

Nematodes in Dryland Field Crops in the Semiarid Pacific Northwest United States

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Abstract: Soils and roots of field crops in low-rainfall regions of the Pacific Northwest were surveyed for populations of plant-parasitic and non-plant-parasitic nematodes. Lesion nematodes (*Pratylenchus* species) were recovered from 123 of 130 non-irrigated and 18 of 18 irrigated fields. *Pratylenchus neglectus* was more prevalent than *P. thornei*, but mixed populations were common. Population densities in soil were affected by crop frequency and rotation but not by tillage or soil type ($P < 0.05$). Many fields (25%) cropped more frequently than 2 of 4 years had potentially damaging populations of lesion nematodes. *Pratylenchus neglectus* density in winter wheat roots was inversely correlated with grain yield ($r^2 = 0.64$, $P = 0.002$), providing the first field-derived evidence that *Pratylenchus* is economically important in Pacific Northwest dryland field crops. Stunt nematodes (*Tylenchorhynchus clarus* and *Geocenamus brevidens*) were detected in 35% of fields and were occasionally present in high numbers. Few fields were infested with pin (*Paratylenchus* species) and root-knot (*Meloidogyne naasi* and *M. chitwoodi*) nematodes. Nematodes detected previously but not during this survey included cereal cyst (*Heterodera avenae*), dagger (*Xiphinema* species), and root-gall (*Subanguina radicolica*) nematodes.

Key words: barley, cereal cyst nematode, *Geocenamus brevidens*, *Heterodera avenae*, lesion nematode, *Meloidogyne chitwoodi*, *Meloidogyne naasi*, non-plant-parasitic nematodes, *Paratylenchus*, pin nematode, *Pratylenchus neglectus*, *Pratylenchus thornei*, root-gall nematode, root-knot nematode, stunt nematode, *Subanguina radicolica*, *Tylenchorhynchus clarus*, wheat, *Xiphinema*.

Wheat (*Triticum aestivum*) is the major field crop in Oregon and Washington, with 5.7 million metric ton produced annually on 1.4 million ha, yielding a farm gate value of \$584 million per annum. Barley (*Hordeum vulgare*) is produced on 240,000 ha and yields 0.9 million metric ton, for a value of \$83 million per annum. Ninety percent of these crops are produced in the semi-arid central and eastern region of each state, where annual precipitation is less than 400 mm and effective precipitation does not occur during summer. In the dryland area 91% of the wheat and barley acreage is not irrigated.

Farm management practices for rain-fed crops in the semiarid Pacific Northwest (PNW) were developed to ensure high yields with minimal season-to-season risk. The dominant cropping system, comprising up to 80% of the production, has been a 2-year rotation of winter wheat and cultivated summer fallow. This rotation includes winter wheat for 10 months and summer fallow for 14 months, and has been characterized as conducive to high rates of soil erosion from water and wind. Socioeconomic concerns regarding the declining qual-

ity and sustainability of soil and water (Duff et al., 1995) have strengthened development of more conservation-oriented farming systems (Allmaras et al., 1985; Cook, 2001; Michalson et al., 1999). Winter wheat production has declined to 64% of the total wheat acreage, and 350,000 ha of land formerly in winter wheat/summer fallow rotation is now planted annually without tillage. Most of this acreage is planted to spring wheat and barley, with much smaller acreages of chickpea (*Cicer arietinum*), canola (*Brassica napus*), mustard (*B. juncea*; *Sinapis alba*), or other broadleaf crops. This transition in farming systems is now being assessed to determine how changes in management affect plant pathogens (Paulitz et al., 2002; Smiley, 1996) and other pests.

Lesion (*Pratylenchus* spp.) and root-knot (*Meloidogyne* spp.) nematodes are well recognized in the PNW for damaging high-value irrigated crops (Jensen, 1961). However, damaging populations of nematodes have been considered unlikely to develop in winter wheat/summer fallow rotations. This view has been validated by a paucity of diagnostic circumstances in which a nematode was considered the causal agent of economic damage in the winter wheat/summer fallow rotations in Oregon and Washington. As a result, populations of these and other plant-parasitic nematodes have not been surveyed in lower-value field crops produced without irrigation in low-rainfall regions of the PNW. It is possible, however, that changes in farming systems may amplify the potential for damage by plant-parasitic nematodes. Gair et al. (1969) reported that lesion nematode populations increased dramatically when dryland fields were shifted to a higher intensity of cereal cropping. Thomas (1978) and Thompson et al. (1983) reported higher lesion nematode populations in no-tilled than in tilled soils.

While little attention has been given to nematodes in dryland field crops in the PNW, high populations of

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lesion nematodes have been occasionally recorded while diagnosing the cause of unthriftiness in cereals and other crops. For example, in 1988 several winter wheat fields at the Columbia Basin Agricultural Research Center, near Pendleton, Oregon, were slow and uneven in resuming growth during the spring. *Pratylenchus thornei* was detected at populations of up to 6,800/kg soil in 16 fields sampled during 1988. A similar observation was made at the same location during 1992, at which time the *P. thornei* population was 3,950/kg soil. An irrigated field of Kentucky bluegrass (*Poa pratensis*) in Union County exhibited a premature decline in seed yield during 1992. In 1993, the field had a lesion nematode population of 34,600/kg soil. Declining yield in a field of wheat planted annually for 20 years in Nez Perce County, Idaho, was determined to have a lesion nematode population of 112,000/kg soil. Lesion nematodes in an irrigated wheat experiment in Union County, during 1998 to 1992, were detected at populations up to 9,000/kg soil. A nearby non-irrigated field of unthrifty winter wheat, following canola, had 30,800 lesion nematodes/kg soil during 1990. William Cobb (pers. comm.) of Cobb Consulting Services, Kennewick, Washington, detected populations up to 11,460 *P. thornei*/kg soil in a winter wheat field examined to determine the cause of growth retardation in Columbia County, Washington, and up to 3,060 *P. thornei*/kg soil in a spring wheat/green pea (*Pisum sativum*) rotation in Umatilla County, Oregon. In summary, high numbers of lesion nematodes occur in at least some nonirrigated and irrigated fields in the PNW.

Reports of significant damage by lesion nematodes in dryland cereal crops have been published elsewhere in the world, mostly during the past 20 years. The most important species in rain-fed semiarid agriculture are *P. thornei* and *P. neglectus*. These species are now known to cause damage to wheat and other crops in non-irrigated regions of Australia (Doyle et al., 1987; Nicol, 2002; Nicol et al., 1999; Taylor et al., 1999; Thompson et al., 1995; Vanstone et al., 1998). *Pratylenchus thornei* in wheat also caused severe stunting and reduced grain yield and test weight in Colorado (Armstrong et al., 1993), Utah (Sher and Allen, 1953), Ontario (Yu, 1997), Israel (Doyle et al., 1987; Orion et al., 1982), and Mexico (Doyle et al., 1987; Nicol et al., 2003; Van Gundy et al., 1974). Assays with *P. thornei* and *P. neglectus* in the greenhouse have shown that *P. thornei*, at high inoculum density, reduced growth of winter wheat seedlings in Washington (Mojtahedi et al., 1986; Mojtahedi and Santo, 1992).

Lesion nematode species tend to have wide host ranges. One or more of the species detected in the PNW have the potential to parasitize all cereals and potential dryland rotation crops including grain legumes, pasture legumes, and oilseeds (Vanstone et al., 1994). A wide range of susceptibility also occurs among

broadleaf and grass weeds and pasture grasses (Griffin and Jensen, 1997; Vanstone and Russ, 2001a, 2001b).

Other nematodes observed previously in non-irrigated cereals in eastern Oregon include *Heterodera avenae* (cereal cyst nematode) and *Subanguina radicumicola* (grass root-gall nematode). *Heterodera avenae* damages non-irrigated cereals in high-rainfall regions of western Oregon (Jensen et al., 1975) and irrigated cereals in eastern Oregon (Smiley et al., 1994). A high population density (4,500/kg soil) of *S. radicumicola* was detected during 1986 in a field of winter wheat exhibiting moderate to severe root deformation and galling in a low-rainfall (250 mm annually) area in Umatilla County. This nematode has not been reported in the semiarid region of eastern Oregon or on wheat in Oregon but does occur naturally on grasses in higher-rainfall areas (1,000 mm annually) of western Oregon (Jatala et al., 1973; Smithson et al., 1963). Lu (1983) reported that the grass root-gall nematode colonized barley and was a "serious pathogen of wheat" in China.

As growers face increasing economic and ecologic pressures to reduce summer fallow acreage by producing more annual crops and to reduce inputs by eliminating primary tillage between crops, it becomes essential to determine whether these trends increase the risk of damage by plant-parasitic nematodes. This paper reports surveys of genera and population densities of plant-parasitic and non-plant-parasitic nematodes in 4 and 11 eastern Oregon and Washington counties during 1999 and 2000, respectively. Emphasis was placed on comparisons of annually cropped fields with winter wheat/summer fallow rotations and on comparisons of tillage systems for annual crops in dryland fields. Additional data on effects of rotations and field management at two locations were acquired during 2003.

MATERIALS AND METHODS

Sampling locations: Emphasis was placed on crops growing in fields planted annually. Many fields fitting this description are managed by planting spring crops without primary tillage. Soil and plant samples during 1999 were collected in 57 research plots representing 21 research sites at five locations in three counties in Oregon (Morrow, Sherman, and Umatilla) and one county (Adams) in Washington (Fig. 1). Sampling sites (148) during 2000 included 49 commercial fields, 26 large experiments in commercial fields, and 34 smaller plots at the Oregon State University (OSU) Columbia Basin Agricultural Research Center (Pendleton and Moro Stations) in Oregon and the Washington State University (WSU) Dryland Research Unit at Lind, Washington. Sites sampled during 2000 were located in seven Oregon counties (Gilliam, Morrow, Sherman, Umatilla, Union, Wallowa, and Wasco) and four Washington counties (Adams, Klickitat, Lincoln, and Walla Walla). Eighteen of the 148 samples during 2000 were

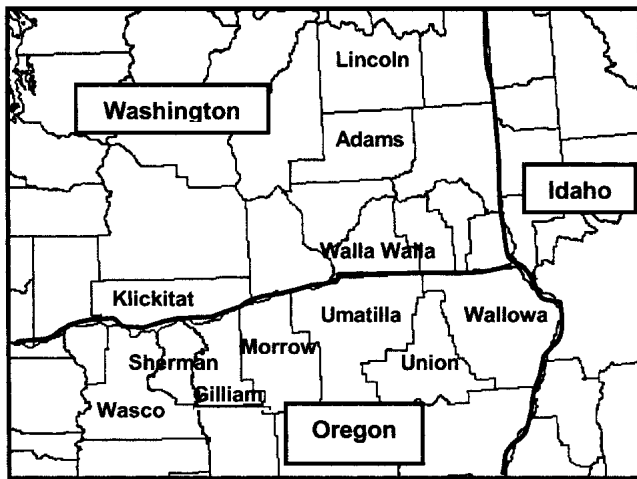


FIG. 1. Oregon and Washington counties from which samples were collected.

from irrigated fields. Additional soil and/or root samples (39) were collected over time to monitor population dynamics through the season at selected sites.

