Suppression of Wheat Growth and Yield by *Pratylenchus neglectus* in the Pacific Northwest

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ABSTRACT

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Many wheat (*Triticum aestivum*) fields planted annually in the Pacific Northwest are infested by high populations of the lesion nematode, *Pratylenchus neglectus*. Spring wheat cultivars varying in tolerance and resistance to *P. neglectus* were treated or not treated with aldicarb to examine relationships between the nematode and growth and yield of annual direct-seeded (no-till) wheat. Increasing initial density of *P. neglectus* in soil was more strongly associated with declining growth and yield of intolerant (Machete and Spear) than moderately tolerant (Frame and Krichauff) cultivars. Yield suppression by *P. neglectus* was generally 8 to 36% for intolerant cultivars, but reached 71% in soil also harboring *Heterodera avenae*, *Rhizoctonia solani* AG-8, and *Gaeumannomyces graminis* var. *tritici*. Intolerant cultivars had lower yields than Krichauff in rainfed but not in irrigated experiments. Density of *P. neglectus* in mature roots was generally lower for moderately resistant Krichauff than for susceptible Machete and Spear. Aldicarb improved yields in irrigated but not in rainfed experiments, and increased plant height and reduced variability in tiller height, canopy temperature, and density of *P. neglectus* in roots. This is the first report of damage to wheat by *P. neglectus* in the Pacific Northwest. Breeding wheat for tolerance and resistance to *P. neglectus* is suggested.

Additional keywords: Fusarium crown rot, *Fusarium pseudograminearum*, *Pratylenchus thornei*, Pythium root rot, *Pythium* spp., *Rhizoctonia* root rot, take-all

Conservation farming systems are becoming more widely practiced in semiarid regions of the Pacific Northwest states of Oregon and Washington. Most rainfed (dryland) wheat (*Triticum aestivum* L.) in the region has traditionally been produced as a 2-year rotation of winter wheat and summer fallow. This low-frequency rotation is the most profitable production system for rainfed fields that receive 250 to 400 mm of annual precipitation, with little rain during the summer. Many wheat-fallow rotations are vulnerable to water erosion, and also contribute to concerns regarding quality of air and water. Interest in conservation tillage systems (4) has led to conversion of land formerly in winter wheat-summer fallow rotation to spring wheat or barley planted annually without tillage. Approximately 20% of dryland spring grains in Oregon and Washington are now planted without tillage, with percentages of 20 to 40% in at least four major cereal-producing counties (35). Most direct-seeded dryland fields are planted

annually to cereals because this is more profitable than rotation with other crop species. Wheat is also produced with supplemental irrigation, usually in long rotations with higher-value crops. However, economic considerations in some regions cause growers to produce irrigated wheat annually.

Populations of the lesion nematode *Pratylenchus neglectus* (Rensch, 1924) Filipjev Schuurmanns & Stekhoven, 1941 may increase dramatically when dryland fields are shifted to a higher intensity of cereal cropping (12). Direct associations between *Pratylenchus* spp. populations and frequency of cereal cropping have been reported (27), and populations are generally much lower following summer fallow than after wheat (22). Populations of *P. thornei* Sher & Allen, 1953 can be reduced to nondamaging levels if wheat is grown no more frequently than once every 3 years in rotation with crops less suitable for multiplication of the nematode (3). Greater populations of *P. thornei* and *P. neglectus* have been detected in annually cropped fields than in winter wheat-summer fallow rotations in the Pacific Northwest wheat belt (34).

P. neglectus causes economic damage to barley in North America (10) and to wheat in Australia, where preplant populations have been negatively correlated with wheat yield (41,44). However, damage relationships between *P. neglectus* population and

wheat yield differ among sites and growing seasons. Yield constraint from root damage depends on the nematode species and numbers in roots; crop species, cultivar, growth stage, and rotation; tillage management; and soil temperature, moisture, and texture. Although high populations of *Pratylenchus* spp. have been reported in annually cropped fields in the Pacific Northwest (34), it is recognized that nematode population estimates are often poor predictors of potential damage (27).

In the Pacific Northwest, *P. neglectus* was reported as a weak parasite of winter wheat cv. Stephens on the basis of slightly reduced foliar growth in a greenhouse seedling assay (19). This plant-parasitic species was subsequently associated with reduction of winter wheat yield under field conditions (34). While the importance of *P. neglectus* on spring wheat has not been examined in the Pacific Northwest, Smiley et al. (36) reported that high populations of *P. thornei* were negatively associated with plant growth, grain yield, and grain quality for annually cropped *P. thornei*-intolerant spring wheat cultivars. Moreover, as the population of *P. thornei* increased, yield stability was often more favorable for moderately tolerant than for intolerant wheat cultivars.

This paper reports the relationships between *P. neglectus* and yield for dryland and irrigated annual no-till spring wheat in eastern Oregon. Procedures and wheat germ plasm were selected to provide direct comparisons with research on *P. neglectus* in Australia (41,44), and with parallel research on *P. thornei* in the Pacific Northwest (36).

