Population Growth of *Pratylenchus penetrans* on Winter Cover Crops Grown in the Pacific Northwest¹

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Abstract: Population growth of Pratylenchus penetrans on 13 fall and winter cover crops was studied in the greenhouse and field. All crops except oat cv. Saia supported population growth of P. penetrans in greenhouse experiments, although the response of P. penetrans to oat cv. Saia varied considerably between experiments. The mean ratio of the final population density/initial population density (Pf/Pi) after 16 weeks for P. penetrans added to a greenhouse soil mix was 0.09, whereas Pf/Pi values after 10 weeks for two experiments with naturally infested soil were 0.95 and 2.3. Although P. penetrans increased on sudangrass cv. Trudan 8 and sudangrass × sorghum hybrid cv. SS 222, subsequent incorporation of sudangrass vegetation into soil reduced P. penetrans populations to preplant levels. Field experiments were inconclusive but suggested that oat cv. Saia or rye cv. Wheeler may be better choices for winter cover than weed-contaminated fallow or other crops on P. penetrans-infested sites in the Pacific Northwest.

Key words: cereal crops, disease management, host range, nematode, oat, pest management, population dynamics, *Pratylenchus penetrans*, soil-borne pathogens, sudangrass, wheat.

Pratylenchus penetrans (Cobb) Filipjev and Schuurmans Stekhoven is an important pathogen of perennial small-fruit and treefruit crops in the Pacific Northwest (Mc-Elroy, 1972). Fumigation is the method most widely used to reduce population densities of P. penetrans before small-fruit and tree-fruit crops are planted in infested fields. Fenamiphos, a non-fumigant nematicide, can reduce *P. penetrans* population densities in established plantings of small-fruit (Lolas et al., 1992; Vrain and Keng, 1986) and treefruit (Santo and Wilson, 1990) crops. Currently there are no effective nonchemical methods for suppressing P. penetrans populations in small-fruit and tree-fruit crops. Crop rotation is not a viable option for managing *P. penetrans* because this nematode is a parasite of all commercially valuable crops grown in the region. P. penetrans population densities are reduced by 1 to 2 years of weedfree fallow, but weed-free fallow requires frequent tillage or herbicide application and is likely to be detrimental to soil fertility and structure. In addition, growers lose revenue when land is out of production.

The presence of cover crops during winter, between successive crops or between rows of established perennial crops, is an important component of sustainable agricultural practices in the Pacific Northwest. Winter cover crops reduce erosion, leaching of nutrients, and weed growth, and also improve soil fertility and structure.

Cover crops that are nonhosts for *P. pen*etrans and that can be grown during late fall or winter in the Pacific Northwest would be useful to suppress the nematode. Previous research indicated that oat cultivars Saia and OAC Woodstock are nonhosts for *P. pen*etrans (Townshend, 1989; Vrain et al., 1996), whereas other cultivars of oat are reported to be good hosts (MacDonald and Mai, 1963; Townshend and Potter, 1976). Some studies have indicated that sudangrass is not a host for *P. penetrans* (Dunn and Mai, 1973; MacDonald and Mai, 1963), although it was reported to be a host in one study (Marks and Townshend, 1973).

The decomposing green vegetation of some crops can be antagonistic to plantparasitic nematodes. Amendment of soil with green vegetation of sudangrass (Mojtahedi et al., 1993a) and oilseed rape (Mojtahedi et al., 1991, 1993b) reduced popula-

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tions of *Meloidogyne hapla* and *M. chitwoodi*. Oilseed rape is a host for *P. penetrans* (Mac-Donald and Mai, 1963; Webb, 1996). However, laboratory and field studies indicated that incorporation of oilseed rape green manures can reduce populations of *P. penetrans* (Porter et al., 1998). Rye is also a host for *P. penetrans* (Dunn and Mai, 1973; Marks and Townshend, 1973; Olthof, 1980; Townshend and Potter, 1976), but decomposing rye vegetation may be toxic to the nematode (Patrick et al. 1965).

The primary objective of our research was to assess population growth of *P. penetrans* on a variety of potentially useful winter cover crops under greenhouse and field conditions. We also studied effects of incorporating chopped vegetation of the same cover crops on survival of *P. penetrans* in soil.