Crop and tillage management systems are briefly described for selected sampling sites in the following paragraphs. Four experimental plots were sampled at the OSU Columbia Basin Agricultural Research Center near Moro in Sherman County. Crops included wheat, canola, and lupin (*Lupinus albus*). The wheat experiments involved annual no-till spring wheat planted for the third and fourth consecutive years (Smiley et al., 1999). Canola and lupin were planted in a field that had been summer-fallowed after a winter wheat crop. These and other rotations were sampled during August 1999 and May, June, and July 2000. In March 2003, plots were sampled following 2 years of safflower (*Carthamus tinctorius*), chickpea, or spring wheat.

Soil samples were collected from 14 plots at the OSU Columbia Basin Agricultural Research Center near Pendleton in Umatilla County. Sites were selected at random to represent a broad range of cropping systems and crops in pre-existing experiments. Summer fallow plots were managed either by chisel plowing in the spring followed by multiple rod weeding during summer or by moldboard plowing followed by disking and rod weeding. Soil samples were collected during July 1999 and in May, June, July, and October 2000.

A spring cropping experiment was sampled on a 20-acre site at a farm near Ralston, in Adams County (Smiley et al., 1999). Four rotations had been established during August 1995. Treatments included conventionally tilled 2-year rotations of spring wheat or winter wheat with summer fallow, and no-tilled annual spring wheat or a rotation of spring wheat/spring barley. Best management practices were used for tillage, residue management, fertilizers, varieties, pesticides, and planting dates. Plots (10 × 150 m) were replicated four times in a randomized complete block design. Soil

and root samples were collected from each replicate of each treatment (32 samples) during July 1999 and June 2000.

Nematode populations were evaluated in a pre-existing crop rotation experiment at a farm near Heppner, in Morrow County. Annual spring crops were produced without tillage in 25 × 275-m non-replicated plots. Three-year rotations included spring barley, spring wheat, and either canola, mustard, or lentil (*Lens culinaris*). Continuous barley or wheat was also examined as annual spring crops without tillage. The spring cropping systems were compared with winter wheat/summer fallow rotations managed with either conventional tillage or chemical fallow. The rotations were sampled during the first (2000) and fourth (2003) years. Samples during 2000 were also collected from a short-term experiment at the same farm. Blocks planted to winter wheat during 1999 were followed in 2000 with flax (*Linus usitatissimum*), safflower, lentil, chickpea, or narrow-leaf lupin (*Lupinus angustifolius*).

A replicated crop rotation-tillage management experiment was established in 1994 near Pilot Rock, in Umatilla County, Oregon. Management practices and grain yields have been reported (Diebel and Ball, 1999). Soil was a Pilot Rock silt loam (Table 1). Seven treatments measuring 12 × 90 m were replicated four times in a randomized complete block design, culminating with all plots planted to winter wheat (cv. Madsen) during 1999. Treatments included (i) 2-year rotation of winter wheat (cv. Madsen or Stephens) and high-residue fallow, using a disk in autumn following harvest and a chisel plow to prepare fallow in spring; (ii) 2-year rotation of winter wheat and high-residue fallow, using chemical fallow in autumn following harvest and chisel plow in standing stubble; (iii) 3-year rotation of winter wheat, spring barley (cv. Baroness or Steptoe), and fallow with tillage as in treatment one; (iv) 3-year rotation of winter wheat, spring barley, and fallow with chemical fallow as in treatment two; (v) 3-year rotation of canola (cv. Arabella and Legend), winter wheat, and fallow with tillage as in treatment one; (vi) 2-year rotation of winter wheat and low-residue fallow using a moldboard plow during the spring (the current “conventional” practice, with wheat stubble standing through winter following harvest); and (vii) continuous no-till spring wheat (cv. Westbred 936R) for 5 years and winter wheat during the sixth year (1998–1999). Standard commercial management practices were used for tillage, residue management, fertilizers, pesticides, planting dates, and grain harvest (Diebel and Ball, 1999). On 28 June 1999, shortly before harvesting the final crop of winter wheat, moist soil samples and root samples were collected 3 days after a rain (12 mm) in an otherwise very dry summer. Samples were collected from two non-adjacent replicates for each of seven treatments. Soil and root sampling procedures are described below.

TABLE 1. Locations and description for selected soils sampled during a survey of nematodes in field crops during 1999 and 2000.

State and county	Nearest town	Soil		Annual precipitation (mm)	Elevation (m)
		Series and texture	Taxonomic name		
Oregon					
Gilliam	Condon	Condon silt loam	fine-silty, mixed, superactive, mesic Typic Haploxerolls	280	822
Morrow	Heppner	Valby silt loam	fine-silty, mixed, superactive, mesic Calcic Haploxerolls	306	766
Sherman	Moro	Walla Walla silt loam	coarse-silty, mixed, superactive, mesic Typic Haploxerolls	280	570
Umatilla	Echo	Ritzville silt loam	coarse-silty, mixed, superactive, mesic Calcic Haploxerolls	250	344
Umatilla	Pendleton	Walla Walla silt loam	coarse-silty, mixed, superactive, mesic Typic Haploxerolls	400	442
Umatilla	Pendleton	McKay silt loam	fine-silty, mixed, superactive, mesic Calcic Argixerolls	400	462
Umatilla	Pilot Rock	Pilot Rock silt loam	coarse-silty, mixed, superactive, mesic Haploxerollic Durixerolls	300	442
Union	La Grande	Imbler fine sandy loam	coarse-loamy, mixed, superactive, mesic Pachic Haploxerolls	460	832
Union	La Grande	Hoopal fine sandy loam	coarse-loamy, mixed, superactive, mesic Typic Duraquolls	460	835
Union	La Grande	Hooley silt loam	medial over loamy, mixed over isolic, nonacid, mesic Typic Endoaquands	460	833
Wasco	Dufur	Walla Walla silt loam	coarse-silty, mixed, superactive, mesic Typic Haploxerolls	305	335
Wasco	Tygh Valley	Maupin silt loam	fine-loamy, mixed, superactive, mesic, Haploduridic Durixerolls	280	500
Washington					
Adams	Lind	Shano silt loam	coarse-silty, mixed, superactive, mesic Xeric Haplocambids	250	488
Adams	Ralston	Ritzville silt loam	coarse-silty, mixed, superactive, mesic Calcic Haploxerolls	280	518
Lincoln	Harrington	Renslow silt loam	coarse-silty, mixed, superactive, mesic Calciargidic Argixerolls	250	653
Walla Walla	Touchet	Ritzville silt loam	coarse-silty, mixed, superactive, mesic Calcic Haploxerolls	230	326

Soils: Soils representative of the sampling sites are described in Table 1. Variability in soil chemical, physical, and biological characteristics was influenced mostly by farming practices. General characteristics were as follows: soil pH = 4.4 to 6.4 (measured in 0.01M CaCl₂, which is typically 0.5 unit lower than measurements in water), soil organic matter = 1.8% to 2.7%, organic N = 0.7 to 1.4 g/kg, organic C = 10 to 18 g/kg, bulk density = 1.1 to 1.3 mg/m³, and microbial biomass from 255 to 1,158 mg C/kg (Smiley et al., 1996).

Soil and root sampling procedures: Each year, soil plus root segments were collected directly in crop drill rows (Armstrong et al., 1993). Plants with attached roots also were collected at two sites during 1999 and at all sites during 2000. In 1999, samples for all except the Pilot Rock experiment were collected during late July and early August, when soil was generally very dry following crop maturation. Twenty 2.5-cm-diam. × 10-cm-deep cores were collected and composited for each plot at all sites. In addition, 20 root systems in each experimental treatment at two locations were collected separately by shovel to 8-cm depth; two plants were collected from each of 10 sub-sampling sites in each plot. Samples were

placed in insulated containers following collection and stored at 4 °C for up to 14 days. Soil was passed through a 6.5-mm sieve and mixed before nematode extraction. Root debris was mostly retained as soil was sieved.

Samples during 2000 were collected from 109 sites during May and June (late spring). At each location, soil plus roots were collected directly in crop drill rows. Soil was collected to a 6 to 8-cm depth using a narrow-blade (10-cm) shovel. A hole was opened and then a 1 to 2-cm slice of soil was removed and placed into a bag. Ten subsamples were collected and composited for each sampling site. Approximately 40 plants with intact root systems also were collected at locations adjacent to those where each soil subsample was collected, using the same shovel and sampling depth. Half the plants were evaluated for nematodes and the remainder were evaluated for root and crown diseases caused by soil-borne plant pathogenic fungi, as described by Smiley et al. (1996). Additional data collected for each sampling site included site location indicators (altitude, latitude, longitude, nearest town, and property owner or operator), tillage (direct drill or cultivated), and cropping history for at least 4 years.

Nematode extraction and identification: Extractions and identifications in 1999 and 2000 were performed at the OSU Nematode Testing Service at Corvallis. In 2003, the samples were processed at Western Laboratories in Parma, Idaho. A wet-sieving density-flotation method was used to extract soil-dwelling nematodes and a 7-day intermittent mist procedure was used to extract endoparasitic nematodes from roots (Ingham, 1994). Plant-parasitic nematodes were counted by genus or genus-complex, and other nematodes were counted as a group and their numbers expressed as "non-plant-parasitic nematodes." Lesion nematode species and stunt nematode genus and species determinations were based on body measurements and ratios thereof as well as other morphological characteristics observed under a compound microscope. Once generic or species identifications were complete, numbers were normalized to equal units of root mass or soil. Numbers are reported as nematodes per kilogram of oven-dry soil or nematodes per gram of fresh root tissue. Cysts were not extracted for the purpose of quantifying *H. avenae* populations.

