Pratylenchus neglectus Reduces Yield of Winter Wheat in Dryland Cropping Systems

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ABSTRACT

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Wheat (*Triticum aestivum*) in low-precipitation regions of eastern Oregon and Washington is grown mostly as rainfed biennial winter wheat (10-month growing season) planted into cultivated fallow (14-month crop-free period). There are increasing trends for cultivated fallow to be replaced by chemical fallow and for spring cereals to be planted annually without tillage. Most fields are infested by the root-lesion nematodes *Pratylenchus neglectus* or *P. thornei*. A replicated multiyear experiment was conducted to compare cropping systems on soil infested by *P. neglectus*. Populations became greater with increasing frequency of the host crops mustard, pea, and wheat. Annual winter wheat had the highest *P. neglectus* populations, the lowest capacity to extract soil water, and a lower grain yield compared with wheat grown biennially or rotated with other crops. Populations of *P. neglectus* did not differ for cultivated versus chemical fallow. Lowest populations occurred in annual spring barley. Winter wheat yield was inversely correlated with the population of *P. neglectus*. Measures to monitor and to reduce the population of *P. neglectus* in Pacific Northwest wheat fields are recommended.

Rainfed wheat (*Triticum aestivum* L.) is planted each year on 1.5 million ha in the low-precipitation region (150 to 300 mm) of north-central Oregon and south-central Washington. Precipitation occurs mostly (75%) from late autumn (October) to early spring (April) and the amount is highly variable from year to year. Winters are cold and intervals of frozen soil are common. Warm to hot days and cool nights prevail during the dry summer period. Maturation of cereal crops is dependent upon healthy root systems capable of extracting water stored deeply in the soil profile.

Ninety percent of hectares planted in this low-precipitation area are managed as a 24-month culture of winter wheat (10-month growing season) alternated with a 14-month fallow (crop-free) period. This production system is known in dryland regions throughout the world as a winter wheat–summer fallow rotation (14) and is referred to as biennial winter wheat in this article. Most fallow in Oregon and Washington (19) is managed as a cultivated "dust mulch" that provides comparatively high yields because it retains as much as 70% of the precipitation occurring during the winter of the fallow period. Each winter wheat crop, therefore, has access to water equivalent to as much as 75% of the precipitation occurring during the rotational sequence. Direct seeding into nontilled (herbicide-maintained) fallow, called chemical fallow, is becoming increasingly popular but still lags behind cultivated fallow because direct-drill (no-till) systems continue to be less profitable than cultivated fallow systems (2,11,18,19). Three-year rotations of winter wheat, a spring crop, and chemical fallow are of interest but have not been widely adopted because they are often less profitable and have greater year-to-year economic risk compared with biennial winter wheat. Direct-seeded fields planted annually to spring crops are also becoming increasingly practiced in the low-precipitation region. However, fields planted annually to no-till spring crops are planted mostly to wheat or barley (*Hordeum vulgare* L.) because these small-grain crops are more profitable than rotations that include broadleaf crops such yellow mustard (*Sinapsis alba* L.) or canola (*Brassica napus* L.). Although of increasing importance, annual no-till spring cropping is not yet widespread because it, too, is less profitable than biennial winter wheat (10,18). In continuous annual cropping systems in an intermediate-precipitation region, spring barley produces 34% greater yield than spring wheat in cultivated systems, 45% greater yield than spring wheat in direct-drill systems, 25% greater yield than biennial winter wheat planted into cultivated fallow, and 5% greater yield than biennial winter wheat planted into chemical fallow (11).

Root-lesion nematodes (*Pratylenchus* spp.) are present in 90% of the fields in low-precipitation regions of the Pacific Northwest (PNW; southern Idaho, eastern Oregon, and eastern Washington) and effects of crop management practices on nematode populations have not been clearly defined (21). Much higher populations of *Pratylenchus neglectus* (Rensch 1924) Filipjev Schuurmanns & Stekhoven 1941 and *P. thornei* Sher & Allen 1953 were detected in annually cropped fields than in biennial winter wheat. Lower populations following fallow (12) and direct associations between *Pratylenchus* spp. population density and frequency of cereal cropping have been reported in other countries (7,17). Barley is generally considered a poorer host than wheat (21,29,32,33).

P. neglectus and *P. thornei* cause substantial constraints to grain yield in rainfed cereals (4,22). *P. neglectus* and *P. thornei* have each reduced yields of annually cropped spring wheat by as much as 70% in the PNW (25,26) but these studies did not compare representative crop management systems for effects on or by species of *Pratylenchus*. Presumptive evidence was presented for reduction of winter wheat yield by *P. neglectus* but the effects of the rotational sequences on potential variability in stored soil water were not defined in that study (21). Thompson et al. (31) reported that the greater tolerance of barley to *P. thornei* compared with wheat enabled barley, in *P. thornei*-infested soil, to have greater efficiency in extracting and be more responsive than wheat to stored soil moisture in a year with limited in-crop rainfall.

A replicated multiyear experiment was established during 2003 to examine the multidisciplinary aspects of eight representative cropping systems at a low-precipitation site known to be infested with *P. neglectus*. This article reports associations between cropping systems, nematode populations, grain yields, and water extraction over the first 5 years of the experiment.

MATERIALS AND METHODS

The experiment was performed at the Columbia Basin Agricultural Research Center 1 km southeast of Moro, Sherman County, OR (45°29.041′ N and –120°43.127′ W). The site is at 575 m of elevation and receives 282 mm of mean annual precipitation, nearly all of which occurs from late

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autumn (October) through spring (May). Mean daily air temperature is –1°C during January and 19°C during July and August. Soil is a moderately deep (mostly >120 cm) Walla Walla silt loam; coarse-silty, mixed, superactive, mesic Typic Haploxeroll. Daily precipitation was measured at a weather station at the experimental site (NOAA–National Climatic Data Center Cooperator No. 355734; "Moro, OR" in http://nowdata.rcc-acis.org/PDT/pubACIS_results).

Crops and crop management. A uniform crop of spring wheat was planted over the intended experimental area during 2003. The experimental area was mapped into 42 plots of 15 by 105 m arranged as three randomized blocks of 14 plots representing eight crop treatments. Numbers of plots in each block were greater than the number of crop treatments because each phase of each multiyear crop sequence was present in all years to allow treatment data to be collected for each year. The eight treatments included annual winter wheat; annual spring wheat; annual spring barley; biennial winter wheat with either cultivated fallow or chemical fallow; a 2-year rotation of winter wheat and winter pea (*Pisum sativum* L. subsp. *arvense* (L.) Poir.); a 3-year rotation of winter wheat, spring barley, and chemical fallow; and two flexible cropping (flex-crop) treatments that allowed annual flexibility in selecting the crop species produced. Flex-cropping decisions were made by an advisory committee of the project leader and producers and were based upon market prices, soil moisture available before planting, and occurrences of weeds and diseases. Flex-crop treatments included winter wheat, chemical fallow, and spring-planted crops of barley, camelina (*Camelina sativa* L.), pea (*P. sativum* L.), mustard, and wheat.