MATERIALS AND METHODS

Locations, climates, and crop management. Five field experiments were performed during 2003 at three locations in northeastern Oregon. Experiments were performed on the Cuthbert farm, 10 km northeast of LaGrande, the Davis farm, 13 km east-southeast of LaGrande, and the Oregon State University Columbia Basin Agricultural Research Center, 1 km south-east of Moro. Annual precipitation averages 480, 395, and 282 mm at the Cuthbert farm, Davis farm, and Moro, respectively. Average daily air temperature is -1°C during January and 19°C during July and August at each location. Soils were an Imbler fine sandy loam at the Cuthbert

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farm, Hoopal fine sandy loam at the Davis farm, and Walla Walla silt loam at Moro. Each soil was deep and well-drained. Two adjacent experiments were performed at the Davis farm and at Moro, and are distinguished as Moro-1 and Moro-2, and Davis-1 and Davis-2. Each field had a recent history of annual cropping without tillage, had been planted to wheat the preceding year, and was naturally infested with *P. neglectus*. Wheat received supplemental irrigation until the soft-dough stage at the Cuthbert farm, to physiological maturity at the Davis farm, and was not irrigated at Moro.

Spring wheat was planted as a direct-seed (no-till) annual crop at each location. Experiments were planted at the Cuthbert and Davis farms on 14 April and at Moro on 10 April. Seed was planted using a drill equipped with a cone-seeder and four openers at 36-cm row spacing. Fertilizer was applied by banding below the seed at the time of planting. Fertilizer and herbicide applications were uniform across each experimental area, and were consistent with standard practices. Wheat seed was treated with fungicides (tebuconazole plus mefenoxam) to suppress seed rot and seedling damping-off.

Wheat cultivars included Frame, Krichauff, Machete, and Spear, each of which is an Australian cultivar characterized by tolerance as well as resistance to *P. neglectus* (40,44,48). Tolerance is defined as the ability of the plant to withstand nematode infection (28), and is generally measured as the ability of the plant to maintain yield potential in the presence of moderate to high populations of plant-parasitic nematodes. Resistance is defined as the ability of the plant to suppress development or reproduction of the nematode (28), and is measured either as final nematode density in roots or soil, or as a multiplication factor consisting of final population (Pf) divided by initial population (Pi) in soil. Reactions to *P. neglectus* by Machete and Spear have been characterized (40,44,48) as moderately intolerant to intolerant, and susceptible to very susceptible. Reactions of Frame have been characterized as moderately intolerant to tolerant, and moderately susceptible to susceptible. Reactions of Krichauff have been characterized as moderately intolerant to tolerant, and moderately resistant to moderately susceptible. Frame and Spear were planted in the Cuthbert farm and Davis-1 experiments, Krichauff and Machete were planted in the Moro-1 and Davis-2 experiments, and Krichauff and Spear were planted in the Moro-2 experiment.

Aldicarb (Temik 15G) was mixed with the seed in the seed cone while planting half of the plots in each experiment. Aldicarb was dispensed at 4.2 kg a.i./ha to suppress damage and reproduction by *Pratylenchus* spp. (41).

The experimental design at each location was a two-way randomized complete block with variables of wheat cultivar and aldicarb treatment in 1.7 × 6.1 m plots. Each treatment (two cultivars, with and without aldicarb) at each location was replicated nine times, for a total of 36 plots. Locations of experiments were marked by burying woven-wire cables vertically into the four corners of each experimental area.

The Moro-1 experiment was replanted uniformly to the Pacific Northwest-adapted spring wheat cv. Zak during March 2004 using a commercial direct-seed drill and standard production practices. Plots were harvested in August, and yields were compared to *P. neglectus* populations prior to planting; the Pf values were determined for the study performed during 2003.

Soil sampling and nematode extraction. Soil was collected to assess *Pratylenchus* spp. populations in individual plots for all experiments. Initial samples (Pi) were collected while soil was moist during early April 2003, 2 days prior to planting. Samples consisted of 15 to 20 cores (2.5 cm diameter × 10 cm deep) composited for each 10 m² plot. Final soil samples (Pf) were collected during late February 2004 to evaluate residual influences, if any, of the cultivar and aldicarb treatments applied during 2003. The Pf sampling was deferred until spring (February) because soils were dry and hard following harvest, which is known to cause a significant underestimate of *Pratylenchus* spp. density in soil (39). To account for vertical distribution of *Pratylenchus* (39,42), the 2004 samples were collected to a depth of 20 cm. Samples were stored moist at 4°C for up to 7 days before being transported to a commercial diagnostic laboratory (Western Laboratories, Parma, ID) for extraction and identification of nematodes. Multiplication factors (Pf/Pi) were calculated for *P. neglectus* in each plot, except at the Cuthbert farm, where farming practices prevented sampling during 2004.