Analysis of data: Populations of parasitic genera and composite non-plant-parasitic nematode genera, and their proportions in the total estimated nematode fauna, were compared between tilled and no-tilled fields during 1999. Fields and/or plots were considered replicate measures for each tillage treatment in a completely randomized analysis of variance using CoStat Statistical Software version 6.101 (CoHort Software, Monterey, CA). Data for samples collected during

2000 were grouped into a matrix to reflect brackets of population levels for each combination of nematode genus or class, crop sequence (winter wheat/summer fallow rotation, cropping frequency greater than 50%, cereal following cereal, cereal following broadleaf, broadleaf following cereal), and tillage system (no-tilled or tilled). Population means were analyzed as described for samples collected in 1999. In addition, frequency distributions for population levels were analyzed to determine if population distributions differed in tilled and no-till fields. Frequency distributions were examined with the Spearman Rank Correlation Coefficient to test the hypothesis that there was no difference between population distributions in the two tillage systems. Coefficients were determined using CoStat statistical software and evaluated for significance using the Spearman Test Statistic table in Conover (1980).

RESULTS

Genera and species: *Pratylenchus* was the plant-parasitic genus detected most often and in highest numbers in soils of dryland field crops in eastern Oregon and Washington. Lesion nematodes were recovered from each of 25 samples collected at 20 research sites in Oregon during 1999, and from none of 32 plots sampled at a research site in Adams County, Washington. Lesion nematodes were therefore detected in samples from 20 of 21 research sites. A summary of data is presented for the 25 samples where lesion nematodes were detected (Table 2). Lesion nematodes also were

TABLE 2. Populations of nematodes^a in no-till (NT) and tilled (T) non-irrigated fields in eastern Oregon and Washington; samples were collected from 7 NT and 18 T fields during 1999, and 98 NT and 32 T fields during 2000.

	Range		Mean				
	NT	T	NT	T	p	CV (%)	1sd _{0.05}
Year: 1999			nematodes per kg soil				
Lesion	50–2,570	10–3,970	782	686	0.86	152	ns
Stunt	0–50	0–570	37	171	0.14	137	ns
Non-parasitic	2,480–7,440	2,150–10,800	4,480	5,020	0.66	50	ns
Total population	2,600–7,690	2,300–12,120	5,298	5,877	0.69	51	ns
			percentage of total nematode population				
Lesion	1–46	0–33	15	8	0.32	120	ns
Stunt	0–3	0–17	1	4	0.18	155	ns
Non-parasitic	55–97	64–100	84	88	0.59	15	ns
Year: 2000			nematodes per kg soil				
Lesion	0–35,960	0–13,260	1,124	1,517	0.62	314	ns
Stunt	0–2,430	0–1,040	133	140	0.92	238	ns
Pin	0–2,690	0–130	36	10	0.59	809	ns
Non-parasitic	680–20,370	330–16,240	5,818	4,835	0.25	74	ns
Total population	920–50,430	490–23,640	7,112	6,501	0.63	89	ns
			percentage of total nematode population				
Lesion	0–75	0–81	11	17	0.14	142	ns
Stunt	0–49	0–71	2	6	0.05	280	4
Pin	0–12	0–3	0.2	0.2	0.95	563	ns
Non-parasitic	25–100	19–100	86	77	0.02	22	9

^a For samples collected during 1999, data are presented for 25 plots in which plant-parasitic nematodes were detected at 20 experimental sites. Data for 32 plots at another site are excluded because plant-parasitic nematodes were not detected. For samples collected during 2000, data are presented for the 130 non-irrigated sampling locations but not 18 irrigated sites. Genera and species were: lesion = *Pratylenchus neglectus* and *P. thornei*, stunt = *Tylenchorhynchus clarus* and *Geocenamus brevidens*, and pin = unspecified species of *Paratylenchus*.

detected in 141 of 148 samples (95%) collected during 2000, including 18 of 18 irrigated fields and 123 of 130 non-irrigated fields (Table 2). Lesion nematodes constituted an average of 13% of the total nematode fauna recovered from non-irrigated fields during 1999 and 2000 (Table 2).

Populations of *Pratylenchus* ranged from zero to 35,960/kg soil in non-irrigated fields during 2000 (Table 2). *Pratylenchus neglectus* was the only species detected in 64% of the soil samples. *Pratylenchus thornei* alone was detected in 6% of samples, and mixtures of *P. neglectus* and *P. thornei* occurred in 30% of the soil samples. Similar species proportions were detected in root samples, where *Pratylenchus* population densities ranged from zero to 2,449/g root (data not presented). *Pratylenchus neglectus* alone was present in 80% of roots containing identifiable adults, *P. thornei* alone was detected in 5% of roots, and mixtures of *P. neglectus* and *P. thornei* occurred in 13% of the roots. Frequency distributions for population density groups of *Pratylenchus* species in roots and soil are presented in Table 3. *Pratylenchus penetrans* was rarely detected during this survey. This species was a significant component of the nematode fauna in only one soil sample and was identified in only 1 of 128 root systems harboring identifiable adult stages.

Stunt nematodes (*Tylenchorhynchus clarus* and *Geocynamus brevidens*) were present in 52 of 148 samples (35%) and detected at populations up to 2,430/kg soil under dryland conditions (Table 2). Stunt nematodes averaged 3% of the total nematode fauna extracted from soil.

Pin nematodes (*Paratylenchus* species) were not detected during 1999. They were, however detected in 15 of 148 soil samples (10%) collected during 2000. *Paratylenchus* was detected at 10 sites during 2000 that coincided with experiments in which this genus was not detected during 1999. Populations during 2000 were as high as 2,690/kg soil under dryland conditions (Table 2) and 20,210/kg under irrigation (Table 4). *Paratylenchus* species were not identified.

Root-knot nematodes (*Meloidogyne chitwoodi* and *M.*

TABLE 3. Relationship of lesion nematode (*Pratylenchus neglectus* and/or *P. thornei*) numbers with tillage and cropping systems in 148 samples from fields in 10 eastern Oregon and Washington counties during April and May 2000; 109 and 39 samples were from no-till (NT) and tilled (T) soil, respectively.

Pratylenchus spp. population category	Crop rotation, crop sampled, and crop or fallow preceding the crop sampled											
	All crops combined; tillage was the main variable		Winter wheat/summer fallow 2-yr rotation		Cropped more than 2 of 4 years		Cereal following a cereal		Cereal following a broadleaf		Broadleaf following a cereal	
	NT	T	NT	T	NT	T	NT	T	NT	T	NT	T
number of fields with lesion nematodes in roots from each tillage and cropping system												
	105	36	7	12	98	24	62	20	19	3	17	1
percentage of fields with nematodes in each population category												
Nematodes in roots <i>no. per g root</i>												
0-10	15	14	29	25	14	8	15	0	10	67	12	0
11-100	21	36	29	58	20	25	19	25	11	33	35	0
101-300	26	19	42	17	25	21	26	20	16	0	29	100
301-1,000	28	17	0	0	30	25	31	30	47	0	12	0
1,001-1,500	5	8	0	0	6	13	5	15	11	0	0	0
1,501-2,000	4	3	0	0	4	4	2	5	5	0	12	0
2,001-2,500	1	3	0	0	1	4	2	5	0	0	0	0
r ^{2a}	0.848		0.884		0.893		0.750		nd		nd	
	ns		ns		ns		ns		—		—	
number of fields with lesion nematodes in soil from each tillage and cropping system												
	105	36	7	12	98	24	68	20	19	3	11	1
percentage of fields with nematodes in each population category												
Nematodes in soil <i>no. per kg soil</i>												
0-10	17	14	14	25	17	8	15	5	20	33	18	0
11-100	14	25	14	34	13	21	12	15	16	67	18	0
101-250	15	17	43	25	13	13	15	10	11	0	9	100
251-500	17	19	29	16	16	21	19	25	11	0	9	0
501-1,000	15	3	0	0	17	4	15	5	21	0	18	0
1,001-2,500	12	11	0	0	14	17	13	20	16	0	9	0
2,501-5,000	4	3	0	0	4	4	3	5	5	0	9	0
5,001-10,000	3	3	0	0	3	4	4	5	0	0	0	0
10,001-20,000	2	5	0	0	2	8	1	10	0	0	9	0
>20,000	1	0	0	0	1	0	1	0	0	0	0	0
r ²	0.673		0.918		0.436		0.476		nd		nd	
	ns		ns		*		*		—		—	

^a r² is the Spearman Rank Correlation Coefficient testing the hypothesis that there is no difference between population distributions in no-tilled and tilled soil, for the two columns being compared. A finding of non-significance (ns) indicates that the hypothesis is true. Significant differences (P = 0.05) among nematode population distributions in tilled and no-till soils are denoted by an asterisk (*). Comparisons were not calculated (nd) if one or both columns contained fewer than four fields in the cropping sequences being compared.

TABLE 4. Relationship of pin (*Paratylenchus* species) and stunt (*Tylenchorhynchus clarus* and *Geocenamus brevidens*) nematode numbers with tillage and cropping systems in 148 samples from fields in 10 eastern Oregon and Washington counties during April and May 2000; 109 and 39 samples were from no-till (NT) and tilled (T) soil, respectively.