Seven of the eight crop treatments were managed without tillage (no-till) using direct-drill technology. All direct-drill treatments were planted using a Fabro disk-type drill (Fabro Ltd., Swift Current, Saskatchewan, Canada) with 30-cm row spacing. A blend of urea and ammonium sulfate was banded 2.5 cm below the seed of all direct-drill small grains crops at application rates based upon industry standards and results of annual soil tests by commercial laboratories. Herbicides were applied to all crop treatments during the growing season in accordance with weed populations and industry standards.

Direct-drill spring wheat and spring barley occurred in the annual crop sequences and in the 3-year and flex-crop rotations (Table 1). These crops were planted at a rate of 222 to 322 seeds/m^2 in April. Cultivars of spring wheat included Zak in 2004 and 2005 and Louise from 2006 to 2008. The spring barley cultivar was Camas from 2004 to 2007 and Haxby during 2008. Direct-drill winter pea occurred in the 2-year rotation and was planted at 78 seeds/m^2 during October or November. Cultivars were Line 706 in 2004 and Spector from 2005 to 2008. Granular inoculant (Nitragin; EMD Crop Bioscience, Brookfield, WI) was applied with the seed and starter fertilizer (N at 9 kg/ha) was banded below the seed at a depth of 7.5 cm. Direct-drill spring camelina (cv. Calena), spring mustard (cv. Tilney), and spring pea (cv. Universal, inoculated with Nitragin) occurred in the flex-crop treatments. These crops were planted in April at rates of 260, 250, and 75 seeds/m^2, respectively.

Direct-drill winter wheat occurred in the annual and biennial crop sequences, the 2- and 3-year rotations, and in flex-crop rotation no. 2 (Table 1). Plots to be planted to direct-drill winter wheat were sprayed once in late September or early October with glyphosate to control summer weeds. Glyphosate was also applied to control weeds two to three additional times during the spring and summer of the fallow phase of the direct-seeded biennial winter wheat treatment managed with chemical fallow. Direct-drill winter wheat was planted in October or November at a rate of 220 to 244 seeds/m^2. Cultivars were Tubbs in 2004, Stephens in 2005, and ORCF-101 from 2006 to 2008.

Compared with direct-drill treatments, management of biennial winter wheat differed considerably when planted into cultivated fallow. After a biennial wheat crop was harvested during the summer, the plots were not cultivated until mid-April of the following year. Glyphosate was applied as needed in the fall and spring. In April, primary tillage was conducted to a depth of 15 cm using a John Deere 1600 (John Deere, Inc., Moline, IL) cultivator fitted with chisel plow turning points, followed by sweep cultivation to a depth of 13 cm

Table 1. Crop management treatments and density of *Pratylenchus neglectus* in the upper 15 to 30 cm of the soil profile during 5 years of eight crop sequences at Moro, OR

	Harvested crop or field management[w]					*P. neglectus* nematodes/kg of soil[x]					
Crop sequence	**2004**	**2005**	**2006**	**2007**	**2008**	**2004**	**2005**	**2006**	**2007**	**2008**	**Mean**
Annual spring barley	SB	SB	SB	SB	SB	297 a	2,409 a	470 bcd	691 cd	413 e	626 b
Annual spring wheat	SW	SW	SW	SW	SW	247 a	2,832 a	1,129 abc	3,617 ab	8,641 ab	1,900 ab
Annual winter wheat	WW	WW	WW	WW	WW	573 a	2,796 a	3,126 a	4,464 a	5,877 ab	2,653 a
Biennial winter wheat (ChF)	WW	ChF	WW	ChF	WW	3,800 a	897 a	1,082 abc	2,932 ab	4,706 abc	2,195 ab
Biennial winter wheat (ChF)	ChF	WW	ChF	WW	ChF	422 a	413 a	216 d	732 cd	3,663 abcd	633 b
Biennial winter wheat (CuF)	WW	CuF	WW	CuF	WW	1,369 a	4,920 a	938 abc	3,253 ab	3,276 abcd	2,321 a
Biennial winter wheat (CuF)	CuF	WW	CuF	WW	CuF	604 a	861 a	984 abc	684 cd	2,440 abcd	969 ab
2-year rotation	WW	WP	WW	WP	WW	838 a	1,483 a	1,187 abc	5,401 a	11,052 a	2,449 a
2-year rotation	WP	WW	WP	WW	WP	335 a	1,356 a	1,691 ab	2,268 abc	7,326 ab	1,665 ab
3-year rotation[y]	WW	SB	ChF	WW	SB	591 a	1,886 a	885 abcd	371 d	931 de	806 ab
3-year rotation	SB	ChF	WW	SB	ChF	709 a	353 a	342 cd	2,160 abc	1,886 bcde	810 ab
3-year rotation	ChF	WW	SB	ChF	WW	1,166 a	1,873 a	1,632 ab	1,668 abc	1,199 cde	1,481 ab
Flex crop rotation no. 1[z]	SB	SW	SM	SW	SP	767 a	2,322 a	670 bcd	1,839 abc	7,708 ab	1,760 ab
Flex crop rotation no. 2	SW	SB	ChF	WW	SC	458 a	1,482 a	1,542 ab	1,100 bcd	2,803 abcd	1,265 ab
$P > F$	…	…	…	…	…	0.313	0.762	0.072	0.005	0.006	<0.001
CV (%)	…	…	…	…	…	16.9	21.2	12.5	10.4	11.3	14.3

[w] ChF = chemical fallow, CuF = cultivated fallow, SB = spring barley, SC = spring camelina, SM = spring mustard, SP = spring pea, SW = spring wheat, WP = winter pea, WW = winter wheat. The experimental area was planted uniformly to spring wheat in 2003. All except the biennial winter wheat (CuF) treatment were direct seeded (e.g., no-till).

[x] Data are from back-transformed means of the $\ln(x + 1)$ transformation used for analysis of variance. Means followed by the same letter within a column are not significantly different at $P = 0.05$ according to the Student-Newman Kuels means test applied to log-transformed data. Sampling was from the surface 15 cm on 10 March 2004 and 7 March 2005, and from the surface 30 cm on 4 April 2006, 2 April 2007, and 14 April 2008. Crops planted during the autumn were in-crop for 5 months prior to sampling. All spring crops and fallow treatments were sampled shortly before or after spring crops were planted.

[y] The three winter wheat plots (replicates) in the 3-year rotation were very dry and compact on 2 April 2007, making it impossible to collect manual core samples to the same depth as for all other plots which had greater soil moisture. Low numbers of *P. neglectus* in those three plots may be biased by a slightly shallower sampling depth during 2007.

[z] Flex crop = rotational sequences were reexamined annually to facilitate real-time management decisions based upon considerations of available stored water, crop prices, and occurrences of weeds and diseases.

using the JD 1600 equipped with 30-cm wide sweeps. Plots were rod weeded (19) at a depth of 8 to 10 cm whenever necessary to maintain weed control and the dust mulch fallow. Plots were generally rod weeded two or three times between May and August. In accordance with industry standards and based on soil sampling, anhydrous ammonia and gypsum were incorporated into fallow treatments during September to meet soil fertility requirements. Winter wheat was planted at 200 to 244 seeds/m^2 in mid-September using a John Deere 7616 HZ drill with 40-cm row spacing. Cultivars were the same as for direct-drill winter wheat.