A modified elutriation method (16) was used to extract all soil-dwelling nematodes from 250-g subsamples. Using an Oosterbrink elutriator, coarse material was collected on a 500-µm sieve, cysts on a 125-µm sieve, and free-living nematodes on a stack of two 38-µm and two 32-µm sieves. Free-living nematodes were washed into 100-ml cups. Cysts were ground to release eggs and larvae, and were added to the 100-ml cups. Suspensions were stored overnight, and settled nematodes were transferred to 50-ml centrifuge tubes and concentrated by 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 for 4 min. The supernatant solution containing nematodes was passed over a 20-µm sieve, transferred 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 mini-vortex mixer for 5 s, removing 4 ml of suspension, placing 1 ml on a Peter's counting slide, and counting and identifying all plant-parasitic nematode genera on the slide. *Pratylenchus* was identified to genus level based on standard morphological characteristics and measurements (11,14). Numbers are reported as nematodes per kilogram of oven-dry soil.

Pratylenchus spp. extracted from each experiment were further identified to species using DNA profiles in a composite of extractions from each plot. During 2003, a subsample of the composite was dried and sent to the Root Disease Testing Service in Adelaide, South Australia, where *P. neglectus* and *P. thornei* were each identified and quantified from extracted DNA (24). Results, in picograms of DNA per gram of soil, were converted through calibrations into estimates for numbers of each *Pratylenchus* species per kilogram of soil. The numerical estimates were used to determine proportions of each species in each experimental area. During 2004, *Pratylenchus* spp. were identified in our laboratory using procedures described by Waeyenberge et al. (47). Extracts returned from Western Laboratories were used to extract DNA from plots with high numbers of *Pratylenchus* spp. Results of DNA analyses in our laboratory were based on intensity, or presence versus absence, of banding patterns for each *Pratylenchus* spp., but these tests have not been calibrated with numbers of *Pratylenchus* spp. in soil in Oregon.

Plant sampling, nematode extraction, and disease assessment. Root systems from 20 plants were collected from each plot in June, between anthesis and grain filling. Roots to 10-cm depth were collected for five plants at each of four subsampling sites in each plot. Whole plants were stored at 4°C before being sent to Western Laboratories. Endoparasitic nematodes were extracted using a standard 7-day root-mist procedure (16), with samples misted for 60 s every 5 min. Nematodes were counted and identified as described for soil extracts. Numbers for each species were normalized to equal units of root mass and reported as nematodes per gram of fresh root tissue and of oven-dry root tissue.

A separate group of plants was also collected to assess incidence and severity of diseases caused by soilborne plant-pathogenic fungi, and to measure plant height and growth stage. Because there were no treatment effects in comparable experiments during 2001 and 2002 (unreported data), diseases were assessed only on 25 plants with intact roots to 10-cm depth collected arbitrarily across each

experimental area during June 2003 (heading stage). Roots were scored visually for incidence and severity of disease (33). Plant height was also measured on 25 plants from each plot and, for the Davis-2 experiment, the Haun plant growth stage (5) was also measured.

Other plant growth and development data were as follows. Seedling emergence was measured 1 month after planting. Leaf canopy temperature at the soft-dough stage was measured as an indicator of the plant water stress differential between aldicarb-treated and control plots (8,21) during mid-afternoon on hot days in July, using a Raynger ST noncontact thermometer (Raytek Corp., Santa Cruz, CA). Plant height, variability in head height, and density of headed tillers were measured immediately before harvest. Variability in head height was calculated by dividing the standard deviation by mean head height. Plots were

harvested with an experimental plot combine to measure grain yield, test weight, and kernel weight.

Statistical analysis. Nematode populations were described by calculating means and standard deviations among plots. All plant growth, disease, and nematode variables among cultivar $\times$ aldicarb treatment combinations were analyzed by analysis of variance for the two-way randomized complete block model, using Co-Stat Statistical Software version 6.101 (CoHort Software, Monterey, CA). When treatment effects were significant at $P < 0.05$, means were separated using the least significant difference test (LSD). Variables were also evaluated by regression analysis using a linear model.

RESULTS

Populations and identities of *Pratylenchus* spp. in soil.

Pratylenchus spp. were highly variable among the 36 plots in each experiment (Table 1). DNA extracts in Australia during 2003 indicated a strong dominance of *P. neglectus* over *P. thornei* at Moro-1 (9,000 versus <1,000 nematodes/kg soil), Moro-2 (4,000 versus 1,000 nematodes/kg soil), Cuthbert farm (6,000 versus <1,000 nematodes/kg soil), and Davis farm (6,000 versus <1,000 nematodes/kg soil). The lower detection limit was 1,000 nematodes/kg, indicating the possibility that populations were entirely *P. neglectus* in experiments at Moro-1 and the Cuthbert and Davis farms. DNA analyses at our laboratory during 2004 also indicated a strong presence of *P. neglectus* and an inability to detect *P. thornei* at all three locations.

Replication and randomization of treatments minimized the impact of high spatial heterogeneity within experiments, as indicated by an absence of difference ($P < 0.05$) in initial *Pratylenchus* populations among treatments subsequently planted to cultivar and aldicarb variables during 2003 (Table 2). Final *Pratylenchus* populations during 2004 were significantly ($P < 0.05$) lower than in 2003 at the Davis-1 and Davis-2 experiments, in response to significantly ($P < 0.05$) lower populations in aldicarb-treated compared to control plots (Table 2). During 2004, a residual influence from the cultivar variable occurred at the Moro-1 and Davis-2 experiments, where the *Pratylenchus* population was lower following Krichauff than Machete. Also during 2004, a cultivar by aldicarb interaction was significant (Table 2), indicating that the suppressive influence of aldicarb on *P. neglectus* population was greater for Machete than for Krichauff.