MATERIALS AND METHODS

Greenhouse experiments: The first greenhouse experiment was conducted in fall 1991. Sixteen replicate 14-cm-diam. plastic pots were planted with strawberry (Fragaria chiloensis cv. Totem), marigold (Tagetes erecta cv. Tangia), barley (Hordeum vulgare cv. Steptoe), oat (Avena sativa cv. Saia), sudangrass (Sorghum sudanense cv. Trudan 8), or oilseed rape (Brassica napus cv. Humus). The soil mix was a steam-pasteurized 1:2 mixture of washed river sand and sandy loam soil. Each cover crop was planted at 20 seeds/pot, except marigold and strawberry, which were planted with 8 seedlings/pot or 1 crown/ pot, respectively. At the time of planting, the soil in each pot was infested with 1,000 P. penetrans (mixed stages) extracted from the roots of mint (Mentha \times piperita). The pots were placed in a completely randomized arrangement in a greenhouse, and the crops were grown at 18 to 24 °C with supplemental lighting to provide a 12-hour photoperiod.

After 8 and 12 weeks, the vegetation in eight replicate pots of each cover crop was clipped to a height of 10 cm to simulate mowing. The nematode populations in all pots were assessed 16 weeks after planting. Roots were shaken vigorously to remove bulk soil, rinsed, blotted, weighed, and cut into 4-cm segments, and nematodes were extracted from a 10-g subsample of the roots. The soil was mixed, and nematodes were extracted from a 100-g subsample from each pot.

The second and third greenhouse experiments were conducted in fall 1994 and spring 1995, respectively. The soil used in these experiments was a Camas sandy loam, naturally infested with *P. penetrans*, from a field of mint on the Willamette River floodplain near Corvallis, Oregon. The soil was collected one day before planting, sieved through a 12-mm-aperture screen to remove stones and plant debris, and mixed with a rotary cement mixer. Three liters of soil were placed in each 20-cm-diam. clay pot.

Eleven cover crops and an unplanted fallow treatment were evaluated in the second experiment. The cover crops included oilseed rape cv. Humus, vetch (Vicia angustifolia cv. Cahaba), hairy vetch (Vicia villosa), sudangrass cv. Trudan 8, sudangrass × sorghum hybrid cv. SS 222, barley cv. Steptoe, barley cv. Micah, rye (Secale cereale cv. Wheeler), oat cv. Amity, oat cv. Saia, and Strawberry cv. Totem. Fourteen pots were planted with each cover crop. All cover crops were planted at 10 seeds/pot except for strawberry with 1 crown/pot. The pots were arranged on a greenhouse bench in randomized complete blocks, with two pots of each cover crop and the fallow treatment in each of seven blocks. The initial nematode population density was determined prior to planting from 100-cm³ subsamples of composited 10-g samples taken from each pot in each block (24 samples/block).

The plants were thinned after germination to 6 plants/pot, and each pot was fertilized with a slow-release fertilizer (15 N:15 P:15 K) at the equivalent of 100 kg N/ha. The crops were grown for 10 weeks at 20 to 22 °C, with supplemental lighting to provide a 12-hour photoperiod. After 10 weeks, one of two pots of each treatment in each block was harvested. Shoots were clipped at the soil surface and weighed. Roots were shaken vigorously to remove adhering bulk soil, weighed, and cut into 2-cm segments. A 10-g root sample was used for nematode extraction. The soil was mixed, and 100 ml was removed for nematode extraction. The shoots were cut into 4-cm fragments, mixed with remaining roots into the soil, and returned to the pot. The pots of soil were kept moist but not waterlogged. After 6 weeks of incubation, the contents of each pot were mixed and another 100-ml sample of soil removed for nematode extraction. After 20 weeks, the remaining plants were weighed, nematode samples taken, and green vegetation incorporated as described for the 10week harvest.

The third experiment was set up in eight blocks, each containing one fallow pot and one pot of each of the following nine cover crops: rapeseed cv. Dwarf Essex, faba bean (Vicia faba cv. Banner), sudangrass cv. Trudan 8, sudangrass × sorghum hybrid cv. SS 222, barley cv. Micah, rye cv. Wheeler, oat cv. Amity, oat cv. Saia, and strawberry cv. Totem. The plants were grown under the same light and fertilizer conditions as for the second experiment. After 10 weeks of growth, the plants were weighed, nematode samples were taken, and green manures were incorporated as described for the 1994 experiment. Nematode populations in soil were assessed again after 6 weeks of incubation with the green manures.