All crops were harvested in late July or early August. A strip following the centerline of each 15-m-wide plot was harvested using a commercial combine with a 5.5-m header. Grain yield was measured using a weigh wagon to determine yield per plot.

Soil water. Measurements of soil water content were conducted throughout the 2006 and 2007 growing seasons using a PR2 probe (Delta-T Devices Ltd., Cambridge, England). Access tubes were inserted by extracting a soil core (27 mm in diameter by 1 m in depth) using a tractor-mounted Giddings GSRTS Model 15-TS Hydraulic Soil Sampler (Giddings Machine Company, Windsor, CO). The PR2 probe senses soil moisture content (percent volume) at 10-, 20-, 40-, 60-, and 100-cm depths by responding to dielectric soil properties. Readings were made on two access tubes located 15 m apart in each plot. At each reading, three measurements were recorded, each time with the probe rotated to a different direction.

Routine soil sampling and nematode extraction. Soil was collected each year to assess *Pratylenchus neglectus* populations in individual treatments when soil was moist shortly before or after spring crops were planted. Sampling dates were 10 March 2004, 7 March 2005, 4 April 2006, 2 April 2007, and 14 April 2008. Samples consisted of 20 cores (2.5 cm in diameter) composited for each of 42 plots; 14 treatments × 3 replicates = 42 samples. Samples were collected to the 15-cm depth during 2004 and 2005 and to the 30-cm depth during 2006 to 2008, in response to our observation that deeper sampling was necessary to adequately quantify populations of lesion nematodes in wheat–fallow rotations (24). Samples were stored moist at 4°C for up to 7 days before being transported to Western Laboratories (Parma, ID) for nematode extraction and identification. A modified elutriation method (9) was used to extract all soil-dwelling nematodes from 250-g subsamples of soil plus root fragments. Using the laboratory's self-constructed Oosterbrink elutriator, coarse material was collected on a 500-µm sieve and nematodes on a stack of two 38-µm and two 32-µm sieves. Nematodes were washed into 100-ml cups, suspensions were stored overnight, and settled nematodes were transferred to 50-ml centrifuge tubes and concentrated at 3,200 rpm for 5 min. Water was discarded, replaced by magnesium sulfate solution at specific gravity 1.80, mixed by spatula, and centrifuged again at 3,200 rpm for 4 min. The supernatant solution containing nematodes was passed over a 20-µm sieve, transferred by gentle washing with tap water to another 50-ml tube, and allowed to settle for at least 2 h before counting.

Enumeration of nematodes was performed by reducing the volume of suspension in the 50-ml tubes to 10 ml, mixing the remaining suspension in a minivortex mixer at 400 rpm for 5 s, removing 4 ml of suspension, placing 1 ml on a Peter's counting slide (Takizawa Nematology Supply Co., Tokyo), counting and identifying all plant-parasitic nematode genera on the slide, and reporting nematodes per kilogram of oven-dry soil. Suspensions were returned to our laboratory for identification of *Pratylenchus* spp. using polymerase chain reaction amplification of DNA (35) extracted from the nematodes quantified by Western Laboratories. Morphological characteristics and measurements were also used to confirm identities of *Pratylenchus* spp. in selected suspensions (8).

Profile depth sampling. Soil cores were collected during 2005 and 2008 using the Giddings Hydraulic Soil Sampler with a 5-cm-diameter, 150 cm-long slotted soil tube and heavy-duty bit. Soil cores were collected to the 120-cm depth and separated into 15-cm intervals from 0 to 60 cm of depth and into 30-cm intervals from 60 to 120 cm of depth during 2005. Cores were separated into four 30-cm-depth intervals during 2008. A pair of soil cores was collected 1 m apart at each sampling location to ensure that sufficient soil was collected for each depth interval and to minimize the effect of the inherent spatial variability of *Pratylenchus* spp. Corresponding depth intervals from the pair of cores taken from each sampling location were composited into samples and stored at 4°C until processing.

During 2005, the deep core samples were taken from 15-by-40-m areas near one end of three replicates in five rotations on 1 June: annual spring barley, annual spring wheat, annual winter wheat, and the in-crop phases of biennial winter wheat managed with either chemical or cultivated fallow. During 2008, the cores were collected across the entire treatment area of all 42 plots during a 10-day period of April 2008. Sampling intensities within treatments were one location per 200 and 525 m^2 during 2005 and 2008, respectively, exceeding the density of one location per 1,575 m^2 considered necessary to effectively characterize populations of *P. thornei* (30).

Nematodes were extracted during 2008 using procedures described above. During 2005, nematodes were extracted by the Whitehead tray method (34). Plastic mesh was cut to fit inside a plastic-coated wire tray that was then placed into a 32-by-40-cm flat-bottomed plastic tub. Two two-ply facial tissues, slightly overlapping, were laid over the plastic mesh. A 200-g subsample from a thoroughly mixed soil sample was spread in a 1-cm layer over the tissues. One liter of tap water was added to the plastic tub so that the water level in the tray was enough to moisten the soil but not to cause waterlogging. Nematodes from soil and root segments were collected in the reservoir of water. Samples were extracted for 48 h in a constant-temperature room (22°C), which would provide an extraction efficiency of approximately 77% (1). The basket was then lifted out of the water and allowed to drain before the tissue and soil were discarded. Water in the tub was agitated and poured through a 20-µm sieve. The tub was rinsed once and the water was passed through the sieve. The sieve was then rinsed twice with minimal water volume (about 25 ml) and the suspension containing nematodes was collected in a 50-ml vial. The volume of extract was determined in relation to an empty vial with etched calibrations and samples were stored at 4°C. Numbers of *P. neglectus* were determined and identified as described previously.

Statistical analysis. Nematode data were transformed using ln(x + 1) to normalize population estimates (15) prior to statistical analysis. Results were analyzed using one-way analysis of variance (ANOVA) and the logarithmic means were back transformed for presentation. Grain yields were also analyzed by one-way ANOVA. Long-term effects of rotations were evaluated by grouping grain yield and nematode data over years for analysis using one-way ANOVA, with crop treatment as the variable and replicates as blocks. Subsets of data were also evaluated by one-way ANOVA. Examples of subsets include soil sampling depth intervals grouped across crop treatments, crop treatments grouped according to the crop or field management treatment immediately preceding a soil sampling date, the two crops, or management treatments before samples were collected. Each analysis was performed using CoStat Statistical Software (version 6.311; CoHort Software, Monterey, CA). Treatment means were either separated using the Student-Newman Kuels means test or the least significant difference (LSD). Associations of grain yields and nematode populations, and results of hand sampling versus mechanized core sampling procedures to assess nematode populations, were evaluated by regression analysis.