The multiplication factor (Pf/Pi) for *P. neglectus* was unaffected by cultivar or aldicarb treatments in two dryland experi-

Table 1. Densities of the *Pratylenchus* populations in soil samples^a collected before planting spring wheat into five experiments at three locations in Oregon

Irrigation Location ^b	Year	Species ^c	<i>Pratylenchus</i> spp./kg soil		
			Mean	Range	SD
Nonirrigated					
Moro-1	2003	Pn	1,538	140-4,120	1,126
	2004	Pn	1,513	180-4,300	979
Moro-2	2003	Pn/Pt	989	140-3,440	678
	2004	Pn/Pt	1,588	260-4,160	1,002
Irrigated					
Cuthbert	2003	Pn	2,556	0-15,300	2,248
Davis-1	2003	Pn	3,217	1,540-5,440	910
	2004	Pn	868	0-2,540	724
Davis-2	2003	Pn	4,601	1,900-11,520	2,012
	2004	Pn	1,618	0-14,440	2,572

^a Samples for each experiment were composed of 15 to 20 soil cores composited for each of 36 plots arranged in adjacent blocks of 12 columns $\times$ 3 rows.

^b Two experiments were at Moro and Davis; sites are differentiated as 1 or 2 for each location; example: Moro-1 or Moro-2.

^c *Pratylenchus* species: Pn = *P. neglectus*, Pt = *P. thornei*, and Pn/Pt = species mixtures and order of decreasing proportions.

Table 2. Populations of *Pratylenchus* spp. in soil during early spring for five experiments at three Oregon locations during 2003 and 2004; samples during 2004 reflect residual influences from the designated cultivar $\times$ aldicarb variables examined the previous year

Irrigation Location ^a	Year ^b	Cultivars ^c	Least susceptible cultivar: K or F ^c		Most susceptible cultivar: M or S ^c		Significance ^d (<i>P</i> > <i>F</i>)		
			Control	Aldicarb	Control	Aldicarb	Cultivar	Aldicarb	Cult. × ald.
Nonirrigated									
Moro-1	2003	K, M	1,351	1,260	1,996	1,549	0.26	0.51	0.66
	2004		1,349	938	1,860	1,909	<0.01**	0.49	0.39
Moro-2	2003	K, S	1,078	1,016	1,067	798	0.60	0.44	0.63
	2004		1,547	1,715	1,404	1,688	0.69	0.30	0.86
Irrigated									
Cuthbert	2003	F, S	2,500	2,209	2,583	2,931	0.77	0.83	0.60
Davis-1	2003	F, S	3,502	3,640	3,140	2,587	0.57	0.12	0.78
	2004		1,569	157	1,493	253	0.83	<0.001***	0.99
Davis-2	2003	K, M	4,916	4,240	4,591	4,671	0.94	0.40	0.50
	2004		1,153	238	4,422	658	0.01*	<0.01**	0.05*

^a Two experiments were at Moro and Davis; sites are differentiated as 1 or 2 for each location; example: Moro-1 or Moro-2.

^b Initial soil populations (Pi) were from samples collected prior to planting wheat during spring 2003. Final soil populations (Pf) were assessed 1 year later, during spring 2004, without soil disturbance over the Pi-to-Pf interval.

^c Cultivars varied among experiments. With regard to reactions to *P. neglectus* in Australia, Krichauff (K) is moderately resistant to moderately susceptible, and tolerant to moderately intolerant; Frame (F) is moderately susceptible to susceptible, and tolerant to moderately intolerant; and Machete (M) and Spear (S) are susceptible to very susceptible, and moderately intolerant to intolerant. In this table, Krichauff and Frame are grouped as "less susceptible/more tolerant" cultivars, and Machete and Spear are grouped as "more susceptible/less tolerant" cultivars.

^d Degrees of freedom for the 36-plot experimental design during 2003, and follow-up sampling during 2004, were nematode (1), cultivar (1), nematode $\times$ cultivar (1), error (25), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*), 99% (**), or 99.9% (***).

ments at Moro (Table 3). The multiplication factor was lower ($P < 0.001$) for Krichauff than for Machete in the Davis-2 experiment, and was lower in aldicarb than control treatments for both cultivars. A significant ($P < 0.001$) cultivar $\times$ aldicarb interaction at the Davis-2 experiment indicated a greater influence of aldicarb on the multiplication rate for *P. neglectus* in Machete than in Krichauff. For the Davis-1 experiment, multiplication rates did not differ between Frame and Spear but were lower ($P < 0.001$) in aldicarb than in control plots. Overall, the multiplication factors for *P. neglectus* were lower ($P < 0.001$) for the two irrigated experiments at the Davis farm than for the two dryland experiments at Moro.