For all greenhouse experiments, Baermann funnels and an intermittent mist chamber were used to extract nematodes from soil and roots, respectively (Ingham 1994). Numbers of *P. penetrans* in each root and soil sample were counted. Nematode population densities were transformed to log(x) values prior to final analyses, and differences among crops were evaluated with blocked one-factor analysis of variance models. Separate analyses were conducted for nematode populations before and after green manure incorporation. The percent reduction in nematode populations after green manure incorporation was calculated for each pot, and the data were analyzed with a blocked analysis of covariance. Cover crops were the classification variable, and biomass of incorporated green manures was the covariate. For all data sets, mean comparisons were conducted with Fisher's protected least significant difference (LSD) calculated at P = 0.05. Strawberry, which is a good host for *P. penetrans*, and the fallow treatment were used as standards for interpretation of effects of the cover crops.

Field plots: The plots were located in a commercial field naturally infested with P. penetrans, near Gresham, Oregon. The soil was a sandy loam, planted with strawberry from spring 1989 through summer 1993. The first experiment was initiated in September 1993. Rye cv. Wheeler, oat cv. Saia, sudangrass × sorghum hybrid cv. SS 222, sudangrass cv. Trudan 8, oilseed rape cv. Humus, and an unplanted fallow treatment were established in five replicate 3×6 -m plots arranged in randomized complete blocks. The cover crops were broadcastseeded at the following densities (in kilograms of seed per hectare): rye, 196; oat, 106; sudangrass cv. SS 222, 45; sudangrass cv. Trudan 8, 34; oilseed rape, 10 kg/ha. The unplanted fallow plots were colonized by indigenous winter weeds and are hereafter referred to as the weedy fallow treatment. Fenamiphos was surface-applied at 8.4 kg a.i./ha to all plots in January 1994. The cover crops were disc-incorporated in May, and strawberry was planted 2 weeks later.

Nematode populations in plots of the cover crops were determined at the time of planting (soil only), and in soil and roots in November 1993 and April 1994. Nematode populations in soil and roots of strawberry plants were determined in July 1994. At each sample date, eight 2.5-cm-diam. × 30-cmdeep cores were taken from each plot and combined into a single sample representing the plot. Root samples (approximately 25 g) were collected from five arbitrarily selected plants from the center of each plot. Nematodes were extracted from 250 g soil from each plot by wet-sieving sucrose-centrifugation and from roots in a mist chamber (Ingham, 1994; Jenkins, 1964).

The second experiment was initiated in fall 1994. Five replicate 3×6 -m plots of eight cover crops were established in randomized complete blocks, adjacent to the first experiment. The treatments were rye cv. Wheeler, oat cv. Saia, sudangrass cv. SS 222, sudan-

grass cv. Trudan 8, rapeseed cv. Humus, meadowfoam (Limnanthes douglasii), weedy fallow (plots allowed to become colonized by weeds), and a weed-free fallow (plots kept free of weeds by hand-weeding). Both cultivars of sudangrass were planted in August 1994 at twice the planting densities used in the first experiment. The remaining cover crops were planted in October. Seeding densities for rye, oat, and rapeseed were the same as for the first experiment, and meadowfoam was planted at 28 kg seed/ha. Above-ground biomass of the cover crops or weeds was determined in three plots of each treatment in April 1995. Quadrats (0.5 m²) were marked in each plot, and the vegetation was clipped at the ground surface, dried, and weighed. The cover crops were disc-incorporated in April 1995. In May, fenamiphos was surface-applied at 10.2 kg a.i./ha to half of each plot, as a strip covering a randomly chosen half of each block of the experimental plots, resulting in five plots of each of 16 cover crop × fenamiphos treatment combinations. Strawberry was planted 11 days after fenamiphos application.

Soil samples were taken from all plots at the time of planting sudangrass (August) and at the time of planting the remaining cover crops (October) as described for the first experiment. In January and April, six 7.5-cm-diam. \times 15-cm-deep cores were taken from each plot and combined into a single composite sample. These cores were more shallow and larger in diameter than cores taken on previous sample dates. The use of larger diameter cores made it possible to obtain samples of roots in proportion to their abundance in the soil. Roots were picked from each soil sample and weighed. Separate root samples were taken from the three dominant weeds in the weedy fallow plots in April. In June the soil and roots of strawberry plants were sampled as described for the first experiment. Nematodes were extracted from roots and soil as described for the greenhouse experiments.