RESULTS

Precipitation totals for crop years (September through August) 2003, 2004, 2005, 2006, 2007, and 2008 were 236, 303, 200, 430, 281, and 222 mm, respectively. Only about 80% of the incipient precipitation infiltrated into soil and became effective for crop use because the total precipitation amounts include rainfall events in which the amount of rain was less than the evaporative potential over the following 24-h period, and snow events in which the snow was sublimated into the vapor phase before it melted and infiltrated soil during the winter.

The only plant-parasitic nematode considered capable of affecting plant health in this experiment was *P. neglectus*. Numbers of this species were vastly greater than for any other plant-parasitic species, which were detected infrequently (usually in fewer than 3 of 42 plots each year) and in low numbers (<30/kg of soil), with no patterns associated with crop rotation, replicate block, or tillage treatment. Other plant-parasitic nematodes included *P. thornei* and species of *Criconemoides*, *Geocenamus*, *Helicotylenchus*, *Heterodera*, *Meloidogyne*, *Paratylenchus*, and *Tylenchorhynchus*.

P. neglectus populations did not significantly differ ($P < 0.10$) among treatments during the first 2 years of this experiment (Table 1). The population during 2006 was significantly ($P = 0.07$) higher in annual winter wheat than in annual spring barley, the fallow phase of the biennial winter wheat (chemical fallow) treatment, and winter wheat following chemical fallow in the 3-year rotation. In 2007 the population of *P. neglectus* was again high in annual winter wheat as well as in annual spring wheat, winter pea of the 2-year rotation, and both types of fallow in the biennial winter wheat treatment. Populations during 2007 were lowest for annual spring barley, biennial winter wheat following both types of fallow, and winter wheat in the 3-year rotation. Populations of *P. neglectus* in both biennial winter wheat treatments were greater in the fallow phase than in the in-crop phase during 2007. During 2008, the *P. neglectus* population was highest in winter wheat of the 2-year rotation and lowest in annual spring barley and each phase of the 3-year rotation.

Populations of *P. neglectus* averaged over the 5-year sampling period revealed that highest mean numbers corresponded in general with the frequency of wheat crops in the crop sequence. The highest mean numbers (Table 1) occurred in annual winter wheat and annual spring wheat (a wheat host in 5 of 5 years), the 2-year rotation, the biennial winter wheat sequences in which wheat was produced in 3 of 5 years, and in the flex-crop rotation no. 1, in which spring wheat and spring mustard were produced in 3 of 5 years. The lowest mean numbers occurred in annual spring barley, the biennial winter wheat sequences in which wheat was produced in only 2 of 5 years, and in the 3-year rotations in which wheat was produced in only 1 or 2 of 5 years. The type of fallow practiced for biennial winter wheat had no long-term effect on populations of *P. neglectus* during this 5-year study.

Populations of *P. neglectus* were also analyzed to determine effects of the preceding crop or fallow treatment from 2005 to 2008. Populations were higher after spring wheat than after spring barley and chemical fallow (Table 2). Although not significantly different, high populations were also measured in soil after production of winter pea and winter wheat. The influence of spring mustard on populations of *P. neglectus* was intermediate between wheat and barley, and there were no differences between cultivated and chemical fallow in biennial winter wheat.

Five rotations were sampled during 2005 using a hydraulic soil probe to examine the distribution of *P. neglectus* through the soil profile. Nematodes were confined mostly to the upper 45 cm of the profile in four rotations but were present to the maximum sampling depth of 120 cm in annual winter wheat (Table 3). Very few *P. neglectus* individuals were detected at any profile depth in annual spring barley. Populations of *P. neglectus* differed significantly ($P < 0.10$) among profile depths in the annual spring wheat and the biennial winter wheat treatments. The maximum density for the spring wheat treatment was detected in the 0- to 15-cm depth interval. Highest nematode densities were detected in the 15- to 30-cm depth interval for the three crop sequences in which winter wheat was produced. In the 15- to 30-cm depth interval, annual spring wheat had a much lower population than the winter wheat sequences. Sampling only the upper 15 cm detected fewer than 10% of the total number of *P. neglectus* nematodes in several of the winter wheat soil profiles, compared with detections of 25 and 64% of total populations in the upper 15 cm of annual spring barley and annual spring wheat. This information was used as the basis for increasing the 15-cm depth for routine soil sampling in 2004 and 2005 to a 30-cm depth from 2006 to 2008.

Results of deep core data collected from the 42 plots during 2008 were similar to those in the five plots sampled during 2005. Low numbers (<300/kg of soil) of *P. neglectus* were detected throughout the profile of annual spring barley (Fig. 1). Populations were higher in annual spring wheat and annual winter wheat but the peak population density was about 30 cm deeper in the profile for winter wheat than for spring wheat. Populations of *P. neglectus* were particularly high following se-

Table 2. Mean density and standard error of the mean for *Pratylenchus neglectus* in the 0- to 30-cm soil-depth profile during the spring following production of a specific crop or fallow management treatment over the 4-year interval 2005 to 2008 in eight crop sequences at Moro, OR

Previous crop or management[y]	*P. neglectus* nematodes/kg of soil[z]
Spring wheat (21)	2,582 ± 338 a
Winter pea (12)	2,520 ± 442 ab
Winter wheat (63)	2,276 ± 162 ab
Spring mustard (3)	1,839 ± 1,217 ab
Cultivated fallow (12)	1,160 ± 654 ab
Chemical fallow (30)	971 ± 212 b
Spring barley (27)	967 ± 309 b
$P > F$	0.0022
CV (%)	16.0
Total df	167

[y] Data are means of the total number of times (shown in parenthesis) each crop or fallow management sequence occurred over the 4-year interval in eight cropping sequences. CV = coefficient of variance.

[z] Nematode data are back-transformed from $\ln(x + 1)$ transformations used for analysis of variance. Means followed by the same letter within a column are not significantly different at $P = 0.05$ according to the Student-Newman Kuels means test applied to log-transformed data.

Table 3. Density of *Pratylenchus neglectus* at 15- to 30-cm depth intervals of the soil profile in five crop sequences at Moro, OR in June 2005

	P. neglectus nematodes/kg of soil[y]				
	Annual			Biennial	
Depth interval (cm)[z]	SB	SW	WW	WW (ChF)	WW (CuF)
0–15	81	1,022	779	9	181
15–30	105	312	3,664	2,781	3,020
30–45	66	183	2,239	770	2,194
45–60	59	62	327	33	64
60–90	9	8	1,160	3	7
90–120	6	0	462	0	4
Mean (0–45 cm)	82	388	1,856	280	1,065
Mean (0–120 cm)	36	56	1,019	37	121
$P > F$	0.3640	0.0785	0.7681	0.0129	0.0178
CV (%)	50.7	65.5	32.5	64.2	44.8
$LSD_{0.05}$	ns	ns	ns	69	49
$LSD_{0.10}$	ns	49	ns	31	23

[y] ChF = chemical fallow, CuF = cultivated fallow, SB = spring barley, SW = spring wheat, WW = winter wheat. All except the biennial winter wheat (CuF) treatment were direct seeded (e.g., no-till). Data are from back-transformed means of the ln(x+1) transformation used for analysis of variance.