Pratylenchus density in roots. The density of *P. neglectus* in mature roots differed ($P < 0.01$) between cultivars in two of five experiments (Table 4). In control plots, the density differed significantly in each of the three experiments in which Krichauff was compared with either Machete or Spear. Densities of *P. neglectus* were always higher in Machete and Spear than in Krichauff. Densities of *P. neglectus*

in control plots did not differ between Frame and Spear at the Cuthbert farm and Davis-1 experiment. Aldicarb treatment significantly reduced *P. neglectus* density in roots in all experiments. Significant cultivar $\times$ aldicarb interactions occurred in two experiments.

The density of *P. neglectus* in mature roots was correlated ($P = 0.005$, $r^2 = 0.40$) with the initial population of *P. neglectus* in soil at the Davis-1 experiment, and with the final soil population of *P. neglectus* ($P < 0.0001$, $r^2 = 0.79$) at the Davis-2 experiment.

Relative *P. neglectus* densities were comparable when evaluated on the basis of either fresh- or dry-root weights during 2003. Densities of *P. neglectus* in roots averaged 5.2 times higher when reported on dry weight rather than the fresh-weight basis reported in Table 4.

Other plant-parasitic nematodes in soil. *Tylenchorhynchus clarus* Allen, 1955, *Heterodera avenae* Wollenweber, 1924, and an unidentified species of *Meloidogyne* were present in fields at Moro (data not presented). Population means for each treatment were never higher than 4

nematodes/kg (range of 0 to 50 in individual plots) for *T. clarus*, 1 nematode/kg (range of 0 to 20) for *H. avenae*, and 2 nematodes/kg (range of 0 to 30) for *Meloidogyne*.

Plant-parasitic nematodes at the Cuthbert and Davis farms included *Criconeimoides* spp., *Geocenamus brevidens* (Allen, 1955) Brzeski, 1991, *H. avenae*, *T. clarus*, *Meloidogyne naasi* Franklin, and *Paratylenchus* spp. The stunt nematode *G. brevidens* was present at a population density of 1 nematode/kg soil at the Cuthbert farm. Populations in the *Tylenchorhynchus/Geocenamus* complex in both experiments at the Davis farm during 2003 averaged 25 nematodes/kg soil (range of 0 to 180), but genera and species were not determined. Mean populations of *M. naasi* were 44 nematodes/kg soil (range of 0 to 490) at the Cuthbert farm and 148 per kg soil (range of 0 to 2,920) at the Davis-1 experiment. *Criconeimoides* spp. occurred at very low densities (1 nematode/kg; range of 0 to 20) at each location, and *Paratylenchus* spp. densities were highly variable (means up to 21,076 nematodes/kg; range of 260 to 55,780).

Table 3. Multiplication factors (Pf/Pi)^a for *Pratylenchus neglectus* in response to cultivar and aldicarb variables for five experiments in Oregon during 2003

Location ^b	Cultivars ^c	Least susceptible cultivar: K or F ^c		Most susceptible cultivar: M or S ^c		Significance ^d ($P > F$)		
		Control	Aldicarb	Control	Aldicarb	Cultivar	Aldicarb	Cult. $\times$ ald.
Moro-1	K, M	1.00	0.74	0.93	1.23	0.81	0.77	0.08
Moro-2	K, S	1.44	1.69	1.32	2.12	0.47	0.24	0.35
Davis-1	F, S	0.44	0.04	0.48	0.10	0.27	<0.001***	0.54
Davis-2	K, M	0.23	0.06	0.96	0.14	<0.001***	<0.001***	<0.001***

^a Multiplication factor was derived from the number of nematodes/kg soil before planting and application of aldicarb during April 2003 (Pi), and resampling 1 year later (Pf). Plots were not tilled or cropped between harvest (August 2003) and collection of Pf samples during March 2004.

^b Experiments at the Davis farm received supplemental irrigation. Experiments were entirely rainfed at the Columbia Basin Agricultural Research Center at Moro. Two experiments were at Moro and Davis; sites are differentiated as 1 or 2 for each location; example: Moro-1 or Moro-2.

^c Cultivars varied among experiments. With regard to reactions to *P. neglectus* in Australia, Krichauff (K) is moderately resistant to moderately susceptible, and tolerant to moderately intolerant; Frame (F) is moderately susceptible to susceptible, and tolerant to moderately intolerant; and Machete (M) and Spear (S) are susceptible to very susceptible, and moderately intolerant to intolerant. In this table, Krichauff and Frame are grouped as "less susceptible/more tolerant" cultivars, and Machete and Spear are grouped as "more susceptible/less tolerant" cultivars.

^d Degrees of freedom for the 36-plot experimental design were nematicide (1), cultivar (1), nematicide $\times$ cultivar (1), error (25), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*), 99% (**), or 99.9% (***).