For all sample dates except June 1995, a blocked one-way analysis of variance model was used to determine the effects of cover crops on nematode population densities in roots, soil from which roots had been removed, and soil containing roots (January and April 1995 samples). Data from the June 1995 sample date were analyzed with a blocked, two-factor split-plot analysis of variance model. Fenamiphos plots were designated as whole plots, and cover crops were subplots within the fenamiphos plots. Nematode densities were transformed to log (x + 1) values before final analyses. Fisher's protected least significant difference (LSD) calculated at P = 0.05 was used to compare means.

RESULTS

Greenhouse experiments: In the first experiment, *P. penetrans* population densities after 16 weeks were lower in pots of unclipped marigold, oat, barley and sudangrass than in pots of strawberry (Table 1). Clipping increased *P. penetrans* population densities in pots of sudangrass and decreased population densities in pots of oat.

In the second and third experiments, *P. penetrans* population densities increased on all cover crops with the exception of oat cv.'s Saia and Amity grown for 10 weeks in the second experiment (Tables 2,3). Population densities on Oat cv. Saia were lower than on strawberry in the second and third experiments. Population densities at the time of

TABLE 1. Numbers of *Pratylenchus penetrans* per 1.5liter pot (total of soil and root populations) in pots of clipped and unclipped cover crops grown in a greenhouse for 16 weeks. The initial population was 1,000 *P. penetrans*/pot. The vegetation was clipped at 8 and 12 weeks after planning.

| Cover crop | Unclipped | Clipped |
|--------------------------|----------------------|----------|
| Totem Strawberry | 2,985 a ^a | _ |
| Dwarf Essex oilseed rape | 4,332 a | 3,765 a |
| Trudan 8 sudangrass | 509 bB | 1,743 aA |
| Steptoe barley | 500 b | 209 b |
| Saia oat | 86 cA | 26 cB |
| Tangia marigold | 6 d | 1 d |
| 0 0 | | |

^a Means (n = 8) within a column labelled with the same lowercase letter are not significantly different according to Fisher's Protected LSD at P = 0.05 performed on data transformed to log(x) values. Means of untransformed data are given. Means within a row labelled with different uppercase letters are significantly different according to Fisher's Protected LSD at P =0.05.

| | 10 week | s' growth | 20 weeks' growth | | |
|---------------------|------------------------|--------------------|-------------------|--------------------|--|
| Cover crop | Pre-incorporation | Post-incorporation | Pre-incorporation | Post-incorporation | |
| Hairy vetch | 57,762 ab ^a | 17,014 a | 236,582 a | 82,277 a | |
| Wheeler rye | 13,599 cd | 6,249 bcde | 62,090 bcd | 53,306 ab | |
| Steptoe barley | 19,978 bcd | 4,063 ef | 78,263 bc | 44,507 ab | |
| Humus oilseed rape | 29,826 abc | 12,433 ab | 71,452 bc | 33,771 ab | |
| Micah barley | 20,292 abcd | 3,956 ef | 95,428 b | 32,100 ab | |
| Cahaba vetch | 63,260 a | 9,819 bc | 85,688 bc | 24,004 bc | |
| Saia oat | 13,376 d | 2,935 ef | 18,193 e | 11,031 c | |
| Totem Strawberry | 15,233 cd | 5,914 cdef | 67,686 cd | 10,603 c | |
| Amity oat | 12,688 d | 4,444 def | 34,462 de | 10,183 c | |
| Trudan 8 sudangrass | 21,877 abcd | 4,269 cdef | 49,585 bcd | 5,893 d | |
| SS 222 sudangrass | 18,315 bcd | 6,690 bcd | 52,143 cd | 4,140 d | |
| Fallow | 4,885 e | 2,721 f | 7,637 f | 3,090 d | |

TABLE 2. Numbers of *Pratylenchus penetrans* per 3-liter pot (total of soil and root populations) before and 6 weeks after incorporation of green manures, from cover crops grown in a greenhouse for 10 or 20 weeks in fall 1994. The initial population was 14,000 nematodes/pot.

^a Means (n = 7) within a column labelled with a common letter are not significantly different according to Fisher's Protected LSD at P = 0.05 performed on data transformed to log(x) values. Means of untransformed data are given.

vegetation incorporation were greater in pots of all cover crops than in fallow pots.