[z] CV = coefficient of variance and LSD = least significant difference; ns = not significant.

quences of spring mustard and spring wheat, and of winter pea and winter wheat. Compared with annual winter wheat, populations of *P. neglectus* diminished when winter wheat was rotated with either chemical or cultivated fallow. As during 2005, populations in several of the soil profiles were more efficiently detected by sampling to the 30-cm depth compared with the 15-cm depth used for routine samplings made during 2004 and 2005.

Populations of *P. neglectus* were also analyzed by combining data for successive pairs of 15-cm depth intervals collected to a depth of 60 cm, then grouping the 30-cm depth intervals across crop sequences and analyzing the data using ANOVA. Higher populations ($P < 0.0001$; $LSD_{0.05} = 814$/kg of soil) occurred in the 0- to 30-cm and 30- to 60-cm intervals (3,524 and 4,409/kg, respectively) than in the 60- to 90-cm (1,569/kg) and 90- to 120-cm (409/kg) intervals. Results of data collected in the 0- to 30-cm interval during 2008 were comparable for three pairs of deep cores collected by hydraulic sampler and 20 cores collected by manual sampling (Fig. 2).

When data were grouped over the entire 120-cm profile depth and also across each phase of each crop treatment, then analyzed by ANOVA, the mean number of *P. neglectus* was higher ($P < 0.0001$) in flex-crop rotation no. 1 (3,679/kg of soil), the 2-year rotation (3,500/kg) and biennial winter wheat with chemical fallow (1,944/kg) compared with the annual spring barley (174/kg) and 3-year rotation (697/kg).

Populations of *P. neglectus* were also averaged over the upper 60 cm of soil and analyzed by ANOVA using the two most recent crops or fallow management prior to sampling as treatments and replicates as blocks. Means and multiple-range separations are shown in Figure 3. Two successive crops of spring barley had fewer ($P <$ 0.0001, coefficient of variance = 9.2%) mean numbers of *P. neglectus* nematodes than all other treatments. Spring barley was also as effective as chemical fallow for reducing numbers of *P. neglectus* nematodes compared with annual winter wheat. Populations of *P. neglectus* were greatest following the 2-year rotation of winter pea and winter wheat, annual spring wheat, and the 2-year sequence of spring wheat and spring mustard in flex-crop no. 1.

Data was also evaluated to determine effects of recent crop history on the proportion of the total *P. neglectus* population detected in each successively deeper 30-cm segment of the soil profile. Proportions of total populations detected in the uppermost 0- to 30-cm interval were highest following 2 years of winter wheat (63%) and lowest following 2 years of spring wheat (19%), with other treatments being intermediate (Fig. 4). Compared with the 0- to 30-cm depth interval, proportions of the total population were much higher in the 0- to 60-cm and 0- to 90-cm depth intervals; 74 to 87% and 92 to 99%, respectively. When averaged across all treatments, the proportion of the total *P. neglectus* population occurring in samples collected to depths of 30, 60-, and 90 cm were 36, 81, and 96%, respectively.

Grain yield differed ($P < 0.05$) among treatments during 2004 (Table 4) but the result was considered to have no importance with respect to crop rotation effects being investigated because 2004 was the first rotational sequence following a uniform crop of spring wheat during 2003. In 2005, spring crops fared poorly due to drought. Highest yields were produced by winter wheat in the 2- and 3-year rotations and in biennial wheat with cultivated fallow. During 2006, spring barley in the annual crop sequence and in the 3-year rotation produced yields statistically equivalent ($P < 0.05$) to biennial winter wheat with cultivated fallow and winter wheat in the 3-year rotation. The lowest yields in 2006 were for annual winter wheat and winter wheat in the 2-year rotation. In 2007, the highest yields were from winter wheat in the 3-year rotation and in the biennial winter wheat with cultivated fallow. The lowest wheat yield during 2007 was the spring wheat in flex-crop no. 1, following a sequence of spring wheat and spring mustard.

Mean grain yields over the three crop years 2005 to 2007 (Table 4) indicated that the highest yields were achieved for winter wheat in the 3-year rotation and in the biennial sequence with cultivated fallow, followed in order by biennial winter wheat with chemical fallow, winter wheat in the 2-year rotation, annual spring barley, and spring barley in the 3-year rotation. The lowest mean cereal grain yields were achieved with annual winter wheat and annual spring wheat. The yields for winter wheat in five crop sequences (all except the flex-crops) from 2005 to 2008 were strongly and negatively correlated with populations of *P. neglectus* in the upper 30

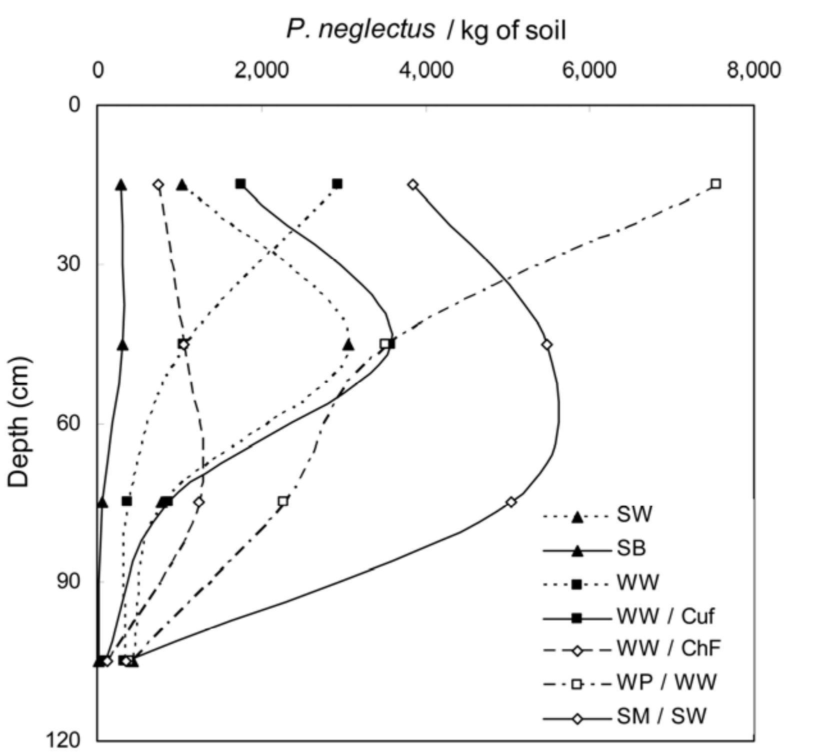

Fig. 1. Profile distribution of *Pratylenchus* spp. in seven crop sequences in the long-term experiment at Moro during April 2008: direct-drill annual spring wheat (SW), direct-drill annual spring barley (SB), direct-drill annual winter wheat (WW), direct-drill spring wheat after spring mustard (SM/SW), biennial winter wheat with either cultivated fallow (WW/CuF) or chemical fallow (WW/ChF), and winter wheat rotated with winter pea (WP/WW).