Nematode population category	Crop rotation, crop sampled, and crop or fallow preceding the crop sampled											
	All crops combined; tillage was the main variable		Winter wheat/summer fallow 2-yr rotation		Cropped more than 2 of 4 years		Cereal following a cereal		Cereal following a broadleaf		Broadleaf following a cereal	
	NT	T	NT	T	NT	T	NT	T	NT	T	NT	T
pin nematodes per kg soil	9	6	number of fields with pin nematodes in soil from each tillage and cropping system									
			0	2	9	4	4	4	4	0	1	0
			percentage of fields with pin nematodes in each population category									
0-10	11	0	—	0	11	0	25	0	—	—	0	—
11-100	45	33	—	0	45	50	50	50	50	—	0	—
101-250	0	33	—	50	0	25	0	25	0	—	0	—
251-500	11	17	—	0	11	25	0	25	0	—	100	—
501-1,000	0	0	—	0	0	0	0	0	0	—	0	—
1,001-2,500	0	0	—	0	0	0	0	0	0	—	0	—
2,501-5,000	11	0	—	0	11	0	25	0	0	—	0	—
5,001-10,000	0	17	—	50	0	0	0	0	0	—	0	—
10,001-20,000	11	0	—	0	11	0	0	0	25	—	0	—
>20,000	11	0	—	0	11	0	0	0	25	—	0	—
r^{2a}		0.239		nd		0.509		0.509		nd		nd
		*		—		*		*		—		—
stunt nematodes per kg soil	38	14	number of fields with stunt nematodes in soil from each tillage and cropping system									
			2	6	39	8	20	10	11	0	5	1
			percentage of fields with stunt nematodes in each population category									
0-10	8	0	0	0	8	0	10	0	0	—	20	0
11-100	31	29	50	17	30	38	25	40	18	—	80	0
101-250	31	35	0	32	35	25	45	40	28	—	0	0
251-500	11	18	50	17	8	25	10	10	9	—	0	100
501-1,000	8	12	0	17	8	12	5	10	18	—	0	0
1,001-2,500	8	6	0	17	8	0	5	0	18	—	0	0
2,501-5,000	3	0	0	0	3	0	0	0	9	—	0	0
r^2		0.929		nd		0.768		0.787		nd		nd
		ns		—		ns		ns		—		—

^a r^2 is the Spearman Rank Correlation Coefficient testing the hypothesis that there is no difference between population distributions in no-tilled and tilled soil, for the two columns being compared. A finding of non-significance (ns) indicates that the hypothesis is true. Significant differences ($P = 0.05$) among nematode population distributions in tilled and no-till soils are denoted by an asterisk (*). Comparisons were not calculated (nd) if one or both columns contained fewer than four fields in the cropping sequences being compared.

naasi) were detected at three sampling sites (data not shown). Non-plant-parasitic nematodes were detected in all soil samples. Populations ranged from 330 to 20,370/kg soil (Table 2). The non-parasitic species represented 19% to 100% of the nematode fauna extracted from soil.

Geographic distribution: Few differences were detected in geographic distribution of plant-parasitic nematodes. Each group was generally recovered from across the region sampled. The notable exception was the near absence of all plant-parasitic nematode populations in soils and roots collected from non-irrigated fields in Adams and Lincoln counties during both years. In Lincoln County, no plant-parasitic nematodes were detected except at one site, where 930 lesion nematodes/g root were recovered in mature wheat roots at a time when no lesion nematodes were detected in soil. In addition, at one site in Adams County, samples from side-by-side irrigated and non-irrigated annual wheat experiments contained 1,381 and 17 lesion nematodes/g root, respectively, and 650 and 0/kg soil, respectively. Soils were very dry, and the soil struc-

ture became fractured as samples were collected at these sites.

Tillage: Lesion nematodes (Table 3) and non-plant-parasitic taxa (Table 5) were detected in nearly all samples collected from both tilled and no-till fields during 2000. Pin nematodes (Table 4) were detected in 9 of 109 no-till fields (8%) and 6 of 39 tilled fields (15%). Stunt nematodes (Table 4) were detected in 38 of 109 (35%) no-till and 14 of 39 (36%) tilled fields.

Populations of lesion, stunt, non-plant-parasitic, and total nematodes were not influenced by tillage during 1999 or 2000 (Table 2). During 2000, however, the proportion of the total nematode fauna composed of stunt nematodes, while low overall, was higher in tilled than in no-till soil ($P < 0.05$). In contrast, the proportion of the total nematode fauna composed of non-plant-parasitic species during 2000 was lower in tilled than no-till soil.

When all crops and crop frequencies were considered together, with tillage as the main variable, rank correlation analysis indicated that there was no overall trend for the distribution of lesion (Table 3), stunt

TABLE 5. Relationship of non-plant-parasitic nematode numbers with tillage and cropping systems in 138 samples from fields in 10 eastern Oregon and Washington counties during April and May 2000.

Nematode population category	Crop rotation, crop sampled, and crop or fallow preceding the crop sampled												
	All crops combined; tillage was the main variable		Winter wheat/summer fallow 2-yr rotation		Cropped more than 2 of 4 years		Cereal following a cereal		Cereal following a Broadleaf		Broadleaf following a cereal		
	NT	T	NT	T	NT	T	NT	T	NT	T	NT	T	
	104	34	7	9	97	25	67	21	19	3	11	1	
	number of fields sampled for each tillage and cropping system												
	percentage of fields with non-plant-parasitic nematodes in each population category												
nematodes per kg soil													
251–500	0	9	0	11	0	8	0	5	0	0	0	100	
501–1,000	2	6	0	0	2	8	3	10	0	0	0	0	
1,001–2,500	18	15	0	45	20	4	15	5	21	0	45	0	
2,501–5,000	33	32	29	22	33	36	31	38	47	33	18	0	
5,001–10,000	28	21	14	22	29	20	31	19	21	34	27	0	
10,001–20,000	18	15	57	0	15	20	18	19	11	33	10	0	
>20,000	1	2	0	0	1	4	2	4	0	0	0	0	
r^{2a}	0.893		0.134		0.616		0.857		nd		nd		
	ns		*		ns		ns		—		—		

^a r^{2a} is the Spearman Rank Correlation Coefficient testing the hypothesis that there is no difference between population distributions in no-tilled and tilled soil, for the two columns being compared. A finding of non-significance (ns) indicates that the hypothesis is true. Significant differences ($P = 0.05$) among nematode population distributions in tilled and no-tilled soils are denoted by an asterisk (*). Comparisons were not calculated (nd) if one or both columns contained fewer than four fields in the cropping sequences being compared.

(Table 4), or non-plant-parasitic (Table 5) nematode populations toward significantly higher or lower numbers in tilled vs. no-till farming systems. Pin nematode populations, present in only 15 samples, were skewed toward higher numbers in no-till than tilled fields (Table 4) ($P < 0.05$).

When rank correlation analysis was applied only to fields managed as winter wheat/summer fallow rotations, there was no difference in the population trends for lesion nematodes in tilled or no-till (chemical fallow) soils or in wheat roots (Table 3). Too few samples were collected to examine tillage effects on pin and stunt nematodes in these fields (Table 4). Non-plant-parasitic nematode populations were significantly skewed toward higher numbers in no-till than tilled wheat-fallow rotation (Table 5).

Although lesion nematode populations in frequently cropped fields differed significantly between tillage systems (Table 3), there was no difference between trend lines when data were plotted (Fig. 2). Pin nematodes were more prevalent in no-till than in tilled soils (Table 4) ($P < 0.05$), but sample sizes leading to this result were low. Non-plant-parasitic nematode populations did not differ among tillage systems when fields were planted more frequently than 50% of the years (Table 5).

There were no differences among populations of any nematode group when annual cereals were compared to cereal/broadleaf rotations in the no-till system. The effect of tillage systems on nematode populations in cereal/broadleaf rotations could not be examined due to the low numbers of tilled fields managed in those rotations.

Crop frequency and rotation: During 2000, all nematode

groups were detected with equal frequency in fields with very different levels of management. Lesion nematodes occurred in 19 of 21 (90%) fields managed as 2-year winter wheat/summer fallow rotations, and in 122 of 127 (96%) fields cropped more frequently than 50% of the years (Table 3). Pin nematodes were detected in 10% of fields under each crop-frequency grouping (Table 4), and stunt nematodes were detected in 37% to 38% of each group (Table 4).

Although crop frequency had relatively little effect on the detection frequency for lesion nematodes, crop frequency did have a strong effect on the population density of these nematodes (Table 3). During 1999, lesion nematode populations in tilled soil were much higher in cereal/cereal annual crop sequences than in summer fallow/cereal rotations (1,425 vs. 27/kg) ($P <$

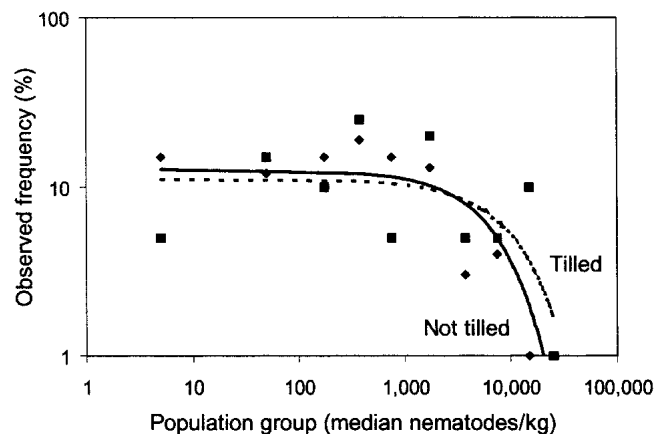


FIG. 2. Absence of tillage effects on lesion nematode populations in fields planted annually to cereal crops; samples were collected during 2000.

0.001). During 2000, populations in winter wheat/summer fallow rotation did not exceed 300/g root. In contrast, more than 40% of samples from higher-intensity cropping systems had populations higher than 300/g root, and more than 10% of samples had populations exceeding 1,000/g root. Populations of lesion nematodes in soil from winter wheat/summer fallow rotations did not exceed 500/kg, but more than 20% of samples from higher-intensity cropping systems had populations higher than 2,500/kg soil. Rank correlation analysis indicated that lesion nematode populations in tilled and no-till farming systems were skewed toward higher numbers in roots collected from fields cropped at more than 50% frequency ($P < 0.05$), compared to fields where winter wheat was rotated with summer fallow.

Crop species: Sampling sizes were too small to fully evaluate effects of crop species on nematode populations. Nevertheless, selected comparisons indicated that cereals and broadleaf crop species differed in ability to support lesion nematode populations.