After incubation with vegetation of crops grown for 10 weeks in the second experiment, *P. penetrans* populations in pots of rye, sudangrass cv. SS 222, vetch cv. Cahaba, hairy vetch, and rapeseed cv. Humus were significantly greater than in fallow pots (Table 2). Sudangrass cultivars Trudan 8 and SS 222 grown for 20 weeks had significantly smaller post-incorporation popula-

TABLE 3. Numbers of *Pratylenchus penetrans* per 3-liter pot before and 6 weeks after incorporation of green manures of potential winter cover crops grown in a greenhouse for 10 weeks in spring 1995. The initial population was 2,571 nematodes/pot.

| Cover crop | Pre-incorporation | Post-incorporation |
|------------------------|-----------------------|--------------------|
| Banner fava bean | 85,580 a ^a | 15,175 a |
| Micah barley | 36,798 abc | 2,826 b |
| Wheeler rye | 69,367 ab | 2,017 b |
| Dwarf Essex | 18,365 cdefg | 1,913 b |
| oilseed rape | | |
| Amity oat | 34,780 bcde | 1,498 b |
| SS 222 sudangrass | 26,853 bcdef | 1,058 b |
| Trudan 8 sudangrass | 15,537 defgh | 771 bc |
| Saia oat | 5,914 h | 770 bc |
| Totem Strawberry | 28,491 bcd | 378 с |
| Fallow | 698 i | 209 d |
| | | |

^a Means (n = 8) within a column labelled with a common letter are not significantly different according to Fisher's Protected LSD at P = 0.05 performed on data transformed to $\log(x)$ values. Means of untransformed data are given. tion densities of *P. penetrans* than strawberry and were the only crops with population densities similar to those in fallow pots (Table 2). In the third experiment (Table 3), post-incorporation population densities in pots of all cover crops except sudangrass cv. Trudan 8 and oat cv. Saia were greater than in pots of strawberry, and all crops had post-incorporation population densities greater than in fallow pots.

Analysis of covariance indicated that the percent reduction in populations of P. penetrans after green manure incorporation did not vary among cover crops grown for 10 weeks in the second experiment (P = 0.16)but did differ among cover crops grown for 20 weeks in the second experiment (P =0.002) and 10 weeks in the third experiment (P = 0.002). However, the rankings of cover crops were different for both harvests of the second experiment and the third experiment (Table 4). The biomass of incorporated vegetation differed among cover crops in both experiments (Table 5) but did not affect the percentage reduction in nematode populations when considered as a covariate in the analyses of covariance (P =0.62, 0.95, and 0.61 for 10-week and 20-week harvests of the second and third experiments, respectively).

Field plots: In the first experiment, sudangrass died in October and the weedy fallow

| | Fall exp | | |
|--------------------------|----------------------|----------|-------------------------------|
| Cover crop | 10 weeks | 20 weeks | Spring experiment 10 weeks |
| Strawberry | 44 abcd ^a | 65 ab | 102 a |
| Micah barley | 82 a | 62 ab | 91 a |
| Wheeler rye | 37 abcd | -6 d | 91 ab |
| Amity oat | 52 abcd | 60 ab | 90 ab |
| SS 222 sudangrass | 38 abcd | 82 ab | 87 ab |
| Saia oat | 75 ab | 32 bcd | 86 ab |
| Trudan 8 sudangrass | 79 ab | 86 a | 84 ab |
| Dwarf Essex oilseed rape | _ | | 80 ab |
| Banner fava bean | _ | | 69 ab |
| Cahaba white vetch | 73 abc | 64 ab | — |
| Hairy vetch | 28 bcd | 63 ab | _ |
| Humus oilseed rape | 20 d | 48 abc | _ |
| Steptoe barley | 81 a | 14 cd | — |
| Fallow | 29 с | 54 abc | 56 b |

TABLE 4. Least-squares estimates (from analysis of covariance) of mean percent reduction in populations of *Pratylenchus penetrans* during 6 weeks' incubation in soil with chopped vegetation of various cover crops.

^a Values within a column labelled with a common letter are not significantly different according to Fisher's Protected LSD at P = 0.05.

and sudangrass plots were subsequently colonized by cornspurry (*Spergula arvensis*) and common groundsel (*Senecio vulgaris*). By April, the dominant weed species in sudangrass and weedy fallow plots was little bittercress (*Cardamine oligosperma*). Consequently, November and April root samples from sudangrass plots were taken from the cornspurry and bittercress plants, respectively, rather than from sudangrass. All other cover crops established satisfactorily with minimal weed invasion. Preplant *P. penetrans* population densities for the first experiment averaged 2,125 *P. penetrans*/kg dry soil across the plot area and did not differ among treatments (Table 6). Cover crops had significant effects on nematode population densities in soil and roots in November; population densities in soil of of rye plots were lower than those in soil of the weedy fallow and other cover crops except oat. Population densities in roots of rye and oat were lower than those in weed roots in the sudangrass and weedy fallow plots.