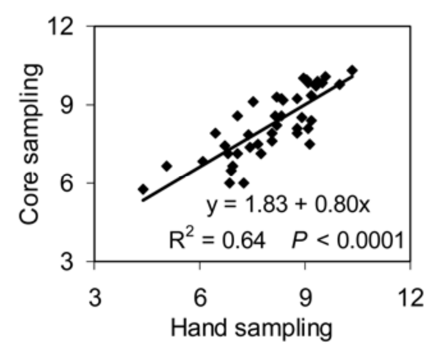

Fig. 2. *Pratylenchus neglectus* populations detected in the surface 30 cm of soil profiles in 42 plots of the long-term experiment at Moro during April 2008; comparison of soils sampled by mechanized deep-coring (three pairs of 5-cm-diameter cores per plot) and by manual hand probing (20 samples of 2.5 cm in diameter per plot). Data are means of $\ln(x + 1)$ transformations of *P. neglectus* nematodes/kg of soil.

cm of soil during the spring (Fig. 5). The lowest yields shown in Figure 5 correspond to the datum points for annual winter wheat. A comparable regression (y = 3,469 – 0.43x, R^2 = 0.46, P < 0.0001, 30 df) was detected when the data in Figure 5 were supplemented with 12 additional datum points for annual spring wheat, annual spring barley, and spring barley in the 3-year rotation.

Soil water content was monitored in the profiles of each crop sequence during the spring and summer of 2006 and 2007. Three soil moisture patterns were evident during 2006 (Fig. 6A). Greater moisture was present at the end of the growing season for the three fallow treatments compared with all winter wheat treatments except annual winter wheat, which was intermediate between the fallow treatments and winter wheat in other crop sequences. Compared with winter wheat in other crop sequences, the annual winter wheat extracted a lower amount of water from soil (Fig. 6A) and had the greatest population of *P. neglectus* (Table 1) and lowest grain yield (Table 3). The soil moisture patterns were similar in 2007, when the fallow treatments again retained more water than planted treatments (Fig. 6B). Extraction of water was slightly less for annual winter wheat compared with winter wheat in all other rotations and also had a high population of *P. neglectus* (Table 1) and a low grain yield (Table 3).

DISCUSSION

P. neglectus population density and vertical distribution in soil profiles were strongly influenced by cropping systems in a low-precipitation region of north-central Oregon. The lowest populations were detected when barley was planted annually and the highest populations occurred when winter wheat was planted annually or rotated with winter pea. These results are in agreement with recognition of barley as generally more tolerant and more resistant than wheat to *P. neglectus* and *P. thornei* (21,24,29,32,33). Our findings are also in agreement with previous observations that *Pratylenchus* spp. become more numerous as host-crop frequency is increased (7,17). Although Strausbaugh et al. (27) detected fewer *Pratylenchus* spp. in chemical than mechanical fallow, no differences between fallow type were detected in this study or by Brmež et al. (3) or Smiley et al. (21). Likewise, observations at another Oregon location indicated that the *P. neglectus* population was comparable following mustard and wheat (24). However, it was unexpected that *P. neglectus* populations in the winter wheat–winter pea rotation would be comparable with those in rotations containing known "good" host species (32,33) every year, as in annual winter wheat and annual spring wheat. Field pea was resistant to *P. neglectus* in Australia (33) but was associated with high populations of *Pratylenchus* spp. in the PNW (16). Our study confirms the necessity to further examine the role of field pea in developing high populations of *Pratylenchus* spp. capable of damaging roots of wheat.

Biennial winter wheat in Oregon is typically planted into cultivated fallow during September and into chemical fallow during October. Seedlings become established and reach the second- through fourth-leaf stage (Feekes scale 1 or Zadoks scale 12 to 14; 5) before onset of semidormancy during winter. Active seedling growth resumes during early spring at a time when spring cereals are being planted. Soil sampling to

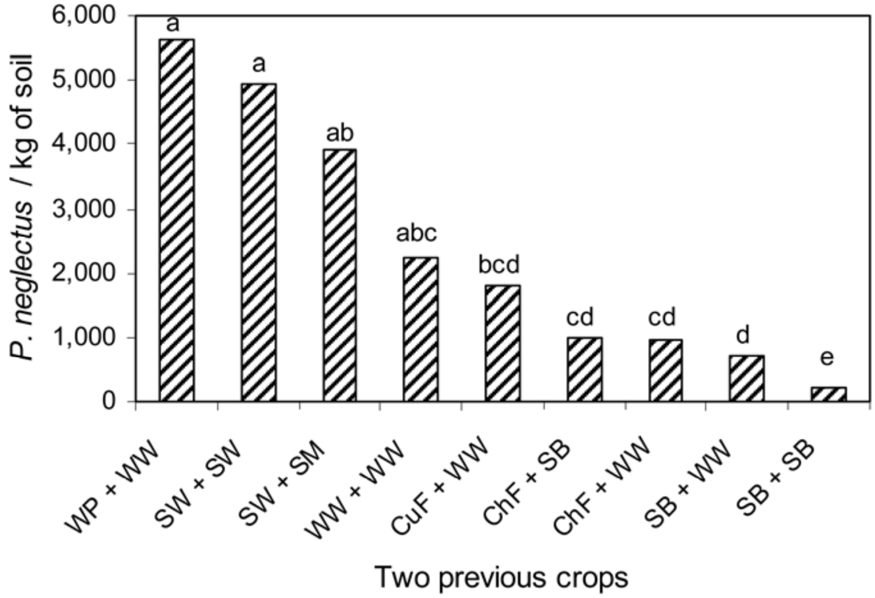

Fig. 3. Mean density of *Pratylenchus neglectus* averaged over the upper 60-cm soil profiles of eight crop sequences when analyzed in relation to the last two crops or treatments prior to collecting deep soil cores in the long-term experiment at Moro during April 2008. Data are means of ln(x + 1) transformations of *P. neglectus* nematodes/kg of soil averaged over the 60-cm depth interval. Treatments with the same letter do not differ at P = 0.05. Each datum bar represents a single observation of a 2-year crop sequence except for WP+WW (two treatments) and CF+WW (five treatments). The treatments and crops were chemical fallow (ChF), cultivated fallow (CuF), spring barley (SB), spring mustard (SM), spring wheat (SW), winter pea (WP), and winter wheat (WW).