Table 4. Density of *Pratylenchus* spp. in mature roots^a in aldicarb-treated and untreated plantings of spring wheat in five experiments at three Oregon locations during 2003

Irrigation Location ^b	Cultivars ^c	Least susceptible, most tolerant cultivar: K or F ^c		Most susceptible, least tolerant cultivar: M or S ^c		Significance ^d (<i>P</i> > <i>F</i>)		
		Control	Aldicarb	Control	Aldicarb	Cultivar	Aldicarb	Cult. × ald.
Nonirrigated								
Moro-1	K, M	1,578	54	6,041	27	0.12	0.01**	0.11
Moro-2	K, S	217	14	752	11	<0.01**	<0.01***	<0.01**
Irrigated								
Cuthbert	F, S	192	13	337	10	0.16	<0.01***	0.76
Davis-1	F, S	354	21	627	97	0.14	<0.01***	0.40
Davis-2	K, M	294	3	2,392	20	0.01**	<0.01***	<0.01***

^a *Pratylenchus* spp. density is reported as numbers of nematodes/g fresh root tissue. Multiply the data by 5.2 to estimate numbers of nematodes/g dry root tissue.

^b Two experiments were at Moro and Davis; sites are differentiated as 1 or 2 for each location; example: Moro-1 or Moro-2.

^c Cultivars varied among experiments. With regard to reactions to *P. neglectus* in Australia, Krichauff (K) is moderately resistant to moderately susceptible, and tolerant to moderately intolerant; Frame (F) is moderately susceptible to susceptible, and tolerant to moderately intolerant; and Machete (M) and Spear (S) are susceptible to very susceptible, and moderately intolerant to intolerant. In this table, Krichauff and Frame are grouped as "less susceptible/more tolerant" cultivars, and Machete and Spear are grouped as "more susceptible/less tolerant" cultivars.

^d Degrees of freedom for the 36-plot experimental design were nematicide (1), cultivar (1), nematicide $\times$ cultivar (1), error (25), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*), 99% (**), or 99.9% (***).

Populations of *H. avenae* were low at the Cuthbert farm and high at the Davis farm. Hatched juveniles were not detected at either location at the time of planting during 2003. Initial densities of eggs plus juveniles released from extracted cysts were 7 nematodes/kg (range of 0 to 160) at the Cuthbert farm. Initial densities for *H. avenae* at the Davis-1 experiment were 1,690 nematodes/kg (range of 100 to 8,020) during 2003 and 1,279 nematodes/kg (range of 0 to 4,400) during 2004, and at the Davis-2 experiment were 784 nematodes/kg (range of 160 to 2,060) during 2003 and 2,070 nematodes/kg (range of 0 to 16,780) during 2004.

At the Davis farm, 1 month after harvest during 2003, a supplemental sampling was performed to determine effects of treatments on populations of *H. avenae* eggs and juveniles from cysts. When compared with initial populations, the multiplication factor (Pf/Pi) was lower ($P < 0.05$) in the aldicarb than control treatment in the Davis-2 experiment, and did not differ between cultivars in either experiment. In the Davis-2 experiment, the multiplication factors were 8.7 and 0.5 for aldicarb and control treatments, respectively ($LSD_{0.05} = 3.0$).

Disease symptoms and associations with nematodes. Disease symptoms during 2003 were caused by a complex of soilborne root-infecting fungal pathogens including *Rhizoctonia solani* Kühn AG-8 and *R. oryzae* Ryker & Gooch (Rhizoctonia root rot), *Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici* J. Walker (take-all), *Fusarium pseudograminearum* O'Donnell & T. Aoki (crown rot), and unidentified species of *Pythium* (Pythium root rot). One or more of these diseases generally occurred together with parasitism by nematodes. Visual estimates of disease incidence (percent plants with symptoms) and severity (0 to 4 scale; 0 = none, 4 = severe) were made for take-all, crown rot, and a "browning" root rot complex consisting of Rhizoctonia root rot, Pythium root rot, and lesion nematode.

Foliar diseases either did not occur or were of no importance in these experiments.

At the dryland sites, take-all was present at low to moderate severity (0.9 to 1.7), variable incidence (19 to 92%), and had no significant relationship ($P < 0.05$) with cultivar or aldicarb treatments. Browning root rot symptoms were also relatively minor, with low to moderate severity (1.0 to 2.2), variable incidence (8 to 92%), and no association with treatments.

At irrigated sites, take-all and browning root rot were of minor severity (0.4 to 0.5) and incidence (24 to 29%) at the Cuthbert farm, and of moderate severity (1.5 to 1.7) and high incidence (95 to 100%) at the Davis-1 experiment. Concise brown-colored lesions and spear-tip type root termini, typical of Rhizoctonia root rot, were of minor severity (0.2) and incidence (24%) at the Cuthbert farm, and were of yield-limiting severity (2.8) and incidence (100%) at the Davis-1 experiment. At both locations, Fusarium crown rot symptoms on subcrown internodes were present at very low severity (<0.2) and incidence (<10%). Witches'-brooms caused by *H. avenae* at the Cuthbert farm were of low severity (0.2) and incidence (16%), and were more prevalent at the Davis-1 experiment, with mean severity of 1.8 on 72% of plants.

Severity of the browning root-rot complex at the Davis-1 experiment was positively associated with initial population of *P. neglectus* in soil ($P = 0.003$, $r^2 = 0.44$) and density of *P. neglectus* in roots ($P = 0.06$, $r^2 = 0.21$). Severity of take-all was negatively associated with severity of the browning root rot complex ($P < 0.0001$, $r^2 = 0.82$).