TABLE 5. Biomass (grams fresh weight) of vegetation of cover crops incorporated into 3 liters of nematodeinfested soil in 1994 and 1995 greenhouse experiments.

| | Fall exp | . · | |
|--------------------------|---------------------|----------|----------|
| Cover crop | 10 weeks | 20 weeks | 10 weeks |
| SS 222 sundangrass | 146 ab ^a | 291 a | 667 a |
| Trudan 8 sudangrass | 140 ab | 223 b | 614 a |
| Wheeler rye | 132 ab | 193 bc | 471 b |
| Dwarf Essex oilseed rape | _ | _ | 455 b |
| Banner fava bean | | | 394 bc |
| Amity oat | 154 a | 178 cde | 330 с |
| Saia oat | 131 ab | 146 def | 233 d |
| Micah barley | 158 a | 166 cde | 206 de |
| Totem Strawberry | 31 d | 68 g | 177 de |
| Cahaba white vetch | 45 cd | 22 h | _ |
| Hairy vetch | 118 b | 136 ef | _ |
| Humus oilseed rape | 72 с | 118 f | _ |
| Steptoe barley | 159 a | 185 bcd | _ |

^a Values within a column labelled with a common letter are not significantly different according to Fisher's Protected LSD at P = 0.05.

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| | 21.4 1000 | 31 November 1993 | | 11 April 1994 | | 15 July 1994 ^a | |
|----------------------|-----------|----------------------|--------------------|---------------|--------------------|---------------------------|-------|
| Cover crop treatment | Soil | Soil | Roots ^b | Soil | Roots ^b | Soil | Roots |
| Weedy fallow | 3,345 | 1,060 a ^c | 209 a | 228 | 246 a | 168 | 13 |
| Saia oat | 1,138 | 356 ab | 76 bc | 100 | 63 bc | 52 | 39 |
| Wheeler rye | 1,045 | 192 b | 41 с | 68 | 36 c | 60 | 0 |
| Humus oilseed rape | 1,257 | 1,000 a | 121 ab | 240 | 49 bc | 152 | 39 |
| Trudan 8 sudangrass | 1,831 | 668 a | 192 a | 136 | 249 a | 88 | 68 |
| SS 222 sundangrass | 4,131 | 1,032 a | 177 ab | 228 | 143 ab | 84 | 13 |
| P^{d} | 0.95 | 0.05 | 0.03 | 0.12 | 0.01 | 0.14 | 0.13 |

TABLE 6. *Pratylenchus penetrans* population densities (nematodes per kilogram of soil and nematodes per gram of root) in field plots of cover crops at Gresham, Oregon, 1993 to 1994.

^a Roots and soil of 1-month-old strawberry plants following respective cover crop treatment.

^b Roots sampled in weedy fallow and sudargrass plots were cornspurry (November) and little bittercress (April).

^c Means (n=5) within a column labelled with a common letter are not significantly different according to Fisher's Protected LSD at P = 0.05 performed on data transformed to $\log(x + 1)$ values. Means of untransformed data are given.

^d *P*-value for effect of cover crop in analysis of variance.

Population densities in roots of rye were also lower than those in roots of oilseed rape. In April, population densities in roots of oat, rye, and oilseed rape were lower than those in weed roots from weedy fallow plots, and population densities in roots of rye were also lower than those in weed roots from sudangrass plots (Table 6). Cover crops did not affect nematode population densities in soil. None of the cover crops had an effect on nematode population densities in soil or roots of strawberry plants in June.

In the second experiment, the most abundant weeds in the weedy fallow and sudangrass plots were annual ryegrass (*Lolium multiflorum*) and pineapple weed (*Matricaria matricarioides*), respectively. Oilseed rape did not germinate properly, and the oilseed rape plots were subsequently left out of the analyses. All other cover crops established satisfactorily. Weed-free fallow plots were periodically colonized by little bittercress and pineapple weed, but not annual ryegrass. The mean aboveground biomass of cover crops in April was as follows: meadowfoam, 214 g dry tissue/m²; oat, 266; and rye, 248. The biomass of weeds in the weed-infested plots was as follows: fallow, 254 g dry tissue/m²; weed-free fallow, 14; and Sudangrass, 302. Annual ryegrass comprised approximately 95% of the biomass of weeds in weeds in weeds in weeds fallow and sudangrass plots.