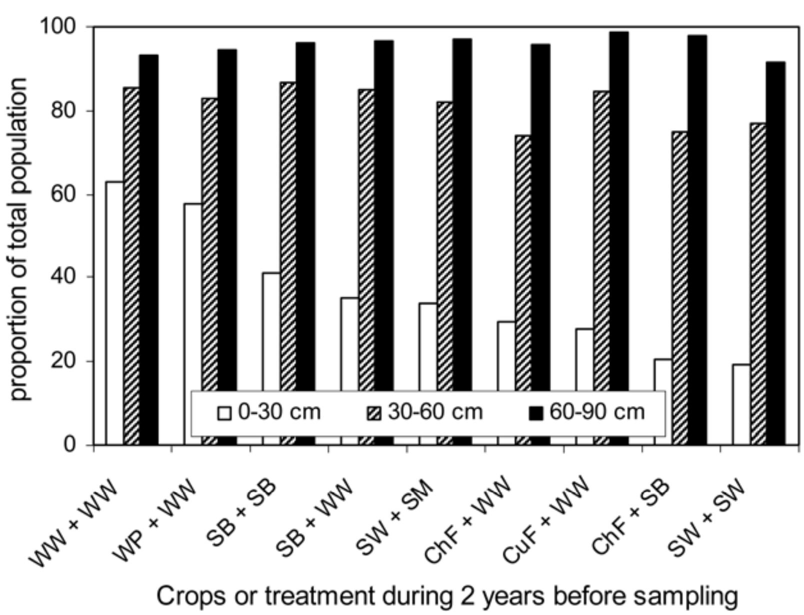

Fig. 4. Cumulative percentage of the total profile population of *Pratylenchus neglectus* detected in three successively deeper 30-cm intervals of soil profiles in eight rotations analyzed by the identity of the last two crops or treatments before deep soil core samples were collected in the long-term experiment at Moro during April 2008. Data are means of ln(x + 1) transformations of *P. neglectus* nematodes/kg of soil in the first three 30-cm depth intervals of the 120-cm sampling depth. The last two crops or treatments were chemical fallow (ChF), cultivated fallow (CuF), spring barley (SB), spring mustard (SM), spring wheat (SW), winter pea (WP), and winter wheat (WW).

assess nematode populations in this experiment was performed as spring cereals were being planted. Populations of *P. neglectus* detected in biennial winter wheat during the springtime, 6 months after the wheat was planted, were numerically higher in the fallow phase than the "in-crop" phase in 4 of 10 comparisons and were significantly lower than the in-crop phase in only 1 of 10 comparisons. An identical phenomenon, with fewer comparisons, also occurred in multiyear samplings of wheat and fallow at other Oregon locations (24). It is commonplace for the majority of *Pratylenchus* spp. to inhabit roots during periods of active root growth, to move into and out of roots throughout the period of active root growth, and to become more prevalent in soil during periods when soil is moist but without the presence of a living host (4).

Smiley et al. (21) reported that *Pratylenchus* spp. populations inside cereal roots were lowest during the spring (May) and increased to a maximum as mature roots died before harvest in July. Populations detected in soil were lowest during June and July and highest during October, after roots had died and new tissue was not yet available for recolonization. Smiley et al. (21) also observed that *Pratylenchus* spp. became active colonists of volunteer cereals and grass weeds (mostly *Bromus tectorum*) that were stimulated into seed germination and seedling growth following the onset of rain during the autumn. They found *Pratylenchus* spp. populations in roots of volunteers and grass weeds during October to be comparable with populations in planted spring and winter cereals the following May. *Pratylenchus* spp. are hosted by a large and diverse number of plant species (4,33). As with most commercial biennial winter wheat practices, winter wheat stubble in this experiment was not treated with herbicide or tillage from early autumn (October) until the following spring (March to April). An interval of zero to several weeks separated the spring weed management program and collection of samples to assess nematode populations in all treatments, including the fallow. Although populations of *Pratylenchus* spp. were not monitored in the volunteer cereals and weed grasses in this experiment, there was ample opportunity for multiplication of nematodes through the 10-month winter wheat growth cycle and also, when temperatures permitted, for as many as 7 months of the 14-month fallow cycle. We conclude that management of *Pratylenchus* spp. populations in the winter wheat–summer fallow region of the PNW must include elimination of the bridging and multiplication potential by unwanted hosts during the fallow period, as has been shown to be essential for reducing risks posed by other pests and diseases of wheat roots and foliage (5,23).

The vertical distribution of *Pratylenchus* spp. is highly variable and influenced by such factors as root distribution and soil moisture, temperature, texture, and depth (4). Sampling to 10- to 20-cm depths was determined adequate in shallow soils (28) but peak populations are known to occur at considerably greater depth in certain deep soil profiles (4,13). Sampling to a 15-cm depth during the first 2 years of this experiment failed to support statistically significant separation of *P. neglectus* populations among crop rotations. Although deeper samplings may have produced a similar result, it is notable that increasing the sampling depth to 30 cm produced statistically separable means over subsequent years of the experiment. Smiley et al. (24) reported that sampling to the 30-cm depth always detected more than 50% of the *Pratylenchus* spp. population in profiles of silt loams in Oregon. Also, sampling to a 45-cm depth detected more than 75% of the population in at least 75% of samples evaluated. Deep-core samplings performed during this experiment revealed that 30-cm-deep samplings enabled us to detect 16 to 63% (mean of 36%) of the total *Pratylenchus* spp. populations in the crop rotations examined. The mean detection level was 81% (range of 74 to 87%) when samples were collected to a 60-cm depth. In concurrence with current recommendations (24), we conclude that the minimally acceptable sampling depth is 30 cm when comparing *Pratylenchus* spp. populations among crop management procedures in deep silt loam soils. Sampling to a 45-cm depth would be more precise where expedient sampling can be performed to that depth using standard manual probes. Precise distinctions among cropping systems will require laborious and expensive sampling to at least a 60-cm depth and segmenting the soil cores into 15- to 30-cm intervals prior to extracting the plant-parasitic nematodes.

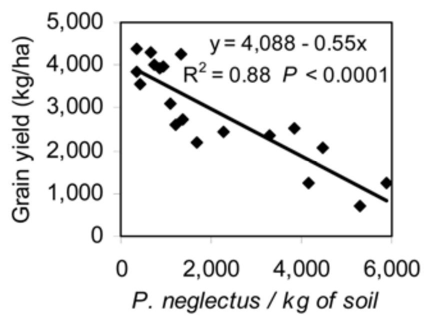

Fig. 5. Relationship between root-lesion nematode populations and grain yields for winter wheat in five crop rotations over four crop years, 2005–08; data are for the treatments annual winter wheat, biennial winter wheat with either cultivated or chemical fallow, 2-year winter wheat-winter pea rotation, and 3-year winter wheat-spring barley-chemical fallow rotation.