At the Davis-2 experiment, Rhizoctonia root rot was more severe in aldicarb-treated than in control plots (ratings of 2.1 versus 1.4, $LSD_{0.05} = 0.3$), and was more severe on Krichauff than Machete (ratings of 2.1 versus 1.5, $LSD_{0.05} = 0.5$). Occurrences of witches'-brooms caused by *H. avenae* were lower in aldicarb-treated than in control plots (ratings of 0.1 versus 2.3,

$LSD_{0.05} = 0.3$), and did not differ among cultivars. Take-all severity ratings (1.0 to 2.8) did not differ significantly between cultivars or aldicarb treatments.

Plant growth and development. Seedling stand density was 10% lower ($P < 0.05$) in aldicarb-treated than in control plots in three of five experiments: Davis-2, Moro-1, and Moro-2 (data not presented). Aldicarb treatment also reduced tillering for both cultivars in the Moro-2 experiment, where there were an average of 113 and 97 tillers/m ($LSD_{0.05} = 7$) in control and aldicarb treatments, respectively. Density of headed tillers ($P < 0.05$) was slightly greater for Krichauff than for Machete at the Davis-2 experiment (data not presented).

Canopy leaf temperature was measured only for the irrigated experiments. Canopy temperature was reduced as much as 4°C by aldicarb treatment at the Cuthbert farm (41.6 versus 37.7°C, $LSD_{0.05} = 1.9$), where irrigation had been terminated before crop maturation. Canopy temperature was 1 and 2°C cooler (not significant at $P = 0.05$) at the Davis-1 (30.9 versus 29.7°C, $P = 0.13$) and Davis-2 (39.9 versus 37.9°C, $P = 0.26$) experiments, where water continued to be applied until the wheat matured.

Aldicarb treatment increased ($P < 0.0001$) plant height by 1 to 3 cm in three of five experiments: Moro-2, Davis-1, and Davis-2 (data not presented). The plant growth stage, measured as the Haun scale, was more advanced during mid-June in aldicarb-treated than in control plots (6.6 versus 6.2, $LSD_{0.05} = 0.3$) at the Davis-2 site, the only experiment where growth stage was measured.

Variability in plant height did not differ among cultivars in control plots (data not presented). Variability in plant height was reduced by aldicarb treatment in three of five experiments. This measure of aldicarb effect in control versus aldicarb-treated plots was 0.21 versus 0.20 ($LSD_{0.05} = 0.01$) at Moro-2, 0.20 versus 0.18 ($LSD_{0.05} = 0.01$) at Davis-1, and 0.19 versus 0.16 ($LSD_{0.05} = 0.03$) at Davis-2.

Table 5. Grain yield (kg/ha) for spring wheat grown in aldicarb-treated and untreated plots in five experiments at three Oregon locations during 2003

Irrigation Location ^a	Cultivars ^b	Most tolerant cultivar: K or F ^b		Least tolerant cultivar: M or S ^b		Significance ^c (<i>P</i> > <i>F</i>)		
		Control	Aldicarb	Control	Aldicarb	Cultivar	Aldicarb	Cult. × ald.
Nonirrigated								
Moro-1	K, M	1,448	1,305	1,140	1,124	<0.01***	0.04*	0.14
Moro-2	K, S	1,530	1,361	1,287	1,394	<0.01**	0.40	<0.01***
Irrigated								
Cuthbert	F, S	2,767	3,192	3,084	3,370	0.39	<0.01**	0.33
Davis-1	F, S	1,451	1,822	1,440	1,952	0.34	<0.01***	0.59
Davis-2	K, M	1,502	2,110	1,601	1,924	0.61	<0.01***	0.19

^a Two experiments were at Moro and Davis; sites are differentiated as 1 or 2 for each location; example: Moro-1 or Moro-2.

^b Cultivars varied among experiments. With regard to reactions to *P. neglectus* in Australia, Krichauff (K) is moderately resistant to moderately susceptible, and tolerant to moderately intolerant; Frame (F) is moderately susceptible to susceptible, and tolerant to moderately intolerant; and Machete (M) and Spear (S) are susceptible to very susceptible, and moderately intolerant to intolerant. In this table, Krichauff and Frame are grouped as "less susceptible/more tolerant" cultivars, and Machete and Spear are grouped as "more susceptible/less tolerant" cultivars.

^c Degrees of freedom for the 36-plot experimental design were nematicide (1), cultivar (1), nematicide × cultivar (1), error (25), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*), 99% (**), or 99.9% (***).

Root weights in the upper 10 cm of soil were determined from samples used to extract endoparasitic nematode species. Fresh and dry root weights did not differ significantly for cultivar and aldicarb treatments in the three irrigated experiments: Cuthbert, Davis-1, and Davis-2. At Moro, dry root weights were higher ($P = 0.03$) for Krichauff than for Spear in the Moro-2 experiment. Dry root weights were higher ($P = 0.05$) for aldicarb than for control treatments in both dryland experiments at Moro. Cultivar $\times$ aldicarb interactions did not differ significantly for root weights in any of the experiments.