Preplant nematode population densities for the second experiment did not vary according to cover crop and averaged 596 *P. penetrans*/kg dry soil (Table 7). Nematode

TABLE 7. *Pratylenchus penetrans* population densities (nematodes per kilogram of soil and nematodes per gram of root, and nematodes per kilogram of soil including roots) in field plots of cover crops at Gresham, Oregon, 1994 to 1995.

| Cover crop treatment | August 8, 1994 Soil | January 11, 1995 | | | April 5, 1995 | | |
|----------------------|------------------------|------------------|--------------|----------|---------------|--------------------|----------|
| | | Soil | Roots | Combined | Soil | Roots | Combined |
| Weed-free fallow | 1,082 | 387 | 0 | 387 | 118 | 578^{a} | 152 |
| Weedy fallow | 510 | 229 | 76 | 239 | 278 | 350 | 1,008 |
| Saia oat | 726 | 141 | 43 | 164 | 58 | 60 | 177 |
| Wheeler rye | 488 | 192 | 23 | 215 | 29 | 30 | 78 |
| Trudan 8 sudangrass | 493 | 286 | $8^{\rm b}$ | 292 | 155 | $77^{\rm b}$ | 305 |
| SS 222 sudangrass | 330 | 494 | $21^{\rm b}$ | 519 | 337 | 422^{b} | 1,643 |
| Meadowfoam | 544 | 144 | 45 | 146 | 146 | 45 | 172 |
| P^{c} | 0.87 | 0.71 | 0.64 | 0.86 | 0.37 | 0.15 | 0.12 |

^a Roots sampled from weed-free fallow plots were approximately 80% little bittercress and 20% pineapple weed.

^b Roots sampled from sudangrass plots were annual ryegrass.

^c P-value for effect of cover crop in analysis of variance.

population densities in roots and soil were not significantly different among cover crops or fallow treatments on the January and April sample dates (Table 7). Nematode population densities in the roots of strawberry were significantly reduced by fenamiphos in June, but did not differ between cover crops and fallow treatments (Table 8). There was no significant effect of the fenamiphos treatment or cover crop on population densities in soil.

DISCUSSION

Of all potential winter cover crops tested under greenhouse conditions, oat cv. Saia consistently supported the lowest population growth of *P. penetrans* and appears to be a good candidate for use as a winter cover crop to suppress P. penetrans in the Pacific Northwest. However, the host-status of oat cv. Saia for P. penetrans appeared inconsistent. Townshend (1989) reported that P. penetrans populations were reduced 88% over 9 weeks in pots with oat cv. Saia, suggesting that the cultivar was a nonhost, and perhaps antagonistic to the nematode. Although we observed a similar decrease in population density (91%) over 16 weeks in our first greenhouse experiment, we also observed net population growth in pots of oat cv. Saia in our second and third greenhouse experiments. The second and third experiments differed from Townshend's experiment (Townshend, 1989) and our first experiment in that they employed considerably larger pots and were conducted in field soil rather than pasteurized soil or potting mix. Experiments designed to assess the influences of rooting density and microbial activity on the response of *P. penetrans* to 'Saia' oat could help explain differences between these experiments.

Wheeler rye appeared to be a host for the nematode in greenhouse experiments, but resulted in some of the lowest populations observed in the field experiments. Additional research is needed to determine whether the response of *P. penetrans* to Wheeler rye is fundamentally different under winter field and greenhouse conditions.

Both cultivars of sudangrass supported substantial nematode reproduction in the greenhouse experiments, but incorporation of their green manures reduced the nematode populations to below pre-plant levels. In contrast, sudangrass did not appear to affect weeds or P. penetrans in the field experiments. Although sudangrass does not survive through the fall in the Pacific Northwest, we expected it to accumulate sufficient biomass in late summer to function as a dead mulch through fall and winter. We hypothesized that the sudangrass mulch would reduce overwinter survivorship of P. penetrans directly by releasing nematotoxic compounds during decomposition of frost-killed

| Cover crop treatment | | Soil | Roots | | |
|----------------------|---------|------------|---------|------------|--|
| | Control | Fenamiphos | Control | Fenamiphos | |
| Weed-free fallow | 263 | 215 | 57 | 11 | |
| Weedy fallow | 454 | 267 | 25 | 14 | |
| Saia oat | 285 | 83 | 97 | 14 | |
| Wheeler rye | 414 | 118 | 39 | 27 | |
| SS 222 sudangrass | 370 | 452 | 107 | 13 | |
| Trudan 8 sudangrass | 412 | 146 | 39 | 125 | |
| Meadowfoam | 213 | 159 | 26 | 24 | |
| mean | 344 | 206 | 56 | 33 | |
| P^{a} | 0.14 | | 0.006 | | |
| P^{b} | | 0.93 | 0.75 | | |