Lesion nematode populations were generally lower in roots of spring barley than in spring or winter wheat during 2000. Only 3 of 13 (23%) barley root samples had lesion nematode populations that exceeded 300/g root. In contrast, 46 of 102 (45%) wheat root samples had lesion nematode populations exceeding 300/g. This trend was exemplified by samples from annual barley and wheat in long-term annual cropping experiments at Pendleton (Table 6) and at Heppner (Table 7).

Comparisons of cropping diversity in no-till systems indicated that lesion nematode populations in roots of cereals rotated with broadleaf crops were generally no lower than populations in roots of annual cereal crops (Tables 3 and 7). There were, however, several notable exceptions to this trend. In an experiment at Heppner during 2000 (data not presented in a table), lesion

nematode populations were lower in roots of safflower (28/g) and flax (99/g) than in lentil (299/g), chickpea (417/g), or narrow-leaf lupin (1,764/g). Sampling in subsequent years revealed that lesion nematode populations detected at Moro in 2003 were 53, 53, and 989/kg soil after 2 consecutive years of safflower, chickpea, or spring wheat production, respectively.

Timing of sample collection: Samples from selected experiments at Pendleton were collected on four dates from spring through autumn. Lesion nematode populations in cereal roots were lowest during the spring (May) and generally built up to their highest level as mature roots died before harvest in July (Table 6). In contrast, populations detected in soil were generally lowest during June and July and were highest in October, after roots had died and new tissue was not yet available for recolonization.

Volunteer cereals and downy brome: Following a summer without rainfall, rain began on 3 September 2000 and continued into the autumn. Volunteer cereal and grass weed seed germinated in September and became established before the sampling date in October. Lesion nematode populations in volunteer cereal seedlings and grass weeds (mostly downy brome; *Bromus tectorum*) during October were comparable to populations in planted spring and winter cereal crops during May (Table 6).

The importance of volunteer cereals and grass weeds as hosts for lesion nematodes was also noted at Heppner during 2003. The grower normally applies glyphosate to kill volunteer cereals and weeds late in the fall. The lack of rainfall during 2002 failed to germinate volunteers and weeds until December, at which time it was too cold to spray. Growth of volunteer cereals and weeds was vigorous during winter, except where the lupin crop failed during the drought of 2002, in which case little revegetation occurred during the following winter. All plots were sprayed on 12 February 2003, and subsequent rain led to rapid re-establishment of volunteer cereals and weeds. When samples were collected on 22 March, before spring crops were planted, all plots except the one following the 2002 lupin crop had vigorous stands of volunteer cereals and grass weeds in the winter wheat and fallow plots. Populations of lesion nematodes in each phase of the winter wheat/summer fallow rotations were as high as populations in annual crop rotations (Table 7), effectively eliminating the sanitizing value of the wheat/fallow rotation.

Relationship between parasitic nematodes and plant-pathogenic fungi: Samples of wheat and barley collected during 2000 were evaluated for symptoms of root diseases caused by fungal root pathogens. Symptoms of Rhizoctonia root rot (*R. solani* and *R. oryzae*) were observed on 75% and 84% of samples collected in May (61 samples) and June (43 samples), respectively (data not shown). Take-all (*Gaeumannomyces graminis* var. *tritici*) was observed on 52% and 49% of samples col-

TABLE 6. Lesion nematode populations at four sampling times in three long-term annual cereal crops^a in tilled fields at the Columbia Basin Agricultural Research Center, Pendleton; 2000.

Annual crop since 1931	May 9	June 9	July 6	October 14
	<i>nematodes per g root</i>			
Spring barley cv. Baronesse	26	83	211	137
Spring wheat cv. Alpowa	565	1,270	1,680	548
Winter wheat cv. Stephens	969	—	1,243	—
	<i>nematodes per kg soil</i>			
Spring barley	350	90	60	210
Spring wheat	13,100	1,130	1,740	13,260
Winter wheat	460	—	2,150	8,350

^a Crops were planted annually without rotation since 1931. The moldboard plow was used for primary tillage. Seed for spring and winter cereals was planted in early April and October, respectively. Winter wheat was nearing the flag leaf stage, and spring grains were small seedlings in May. Winter wheat was at anthesis and spring cereals were heading in June. Each crop was mature and nearing harvest in July. In October, winter wheat was just emerging (too small for sampling) and volunteer cereals and downy brome were well established after rains in September germinated seeds lying on the soil surface.

TABLE 7. Lesion nematode (*Pratylenchus neglectus*) populations in soil following various crop sequences^a at the Jepsen Farm near Heppner, OR.

Harvest year and crop or management					Lesion nematode population		
1999	2000	2001	2002	2003	May 2000	May 2000	March 2003
Annual no-till spring crops ^b					nematodes per g root		nematodes per kg soil
Can	SW	SB	Can	SW	689	1,940	2,660
Lent	SW	SB	Lup	SW	1,041	440	780
Must	SW	SB	Must	SW	908	1,080	9,080
SB	Can	SW	Sb	Can	—	—	5,500
SB	Lent	SW	SB	Lent	—	—	3,780
SB	Must	SW	SB	Must	—	—	1,560
SW	SB	Can	SW	SB	—	—	3,780
SW	SB	Lup	SW	SB	—	—	8,680
SW	SB	Must	SW	SB	—	—	5,260
SB	SB	SB	SB	SB	117	410	1,800
SW	SW	SW	SW	SW	314	580	3,960
Winter wheat/summer fallow rotation ^c							
WW	Chem	WW	Chem	WW	—	—	1,800
WW	Conv	WW	Conv	WW	—	—	4,820
Chem	WW	Chem	WW	Chem	105	74	2,160
Conv	WW	Conv	WW	Conv	44	42	3,120

^a Crops prior to 1999 were no-till spring barley during 1996 and 1997, and no-till spring mustard during 1998.

^b Spring-planted crops from 1999 to 2003; Can = canola cv. Hyola 308RR, RideR, and Hyola 401; Lent = lentil cv. Crimson and Mason; Lup = lupin cv. Belarus, Must = mustard cv. Tilney, SB = spring barley cv. Baronesse, and SW = soft white spring wheat cv. Penawawa.

^c Soft white winter wheat (WW; cvs. Gene and Stephens) was rotated with either chemical fallow (Chem) or conventionally tilled fallow (Conv). Glyphosate herbicide was applied on 12 February 2003 to kill volunteer cereals and grass weeds in the spring crop rotations and chemical fallow. Spring crops were planted on 21 February. Rain and mild temperature led to re-establishment of volunteer and weeds, which became prolific on all winter wheat/fallow rotations and most spring crop rotations before soil plus roots in crop drill rows were sampled on 22 March. Conventional fallow was not tilled until 23 April, after samples were collected.

lected in May and June, respectively. There was no detectable relationship between the incidence of fungal diseases and plant-parasitic nematodes (data not presented).

Relationship between nematodes and yield of winter wheat: Root and soil samples were systematically collected from only one replicated experiment for which yields were also monitored—the crop rotation-tillage management experiment near Pilot Rock. Tables 3 through 5 include data for plant-parasitic (*P. neglectus*, *P. thornei*, and a species of *Tylenchorhynchus*) and non-plant-parasitic nematodes detected in the experiment. Populations of *Pratylenchus* in soil (up to 303/kg of soil) were very low at the time of sampling, consistent with the observation throughout the survey that populations in soil were low in very dry soil during the summer. There was no difference in *Pratylenchus* population density among cultivated- vs. chemical-fallow treatments, again consistent with results of the overall survey. For example, average density of *P. neglectus* in roots averaged 250/g root for three winter wheat/summer fallow rotations, regardless of tillage intensity (chemical fallow to moldboard plow) and averaged 1,059/g root for winter wheat following no-till annual spring wheat and 4,367/g root for wheat in the winter wheat/fallow/canola rotation that included tillage at least twice each year. In addition, *P. neglectus* densities in winter wheat roots averaged 216/g in the two wheat/barley/fallow rotations differing in tillage intensity, 4,367/g in the wheat/fallow/canola rotation, and 1,059/g following no-till annual spring wheat. *Pratylenchus* densities in

roots were therefore especially high for rotations where cropping frequency exceeded 50%, except for rotations that included barley. These results are in agreement with data presented for the overall survey. *Pratylenchus neglectus* density in roots was inversely correlated ($P = 0.002$) with yield of winter wheat (Fig. 3). Although soil moisture was not measured and may have varied among crop rotation and tillage variables in this

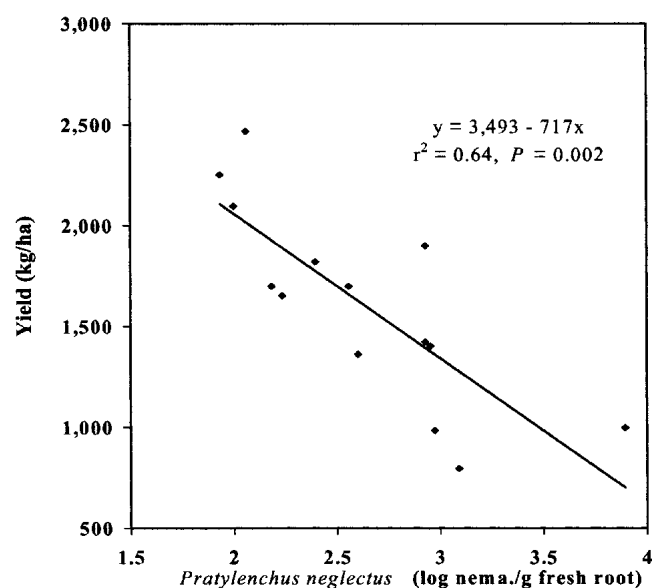


FIG. 3. Association of yield and density of *Pratylenchus neglectus* in roots for a uniform planting of Madsen winter wheat following 5 years of seven crop rotation and tillage management treatments at Pilot Rock, Oregon.

experiment, the high correlation coefficient for the regression suggests that winter wheat yield was influenced more by *P. neglectus* density than by availability of water.

