), and 120 d (this study). Depending on the temperatures at which these experiments were conducted, anywhere from 2.6 to 5.5 *P. penetrans* generations could have occurred based on constant temperatures of 17 and 27 °C, respectively (Mizukubo and Adachi, 1997). Another difference could be initial inoculation densities used across experiments. In the aforementioned studies, initial inoculation densities ranged from 2.2 to 4.0 *P. penetrans*/g soil (Vrain and Daubeny, 1986), 5.0 *P. penetrans*/g soil (Bristow et al., 1980), and 0.7 to 1.0 *P. penetrans*/g soil in our study. However, inoculation density does not seem to be a plausible explanation for the variation because the lowest RF value reported for 'Willamette' by Vrain and Daubeny (1986), 0.82, occurred when plants were inoculated with the highest initial population density (4.0 *P. penetrans*/g soil). In fact, in our study, when the same initial inoculation density was used in 2011 and 2012 (1.0 *P. penetrans*/g soil), RF values were 0.6 and 2.1 on *R. idaeus* 'Meeker', respectively.

Pratylenchus penetrans is a significant production constraint in raspberry and having a commercially acceptable cultivar with resistance to *P. penetrans* would be a useful tool for raspberry growers to combat this pest. Our research demonstrates that some

sources of *R. niveus* and *R. leucodermis* are poor hosts for *P. penetrans* and may provide a source of resistance genes that can be transferred to red raspberry. There was minimal sampling of variability within *Rubus* species and resistance may be present in specific accessions of other species. In addition, our results indicate that more research is needed to learn about the inheritance of the putative resistance. To truly understand the potential of *R. niveus* and *R. leucodermis* as sources of resistance, these species should be evaluated in the field.

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