Table 4. Grain yield for wheat and barley crops produced over four crop years in eight crop sequences at Moro, OR

Crop and crop sequence[x]	Grain yield (kg/ha)[w] 2004	2005	2006	2007	2008	4-yearr mean[y]
Spring barley						
Annual spring barley	3,045 a	651 c	3,564 a	2,204 d	1,255 c	1,919 b
3-year rotation	2,277 c	715 c	3,251 a	2,008 de	523 e	1,624 bc
Flex-crop rotations[z]	2,345 c	755 bc	…	…	…	…
Spring wheat						
Annual spring wheat	2,656 c	681 c	2,543 bc	2,158 e	902 d	1,571 bc
Flex-crop rotations	2,492 c	868 c	…	1,955 f	…	…
Winter wheat						
Annual winter wheat	3,431 ab	713 c	1,241 d	2,074 ef	1,238 c	1,317 c
Biennial winter wheat (ChF)	3,293 ab	3,568 ab	3,094 b	3,991 b	2,522 ab	3,294 a
Biennial winter wheat (CuF)	3,241 b	3,910 a	3,953 a	4,312 ab	2,365 b	3,635 a
2-year rotation	3,272 ab	2,732 ab	2,209 c	2,425 de	799 d	2,041 b
3-year rotation	3,377 ab	4,264 a	3,839 a	4,386 a	2,605 a	3,774 a
Flex-crop rotation no. 2	…	…	…	3,471 c	…	…

[w] Means followed by the same letter within a column are not significantly different at $P = 0.05$ according to the Fisher's least significant difference test.
[x] Grain yields in eight crop sequences. ChF = chemical fallow and CuF = mechanical fallow. All plots were direct seeded (no-till) except biennial winter wheat in the CuF treatment.
[y] Mean of grain yields for crops harvested during the last four years, 2005–08.
[z] Flex-crop = rotational sequences were re-examined annually to facilitate real-time management decisions based upon considerations of available stored water, crop prices, and occurrences of weeds and diseases.

P. neglectus and *P. thornei* were only recently reported as being common and in high numbers in many fields of the low-precipitation regions of the PNW (21,27), and potential impacts of these species on yield of spring wheat were reported (25,26). Presumptive evidence that *P. neglectus* also restricted yields of winter wheat was reported (21) but that observation did not provide evidence that the wheat yield was not also influenced by availability of stored soil water, even though the experiment was performed on a shallow silt loam soil where all stored water would be expected to be extracted by each crop each year. In this article, we report that high populations of *P. neglectus* were associated with reduced yields of winter wheat, and that the greatest yield reduction occurred in the rotation in which the least amount of water was extracted during the growing season. It is reasonable to assume that root dysfunction caused by *Pratylenchus* spp. or any other root pathogen will also reduce the capacity of wheat to extract water and nutrients in amounts comparable with those extracted by plants with healthy roots. Thompson et al. (31,32) reported that *Pratylenchus* spp.-affected roots became less capable of extracting water, nitrogen, phosphorus, and zinc and induced premature moisture stress, particularly toward the end of the growing season or in dry years. Wheat in the PNW often receives little effective rainfall late in the growing season and generally depletes stored water in the soil profile before plant maturity. Smiley et al. (25,26) demonstrated that spring wheat with roots heavily infested by *P. neglectus* and *P. thornei* had canopy temperatures elevated as much as 4°C higher than canopy temperatures in adjacent plots where nematode populations were suppressed by applying the nematicide aldicarb. Plant canopy temperature is directly correlated with water stress in wheat (6,20). It was concluded that root dysfunction caused by *Pratylenchus* spp. reduced the capacity of plants to extract deeply stored water late in the growing season. In this study, we determined that the cropping system that resulted in the greatest *P. neglectus* population also became least efficient for extracting deeply stored soil water. Therefore, this is the first definitive report of winter wheat yield being reduced by *Pratylenchus* spp. in the PNW.

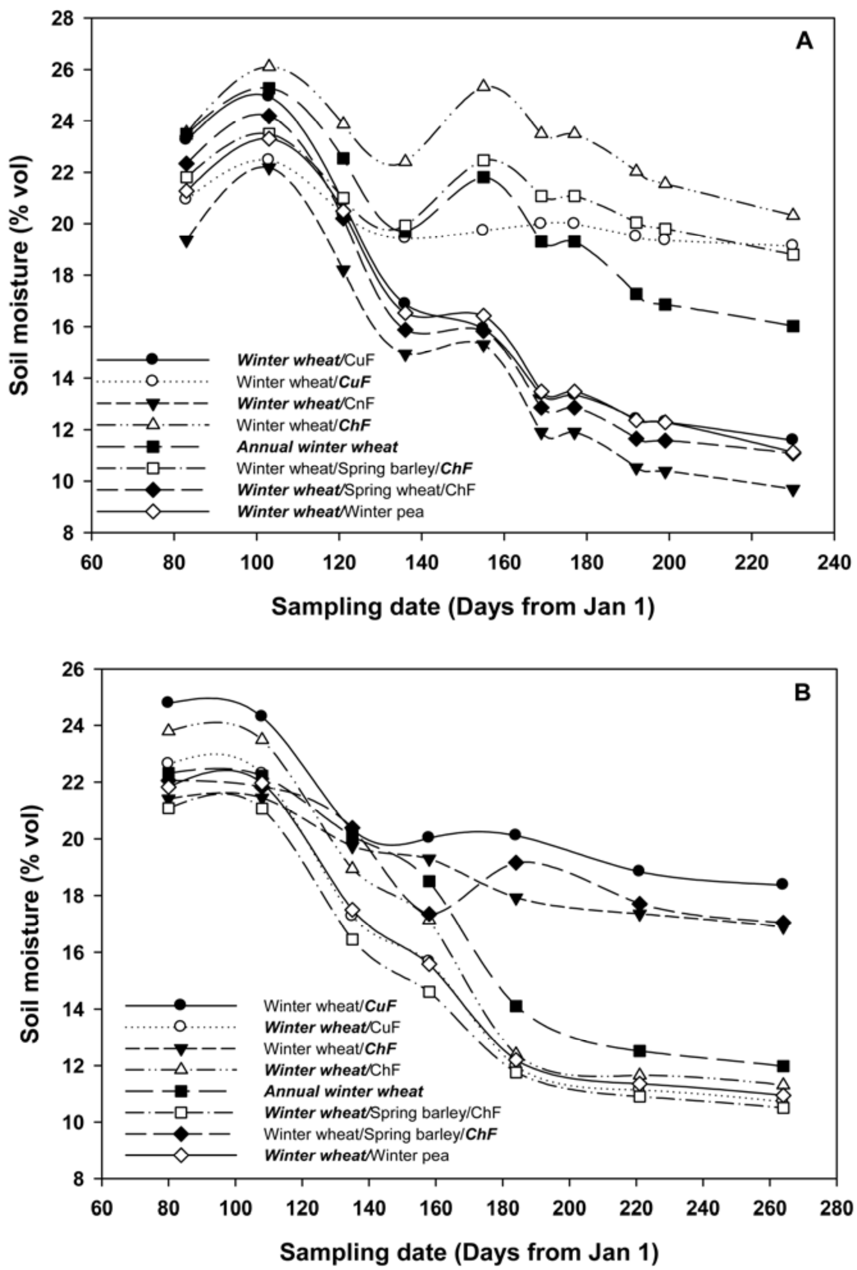

Fig. 6. Mean soil water content under all rotations in the 0- to 100-cm depth profile at Moro from March to September during **A,** 2006 and **B,** 2007. Data is for the crop or treatment shown in boldface and italics of a crop or management sequence; CuF = cultivated fallow and ChF = chemical fallow. Symbols and line styles are consistent for individual crop sequences over 2 years (e.g., the solid circle and continuous line designate the in-crop phase of the biennial winter wheat treatment during 2006 and the cultivated fallow phase of the same treatment during 2007).

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