DISCUSSION

Plant-parasitic nematodes detected in dryland field crops in low-rainfall regions of eastern Oregon and Washington included species of *Pratylenchus* (lesion nematode), *Tylenchorhynchus* and *Geocenamus* (stunt nematodes), *Paratylenchus* (pin nematode), and *Meloidogyne* (root-knot nematode). Lesion nematodes were present in most fields, and stunt nematodes were common. Pin and root-knot nematodes were present at fewer locations, but pin nematodes were occasionally detected in high numbers. *Subanguina* (root-gall nematode) and juvenile stages of *Heterodera avenae* (cereal cyst nematode) were not detected. Soil samples for the present survey were collected during July and August 1999 and late May and June 2000. Hatching of the cyst nematode population in Union County was previously determined to be initiated in March, peak in April, and decline to undetectable levels during late May (Newcomb et al., 1989). It was not surprising, therefore, that cyst nematode juveniles were not detected in the small numbers of soil samples collected from the infested region of Union County during this survey.

Pratylenchus neglectus and (or) *P. thornei* were present in 94% of the dryland field crops in low-rainfall regions of the PNW. Hafez et al. (1992) also reported the occurrence of *Pratylenchus* species in 92% of mostly irrigated fields in Idaho. In contrast to results of the current study, Hafez et al. reported much lower percentages of *Pratylenchus* (32%) from the 128 wheat fields sampled and, in particular, much lower percentages of *P. neglectus* (16%) and *P. thornei* (13%). In the present survey, high populations of *Pratylenchus* (mostly *P. neglectus* but some *P. thornei*) were detected in Union County, Oregon, compared to no *Pratylenchus* species reported from soils collected in that county by Hafez et al. (1992). The diversity of *Pratylenchus* species on wheat was considerably greater in the study by Hafez et al. than reported in this paper, presumably reflecting the different environments (elevation, temperature, supplemental irrigation) and focus (irrigated vs. dryland fields) for these studies.

Nicol (1996) also reported that *P. neglectus* and *P. thornei* could be extracted from 90% of South Australian fields. Populations of *Pratylenchus* species were strongly influenced by crop frequency. One crop per year is the maximum management frequency practiced in PNW dryland fields. Where crop frequency exceeded 50%, high populations of lesion nematodes occurred in roots and soil collected from more than 40% of fields. None of the root and soil samples collected from winter wheat/summer fallow rotations (50% cropping frequency) during 1999 and 2000 contained high popula-

tions of lesion nematodes, except where over-wintering grass weeds simulated an annual cropping system.

Volunteer wheat and grass weeds were heavily infested by lesion nematodes. Many growers allow volunteers to survive through the winter. If a spring crop is to be planted, the volunteers and weeds are killed several weeks before the new crop is planted. If a winter wheat crop is to be planted, the field is usually cultivated, fertilized, and maintained weed-free by multiple mechanical "rod" weedings during the summer. In each case, however, the presence of volunteers surviving through the winter greatly reduces the effective interval of the break from one harvest to the next planting. In the case of spring cereals colonized by *Rhizoctonia solani*, grain yield can be increased as much as two-fold by killing volunteer cereals and weeds during the early winter rather than waiting until early spring (Smiley et al., 1992). This phenomenon, called the "green bridge" between planted crops, appears equally applicable to plant-parasitic nematodes.

Tillage systems in the field crops sampled in this study did not have a strong effect on lesion nematode populations. Similar observations have been reported elsewhere (Stinner and Crossley, 1982), although it also has been reported that populations have been favored by conventional tillage (Caveness, 1974; Overhoff, 1991) or by zero tillage (Thomas, 1978; Thompson et al., 1983). Taylor and Evans (1998) reported recovery of *P. neglectus* and *P. thornei* to depths of 60 cm to 90 cm and, at only one of five sites, recovered significantly more lesion nematodes from inside rather than outside plant rows. These findings underscore the vertical and horizontal migratory capabilities of these species.

Soil texture had no apparent relationship with distribution of *P. thornei* and *P. neglectus*. Although the dominant soil textures are silt loams in the wheat belt of the PNW, soil textures from sandy loams to clay loam were included in the two-state survey during 2000. Kort (1972) stated that *P. neglectus* is more prevalent in loams and *P. thornei* in heavier soils. Nicol (1996) also summarized international literature indicating *P. thornei* was associated mostly with clays, clay loams, and loams. However, in a survey of South Australian soils, Nicol (1996) found that *P. thornei* tended to be more prevalent than *P. neglectus* in heavier soils in some regions, but the relationship did not always appear directly related to soil texture. Nicol concluded that the distinction between proportions of species in a given region or soil type might be a reflection of the sampling year, previous rotation, management practices, or other soil characteristics.

Relationships between nematode populations and yield reductions are difficult, if not impossible, to generalize over large areas. Crop yield loss resulting from root damage depends on nematode species and numbers in roots; on crop species and variety, crop growth stage, and crop rotation and tillage management; and

on soil temperature, moisture and texture. As such, high numbers alone do not necessarily equate to high potential for damage, and threshold values for economic damage by lesion nematodes are not known for dryland field crops in the PNW. However, it is anticipated that threshold values for lesion nematodes in dryland crops will be lower than in irrigated crops or dryland crops in regions with summer-dominant rainfall distribution, because damage from biotic stress early in the crop growth cycle undoubtedly predisposes plants to greater damage as abiotic stresses occur later in the growing season. Dryland cereal crops usually deplete soil water reserves before maturity in the PNW. Compared to plants with healthy roots, plant growth is suppressed much more readily in drying soils if the root system is already partially dysfunctional due to reduced branching, such as occurs when lesion nematodes damage root tissue.

Although root and soil samples from winter wheat/summer fallow rotations contained low populations of lesion nematodes, about 25% of the more-frequently cropped fields contained lesion nematode populations high enough to create potential risk to production of susceptible crops. Samples collected from frequently cropped fields during 2000 included 24% to 33% with *Pratylenchus* populations exceeding 1,000/kg, 10% to 16% exceeding 2,500/kg, and 6% to 12% exceeding 5,000/kg. Vanstone et al. (1998) reviewed reports from a *Pratylenchus* workshop indicating that damage could be anticipated when populations of *P. thornei* exceeded 2,500/kg in Queensland, Australia, where rainfall is plentiful during the summer. Doyle et al. (1987) investigated wheat fields in New South Wales, Australia, where yields were consistently low. Grain yields were commonly half of what was expected in the region. Wheat plants over entire fields were stunted, had reduced tillering, and sometimes had yellowing of the lower leaves. Application of the nematicide aldicarb reduced *P. thornei* numbers from 400/kg to zero and increased yield of nematode-susceptible wheat by up to 51% and nematode-resistant barley by 10%. A strong negative correlation between grain yield and lesion nematodes (5,300 *P. thornei*/kg soil) was also reported for a winter wheat field recropped a second year without rotation to summer fallow in Colorado (Armstrong et al., 1993). Soil fumigation in Colorado reduced the nematode count to 500/kg soil and was correlated with winter wheat yield increases of up to 50%.

We report evidence that *P. neglectus* reduced yield of winter wheat in the experiment near Pilot Rock. This is the first field-derived evidence that *Pratylenchus* spp. are of economic importance in PNW dryland field crops. Previous reports of root damage were from seedling assays with non-vernalized winter wheat in the greenhouse (Mojtahedi and Santo, 1992; Mojtahedi et al., 1986). *Pratylenchus* are likely to restrict winter wheat productivity only when this crop is produced in rota-

tions that include susceptible crops grown more than 50% of the years. It would not appear likely for *Pratylenchus* to significantly damage winter wheat produced in 2-year rotations with summer fallow, except when winter-annual weeds and volunteer cereals are allowed to grow throughout the winter "fallow" period, effectively eliminating the sanitizing effect of the fallow cycle. Our observation that populations of *Pratylenchus* are similar following chemical fallow and cultivated fallow makes it unlikely that fallow-preparation practices will alter the influence of *Pratylenchus*, provided that weed and volunteers are controlled in a timely manner in each system.

The DNA-based Root Disease Testing Service in Adelaide, South Australia (Ophel-Keller and McKay, 2001) considers *P. thornei* and *P. neglectus* to be of low risk at populations from 1,000 to 6,000/kg, moderate risk from 6,000 to 18,000/kg, and high risk at more than 18,000/kg dry soil. While it is not possible to directly relate risk management levels in Australia to climates and soils in Oregon and Washington, it is of interest to note that about 10% of all samples reported here would be categorized in the moderate risk class based on the extraction of nematode DNA from soil in South Australia. This is likely a conservative risk estimate because nematode population densities reported from DNA-extraction from soil are likely to be considerably higher than densities determined through physical extraction and counting of motile nematode stages. This could be particularly pronounced for this study because some of the samples reported in this survey were collected from very dry soil, extensively disrupting the soil structure at the time of collection. Following routine procedures for nematode diagnostic laboratories in the PNW (Hafez et al., 1992; Ingham, 1994), the dry soil was then thoroughly mixed and sieved before subsamples were collected to extract nematodes. It is now known that, for dry soil, disruptive sampling and handling procedures, including mixing and sieving, are each likely to reduce the efficiency for recovering *P. neglectus* and *P. thornei* (Taylor and Evans, 1998). These species survive extended dry periods in a state of anhydrobiosis (Glazer and Orion, 1983), during which time they are very brittle and easily broken by practices that break the soil structure. Individuals broken by tillage, sampling, or sieving are not recovered by extraction procedures requiring nematode motility. Extraction of DNA would presumably count broken as well as unbroken *Pratylenchus*, leading to higher population estimates compared to extractions of living nematodes capable of moving through moist soil columns.

With few exceptions, populations of lesion nematodes were lower in roots of spring barley than spring or winter wheat in this study. Although numbers of observations were very small, lesion nematode populations appeared to be quite low in safflower and flax compared to cereals, chickpea, and lupin. Variable results

were obtained for canola. Lesion nematodes have wide host ranges. *Pratylenchus neglectus* attacks all cereals as well as rotational crops such as grain legumes, pasture legumes and grasses, and oilseeds (Griffin and Jensen, 1997; Vanstone et al., 1994), and many broadleaf and grass weeds (Vanstone and Russ, 2001a, 2001b). However, nematode multiplication differs greatly in roots of various crop species and among varieties within crop species (Taylor and Vanstone, 1996). Taylor et al. (2000) concluded that chickpea, wheat, and canola were good hosts for *P. neglectus*, whereas barley, oat (*Avena sativa*), and durum wheat (*Triticum durum*) were moderate hosts, and field pea and triticale (*Triticosecale*) were poor hosts.