TABLE 8. *Pratylenchus penetrans* population densities (June 1995) in soil (nematodes per kilogram soil) and strawberry roots (nematodes per gram root) in plots previously planted with winter cover crops and treated with fenamiphos.

^a Probability for main-factor effect of fenamiphos, analysis of variance of data transformed to $\log (x + 1)$ values.

^b Probability for main-factor effect of cover crops

tissues or, indirectly, by minimizing growth of weed hosts. Earlier planting dates to maximize biomass accumulation before fall and incorporation of the vegetation in fall have not yet been evaluated. MacGuidwin and Layne (1995) also found that sudangrass and sorghum × sudangrass hybrids did not reduce field populations of *Pratylenchus*, *Xiphinema*, or *Paratrichodorus* spp., either during summer growth or after the incorporation of green manures in late summer.

In the greenhouse, both cultivars of oilseed rape supported substantial P. penetrans population growth in our experiments and in a previous study (MacDonald and Mai, 1963). Although oilseed rape green manures have been reported as antagonistic to M. chitwoodi (Mojtahedi et al., 1991, 1993b) and P. penetrans (Porter et al., 1998), they did not reduce populations of P. penetrans any more than the green manures of strawberry or cereal crops in our experiments. Meadowfoam resulted in the smallest P. penetrans population densities observed in the 1994-1995 field trial and deserves additional research. Like oilseed rape, meadowfoam contains high concentrations of glucosinolates (Vaughn et al., 1996), which have been implicated in the suppressive action of Brassica green manures to M. hapla and M. chitwoodi (Mojtahedi et al., 1991, 1993b).

Legumes, alone or mixed with cereals, are desirable cover crops because they increase soil nitrogen. White clover (Townshend and Potter, 1976), sweet clover and hairy vetch (MacDonald and Mai, 1963), and alfalfa, red clover, and birdsfoot trefoil (Townshend and Potter, 1976; Willis et al., 1982) support substantial growth of populations of *P. penetrans.* In the current study, hairy vetch, vetch cv. Cahaba, and fava bean cv. Banner were also good hosts for *P. penetrans.* When *P. penetrans* is present, none of the legumes tested to date would be good choices for cover crops.

Fenamiphos, the only nematicide registered for use on small-fruit crops in the United States, appears to be effective at reducing population densities of *P. penetrans*. In the second field experiment, spring application of fenamiphos resulted in reduced population densities of *P. penetrans* in roots of strawberry. Population densities in soil were not reduced.

Many common weeds are good hosts for P. penetrans (Townshend and Davidson, 1960), and our field experiments highlight the importance of winter weed control for management of this nematode. Winter fallow in the Pacific Northwest is usually compromised by weeds that are likely to maintain or increase P. penetrans populations through the winter. Rye cv. Wheeler and oat cv. Saia both established well in the fall and grew well through winter; consequently, the plots were less colonized by weeds than were the oilseed rape and sudangrass plots. Differences among field treatments were detected only in the November and April samples of the 1993-1994 experiment, but oat cv. Saia and rye cv. Wheeler appeared to harbor lower P. penetrans population densities than oilseed rape and sudangrass at all sample dates in both experiments. These results are consistent with previous field research in which oat cv. Saia suppressed P. penetrans populations relative to weedy fallow and various other cover crops except redtop and red fescue (Vrain et al., 1996), marigold (Merwin and Stiles, 1989), and brome grass (Colbran, 1979). Although Saia oat and Wheeler rye appeared to support lower population densities than weedy fallow in winter and spring, there were no differences in population densities in roots of the succeeding strawberry crop. Because Saia oat and Wheeler rye supported some P. penetrans population growth in greenhouse experiments, we hypothesize that the apparent effects of these cover crops on nematode populations in the field are due to their suppression of weeds that support even greater growth of P. penetrans populations.

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