A range in host suitability also has been detected within varieties of wheat, barley, and oats. Hollaway et al. (2000) reported that most commercial wheat varieties grown in southeast Australia are susceptible to *P. thornei* and that barley varieties were resistant or moderately resistant, canola was moderately resistant, and lentil, field pea, and flax were resistant. Hollaway and Eastwood (1997) reported that plots planted to five barley and two durum varieties had lower numbers of *P. thornei* (800 to 2,000/kg soil) than all except the most resistant varieties of wheat (1,800 to 9,000/kg soil) in Australia. Six lentil and seven field pea varieties also had comparatively lower populations (500 to 2,200/kg soil). Intermediate populations occurred in plots of faba bean (*Vicia faba* L.) (3,500 to 4,100/kg soil), and high populations developed in plots planted with two vetch (*Vicia sativa* L.) varieties (7,800 to 17,000/kg soil). Hollaway and Eastwood (1997) considered pea and lentil as resistant, faba bean moderately susceptible, and vetch highly susceptible to multiplication of *P. thornei*. The nematode population increased during production of all wheat varieties except the few with resistance. With minor exceptions, results of this survey indicate that similar relationships are likely to occur with similar crop species in the PNW, although it remains unknown whether any resistant wheat varieties are currently available in the region.

Wheat roots with *P. neglectus* and/or *P. thornei* numbers as low as 300/g root have been considered highly infested in some studies (Griffin, 1984; Rivoal and Cook, 1993). In this study, *P. neglectus* and/or *P. thornei* populations in wheat root samples collected from more frequently cropped fields during 2000 exceeded 300/g in 41% to 46% of the samples, exceeded 1,000/g in 11% to 21% of the samples, and exceeded 1,500/g in 5% to 8% of the samples. It is therefore probable that *Pratylenchus* reduces yields of spring cereals in annually cropped fields in low-rainfall regions of the PNW.

Root diseases caused by soilborne plant pathogenic fungi are common in the PNW (Paulitz et al., 2002; Smiley, 1996). Samples collected for these assays of nematodes during 1999 and 2000 also were evaluated for other diseases. Symptoms of take-all and Rhizocto-

nia root rot were particularly prevalent. Fungal pathogens may cause greater damage in roots initially wounded by lesion nematodes (Taheri et al., 1994). *Pratylenchus neglectus* was associated closely with Rhizoctonia root rot of winter wheat in Ontario, Canada (Benedict and Mountain, 1956). Although the fungal pathogen was considered most important in Canada, it was thought that *P. neglectus* assisted initiation of the root rot disease. Pathogens causing Rhizoctonia root rot and take-all each were found to increase lesion nematode reproduction in roots (Taheri et al., 1994). However, when both of these fungi occupied the same root tissue, the combination greatly reduced nematode reproduction. This apparently occurred because the roots were so heavily damaged by the fungi that there were few healthy cells available for nematode feeding and multiplication. Multiplication rates of lesion nematodes also were amplified when they entered root tissue already breached by fungal pathogens. It is clear that complex interactions occur among agents that cause root dysfunction, and that the potential exists for damage to be greater from combinations of organisms than from an organism acting alone.

The importance of stunt nematodes (*Tylenchorhynchus clarus* and *Geocenamus brevidens*) in PNW dryland field crops remains unknown. In our survey, stunt nematodes were detected in 37% of fields sampled during 2000. Hafez et al. (1992) reported that *Tylenchorhynchus* species, including *T. clarus*, were present in 10% of 128 wheat field samples in Idaho and eastern Oregon and that *G. brevidens* was present in 38% of fields. Stunt nematodes in this study were widespread and were not affected by tillage. Langdon et al. (1961) reported that wheat, barley, and oats each favored reproduction of *G. brevidens*, and that populations exceeding about 2,000/kg were associated with plant stunting and reduced grain yield in Oklahoma. Schlehner et al. (1965) attributed yield reductions to "high populations" of *G. brevidens* but did not provide quantitative data on populations. In this study, populations of stunt nematodes exceeded 1,000/kg soil in about 10% of the fields where this group of nematodes was detected. However, stunt nematodes always occurred in soils that were also inhabited by lesion nematodes and soilborne root-infecting fungal pathogens. Boag et al. (1990) concluded that yield reductions in Scotland were more likely to be attributable to combined populations of *Pratylenchus*, *Tylenchorhynchus*, and other genera than to individual genera of parasitic nematodes. Langdon et al. (1961) reported that damage caused by *G. brevidens* alone was less severe than when soils were infested with *G. brevidens* and the parasitic fungus *Olpidium brassicae*.

Pin nematodes (*Paratylenchus* spp.) were detected in high numbers in several dryland and irrigated fields, but their importance in cereals remains unknown. Hafez et al. (1992) also reported *Paratylenchus* spp. in

4% of wheat fields sampled in Idaho and eastern Oregon.

Populations of root-knot nematode (*Meloidogyne chitwoodi* and *M. naasi*) were comparatively low in this survey. None of the populations detected in the low-rainfall region exceeded 500 *Meloidogyne* spp./kg soil. While root-knot nematodes cause severe damage in some spring-planted cereals in irrigated fields in the PNW, populations at which damage has been documented (Griffin, 1993; Nyczepir et al., 1984; Patel and Patel, 1988; Rivoal and Cook, 1993; Santo and O'Bannon, 1981) were higher than populations detected in this study.

Non-plant-parasitic nematodes were generally present in significant proportions of the nematode fauna at all sites. In fields managed as winter wheat/summer fallow rotations, the population of non-plant parasites was higher in no-till than in tilled fields. Where fields were cropped more frequently than 50% of the years there was no influence of tillage on the population of non-plant-parasitic nematodes. Plant-parasitic nematodes typically constitute 50% or more of the total nematode fauna (Ferris and Ferris, 1974). In this study in low-rainfall environments with a winter-dominant rainfall distribution, the proportion of plant parasites varied from 6% to 62% of the total nematode population.

Further evaluations are warranted to more precisely define populations and potential damage associated with plant-parasitic nematodes and combinations of nematode and fungal pathogens in low-rainfall regions of the PNW. There is a particularly acute need to define the potential risk posed by lesion nematodes.

LITERATURE CITED

- Allmaras, R. R., P. W. Unger, and D. W. Wilkins. 1985. Conservation tillage systems and soil productivity. Pp. 357–412 in R. F. Follett and B. A. Stewart, eds. Soil erosion and crop productivity. Madison, WI: American Society of Agronomy.
- Armstrong, J. S., F. B. Peairs, S. D. Pilcher, and C. C. Russell. 1993. The effect of planting time, insecticides, and liquid fertilizer on the Russian wheat aphid (Homoptera: Aphididae) and the lesion nematode (*Pratylenchus thornei*) on winter wheat. *Journal of the Kansas Entomological Society* 66:69–74.
- Benedict, W. G., and W. B. Mountain. 1956. Studies on the etiology of a root rot of winter wheat in Southern Ontario. *Canadian Journal of Botany* 34:159–174.
- Boag, B., S. Bowen, A. M. Spaul, G. Wright, and B. F. L. Smith. 1990. Migratory plant-parasitic nematodes associated with cereals in Scotland. *Annals of Applied Biology* 117:399–406.
- Caveness, F. E. 1974. Plant-parasitic nematode population differences under no-tillage and tillage soil regimes in western Nigeria. *Journal of Nematology* 6:138.
- Conover, W. J. 1980. *Practical nonparametric statistics*, 2nd ed. New York: John Wiley and Sons.
- Cook, R. J. 2001. *Retooling agriculture: A report on direct-seed cropping systems research in the Pacific Northwest*. Washington State University PNW Extension Publication.
- Diebel, P. L., and D. A. Ball. 1999. Economic analysis of conservation farming systems for eastern Oregon wheat production. Oregon State University Agricultural Experiment Station Special Report 1004.
- Doyle, A. D., R. W. McLeod, P. T. W. Wong, S. E. Hetherington, and R. J. Southwell. 1987. Evidence for the involvement of the root lesion nematode *Pratylenchus thornei* in wheat yield decline in northern New South Wales. *Australian Journal of Experimental Agriculture* 27:563–570.
- Duff, B., P. E. Rasmussen, and R. W. Smiley. 1995. Wheat/fallow systems in semi-arid regions of the Pacific NW America. Pp. 85–111 in V. Barnett, R. Payne, and R. Steiner, eds. *Agricultural sustainability: economic, environmental, and statistical considerations*. London: John Wiley and Sons.
- Ferris, V. R., and J. M. Ferris. 1974. Inter-relationships between nematode and plant communities in agricultural ecosystems. *Agro-Ecosystems* 1:275–299.
- Gair, R., P. L. Mathias, and P. N. Harvey. 1969. Studies of cereal nematode populations and cereal yields under continuous or intensive culture [*Heterodera avenae*, *Pratylenchus neglectus*, *Trichodorus primitivus*]. *Annals of Applied Biology* 63:503–512.
- Glazer, I., and D. Orion. 1983. Studies on anhydrobiosis of *Pratylenchus thornei*. *Journal of Nematology* 15:333–337.
- Griffin, G. D. 1984. Nematode parasites of alfalfa, cereals, and grasses. Pp. 243–321 in W. R. Nickle, ed. *Plant and insect nematodes*. New York: Marcel-Dekker Inc.
- Griffin, G. D. 1993. Influence of temperature on the virulence of two races of *Meloidogyne chitwoodi* on wheat and barley. *Journal of Nematology* 25:454–460.
- Griffin, G. D., and K. B. Jensen. 1997. Differential effects of *Pratylenchus neglectus* populations on single and interplantings of alfalfa and crested wheatgrass. *Journal of Nematology* 29:82–89.
- Hafez, S. I., A. M. Golden, F. Rashid, and Z. Handoo. 1992. Plant-parasitic nematodes associated with crops in Idaho and eastern Oregon. *Nematropica* 22:193–204.
- Hollaway, G., and R. Eastwood. 1997. Root lesion nematode: Tolerance, resistance, and management strategies: What did we learn in 1996. *Crop Science Society of South Australia Newsletter* No. 157.
- Hollaway, G. J., S. P. Taylor, R. F. Eastwood, and C. H. Hunt. 2000. Effect of field crops on density of *Pratylenchus* in southeastern Australia, part 2: *P. thornei*. *Journal of Nematology* 32:600–608.
- Ingham, R. E. 1994. Nematodes in methods of soil analysis, part 2. Pp. 459–490 in R. W. Weaver, ed. *Microbiological and biochemical properties*. Madison, WI: American Society of Agronomy.
- Jatala, P., H. J. Jensen, and R. A. Shimabukuro. 1973. Host range of the "grass root-gall nematode," *Ditylenchus radicolica*, and its distribution in Willamette Valley, Oregon. *Plant Disease Reporter* 57:1021–1023.
- Jensen, H. J. 1961. Nematodes affecting Oregon agriculture. Oregon Agricultural Experiment Station Bulletin 579.
- Jensen, H. J., H. Eshtiaghi, P. A. Koepsell, and N. Goetze. 1975. The oat cyst nematode, *Heterodera avenae*, occurs on oats in Oregon. *Plant Disease Reporter* 59:1–3.
- Kort, J. 1972. Nematode diseases of cereals of temperate climates. Pp. 97–126 in J. M. Webster, ed. *Economic nematology*. London: Academic Press.
- Langdon, K. R., F. B. Struble, and H. C. Young, Jr. 1961. Stunt of small grains, a new disease caused by the nematode *Tylenchorhynchus brevidens*. *Plant Disease Reporter* 45:248–352.
- Lu, Z. P. 1983. The root gall disease of wheat. *Plant Protection* 9:41.
- Michalson, E. L., R. I. Papendick, and J. E. Carlson. 1999. Conservation farming in the United States: The methods and accomplishments of the STEEP program. Boca Raton, FL: CRC Press.
- Mojtahedi, H., and G. S. Santo. 1992. *Pratylenchus neglectus* on dryland wheat in Washington. *Plant Disease* 76:323.
- Mojtahedi, H., G. S. Santo, and J. M. Kraft. 1986. First report of *Pratylenchus thornei* on dryland wheat in Washington State. *Plant Disease* 72:175.
- Newcomb, G. B., R. E. Ingham, R. W. Smiley, and J. A. Pinkerton. 1989. Effects of nematocidal treatment on *Heterodera avenae* and wheat yield in Northeast Oregon. *Journal of Nematology* 21:576.
- Nicol, J. M. 1996. The distribution, pathogenicity, and population dynamics of *Pratylenchus thornei* (Sher and Allen, 1954) on wheat in South Australia. Ph.D. thesis. The University of Adelaide, Adelaide, Australia.
- Nicol, J. M. 2002. Important nematode pests of cereals. Pp. 345–

- 366 in B. C. Curtis, ed. Bread wheat: Improvement and production. Rome, Italy: FAO Plant Production and Protection Series.
- Nicol, J. M., K. A. Davies, T. W. Hancock, and J. M. Fisher. 1999. Yield loss caused by *Pratylenchus thornei* on wheat in South Australia. *Journal of Nematology* 31:367–376.
- Nicol, J., R. Rivoal, S. Taylor, and M. Zaharieva. 2003. Global importance of cyst (*Heterodera* spp.) and lesion nematodes (*Pratylenchus* spp.) on cereals: Yield loss, population dynamics, use of host resistance, and integration of molecular tools. *Nematology Monographs and Perspectives* 2:1–19.
- Nyczepir, A. P., R. N. Inserra, J. H. O'Bannon, and G. S. Santo. 1984. Influence of *Meloidogyne chitwoodi* and *Meloidogyne hapla* on wheat growth. *Journal of Nematology* 16:162–165.
- Ophel-Keller, K., and A. McKay. 2001. Root disease testing service: Delivery and commercialisation. Pp. 17–18 in I. J. Porter, ed. *Proceedings of the Second Australasian Soilborne Diseases Symposium*. Victoria, Australia: Department of Natural Resources & Environment.
- Orion, D., J. Kirkun, and J. Amir. 1982. Population dynamics of *Pratylenchus thornei* and its effect on wheat in a semiarid region. *Proceedings of the 16th International Symposium*. European Society for Nematology, St. Andrews, Scotland. p. 48.
- Overhoff, A. 1991. A vertical distribution of the plant-parasitic nematode community and nematophagous fungi under different tillage regimes. *Journal of Nematology* 23:546.
- Patel, Y. C., and D. J. Patel. 1988. Assessment of losses due to root-knot nematodes in wheat. *Pakistan Journal of Nematology* 6:45–47.
- Paulitz, T., R. Smiley, and R. J. Cook. 2002. Insights into the prevalence and management of soilborne cereal pathogens under direct seeding in the Pacific Northwest U.S.A. *Canadian Journal of Plant Pathology* 24:416–428.
- Rivoal, R., and R. Cook. 1993. Nematode pests of cereals. Pp. 259–3 in K. Evans, D. L. Trudgill, and J. M. Webster, eds. *Plant-parasitic nematodes in temperate agriculture*. Wallingford, UK: CAB International.
- Santo, G. S., and J. H. O'Bannon. 1981. Pathogenicity of the Columbia root-knot nematode (*Meloidogyne chitwoodi*) on wheat, corn, oat, and barley in the Pacific Northwest. *Journal of Nematology* 13:548–550.
- Schlehuber, A. M., J. Pass, and H. C. Young, Jr. 1965. Wheat grain losses caused by nematodes. *Plant Disease Reporter* 49:806–809.
- Sher, S. A., and M. W. Allen. 1953. Revision of the genus *Pratylenchus* (Nematoda: Tylenchidae). University of California Publications on Zoology 57:441–470.
- Smiley, R. W. 1996. Diseases of wheat and barley in conservation cropping systems of the semiarid Pacific Northwest. *American Journal of Alternative Agriculture* 11:95–103.
- Smiley, R. W., H. P. Collins, and P. E. Rasmussen. 1996. Diseases of wheat in long-term agronomic experiments at Pendleton, Oregon. *Plant Disease* 80:813–820.
- Smiley, R. W., R. E. Ingham, W. Uddin, and G. H. Cook. 1994. Crop sequences for winter wheat in soil infested with cereal cyst nematode and fungal pathogens. *Plant Disease* 78:1142–1149.
- Smiley, R. W., A. G. Ogg, Jr., and R. J. Cook. 1992. Influence of glyphosate on Rhizoctonia root rot, growth, and yield of barley. *Plant Disease* 76:937–942.
- Smiley, R., L. Patterson, K. Rhinhardt, and E. Jacobsen. 1999. Disease management for annual crops in low-rainfall regions. Oregon Agricultural Experiment Station Special Report 999:59–67.
- Smithson, H., L. B. Loring, and H. J. Jensen. 1963. The “grass root-gall nematode” found on annual bluegrass roots in Oregon. *Plant Disease Reporter* 47:440–441.
- Stinner, B. R., and D. A. Crossley, Jr. 1982. Nematodes in no-tillage agroecosystems. Pp. 14–28 in D. W. Freckman, ed. *Nematodes in soil ecosystems*. Austin, TX: University of Texas Press.
- Taheri, A., G. J. Hollamby, V. A. Vanstone, and S. M. Neate. 1994. Interaction between root lesion nematode, *Pratylenchus neglectus* (Rensch 1924) Chitwood and Oteifa 1952, and root rotting fungi of wheat. *New Zealand Journal of Crop and Horticultural Science* 22:181–185.
- Taylor, S. P., and M. L. Evans. 1998. Vertical and horizontal distribution of and soil sampling for root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) in South Australia. *Australasian Plant Pathology* 27:90–96.
- Taylor, S. P., G. J. Hollaway, and C. H. Hunt. 2000. Effect of field crops on population densities of *Pratylenchus neglectus* and *P. thornei* in southeastern Australia, part 1: *P. neglectus*. *Journal of Nematology* 32:591–599.
- Taylor, S. P., and V. A. Vanstone. 1996. Nematodes don't have to be the root of all crop problems. *Australian Grain* 6 (2):54–55.
- Taylor, S. P., V. A. Vanstone, A. H. Ware, A. C. McKay, D. Szot, and M. H. Russ. 1999. Measuring yield loss in cereals caused by root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) with and without nematocides. *Australian Journal of Agricultural Research* 50:617–622.
- Thomas, S. H. 1978. Population densities of nematodes under seven tillage regimes. *Journal of Nematology* 10:24–27.
- Thompson, J. P., J. MacKenzie, and R. Amos. 1995. Root-lesion nematode (*Pratylenchus thornei*) limits response of wheat but not barley to stored soil moisture in the Hermitage long-term tillage experiment. *Australian Journal of Experimental Agriculture* 35:1049–1055.
- Thompson, J. P., J. MacKenzie, and J. McCulloch. 1983. Root-lesion nematode (*Pratylenchus thornei*) on Queensland wheat farms. *Proceedings of the 26th International Congress of Plant Pathology*, Melbourne, Australia. Abstract 214.
- Van Gundy, S. D., B. Jose Gustavo Perez, L. H. Stolzy, and I. J. Thomason. 1974. A pest management approach to the control of *Pratylenchus thornei* on wheat in Mexico. *Journal of Nematology* 6:107–116.
- Vanstone, V., M. Farsi, T. Rathjen, and K. Cooper. 1994. Resistance of triticale to root lesion nematode in South Australia. *Proceedings of the 3rd International Triticale Symposium*, Lisbon, Portugal. The Netherlands: Kluwer Academic Press.
- Vanstone, V. A., A. J. Rathjen, A. H. Ware, and R. D. Wheeler. 1998. Relationship between root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) and performance of wheat varieties. *Australian Journal of Experimental Agriculture* 38:181–189.
- Vanstone, V. A., and M. H. Russ. 2001a. Ability of weeds to host the root lesion nematodes *Pratylenchus neglectus* and *P. thornei*. I. Grass weeds. *Australasian Plant Pathology* 30:245–250.
- Vanstone, V. A., and M. H. Russ. 2001b. Ability of weeds to host the root lesion nematodes *Pratylenchus neglectus* and *P. thornei*. II. Broad-leaf weeds. *Australasian Plant Pathology* 30:251–258.
- Yu, Qing. 1997. First report of *Pratylenchus thornei* from spring wheat in southern Ontario. *Canadian Journal of Plant Pathology* 19:289–292.