Grain yield. Moderately tolerant cultivars yielded significantly more grain than intolerant cultivars for each of the nonirrigated experiments at Moro (Table 5). Cultivars did not differ in yield in the three irrigated experiments.

Aldicarb did not improve yields in the nonirrigated experiments and improved ($P < 0.01$) yield in each of the irrigated experiments (Table 5). Compared with aldicarb-treated plots in the irrigated experiments, yield suppression for individual cultivars in control plots ranged from 8 to 29%. Averaged across cultivars, yield suppressions of 11, 23, and 23% were associ-

ated with elevated populations of *P. neglectus* at the Cuthbert farm and the Davis-1 and Davis-2 experiments, respectively. The proportional increase in yield due to aldicarb treatment was lower ($P < 0.05$) at the Cuthbert than in the Davis experiments. Irrigation at the Cuthbert farm was terminated at a time when the surrounding winter wheat crop became mature and the spring wheat in the experiment was in the early soft-dough stage. Spring wheat was watered to full maturation at the Davis farm. Aldicarb slightly reduced ($P < 0.05$) yield at the Moro-1 experiment, which was among the driest sites studied.

During 2004, at Moro-1, yield of Zak averaged 2,888 kg/ha. Treatments did not differ significantly when the 2004 yield was analyzed according to cultivar and aldicarb treatments applied to plots during 2003.

Grain quality. Grain test weight was lower ($P < 0.05$) in aldicarb than in control treatments at both Moro-1 and Moro-2 (data not presented). Grain kernel weight was also lower ($P < 0.05$) in aldicarb than in control treatments at Moro-2 but not Moro-1.

Grain at the Cuthbert farm became shriveled after irrigation was terminated in the

early soft-dough stage. Aldicarb treatment at the Cuthbert farm led to improvement in test weight (653 versus 665 kg/m³, $LSD_{0.05} = 11$) but not kernel weight. At the fully watered Davis-1 experiment, aldicarb treatment improved test weight (805 versus 811 kg/m³, $LSD_{0.05} = 3$) and kernel weight (35 versus 37 mg/kernel, $LSD_{0.05} = 1$). Results were similar for the Davis-2 experiment, where test weights in aldicarb and control plots were 794 and 786 kg/m³ ($LSD_{0.05} = 4$) and kernel weights were 37 and 34 mg/kernel ($LSD_{0.05} = 2$), respectively.

Associations between *P. neglectus* and grain yield. Significantly negative correlations were common between grain yields and initial populations of *P. neglectus*. The likely bias from aldicarb and cultivar variables was avoided by placing emphasis on control plots for individual cultivars. Under dryland conditions at the Moro-1 experiment, the *Pratylenchus* population in control plots was negatively correlated with yield (Fig. 1A). As the initial population of *P. neglectus* increased in plots with 0 to 4,000 nematodes/kg, the yield of Krichauff (moderately resistant and moderately tolerant) was unaffected and yield of Machete (susceptible and intolerant) was reduced ($P = 0.10$) by 22%. Slopes of the regressions for the two cultivars (Fig. 1A) differed significantly ($P < 0.05$). A similar but more statistically significant relationship occurred for these same cultivars at the irrigated Davis-2 experiment, where Krichauff yield was unaffected and yield of Machete declined ($P = 0.02$) by 71% as the *P. neglectus* population increased in plots with 1,800 to 7,600 nematodes/kg (Fig. 1B). Again, the regression slopes for these cultivars differed significantly ($P < 0.05$).

Similar relationships occurred for Frame (moderately susceptible and moderately intolerant to tolerant) and Spear (susceptible and intolerant) at the irrigated Cuthbert (Fig. 2A) and Davis-2 (Fig. 2B) experiments. At the Cuthbert farm, yield of Frame was unaffected and yield of Spear declined 29% as the preplant *P. neglectus* population increased in plots with 0 to about 6,000 nematodes/kg. At the Davis-2 experiment, yields of Frame and Spear declined 11 and 36%, respectively, as the *P. neglectus* population increased in plots with 0 to 4,000 nematodes/kg.

There also were negative correlations between yield and *P. neglectus* density in roots for three experiments. The intolerance of Spear to *P. neglectus* was particularly evident in aldicarb-treated plots at the Moro-2 experiment (Fig. 3), where yield declined rapidly in plots with greater than 20 *P. neglectus*/g of fresh root tissue (about 80 *P. neglectus*/g on an oven-dry basis). Densities of *P. neglectus* in roots of Krichauff at this very dry nonirrigated site were mostly less than 8 per g of fresh root tissue, and were unrelated to yield. Root weights were higher for Krichauff than for

Fig. 1. Relationships between initial population of *Pratylenchus neglectus* and yield of spring wheat cvs. Krichauff and Machete in control plots (not treated with aldicarb) at the **A**, Moro-1 and **B**, Davis-2 experiments during 2003.

Spear in this experiment, but grain yields did not differ between cultivars.

During 2004, at the only experiment (Moro-1) replanted to evaluate residual responses of treatments on yield of the locally adapted cultivar Zak, yield was negatively correlated ($P < 0.001$) with initial density of *P. neglectus* in soil (Fig.

4). Yield of Zak declined 16% as the initial population of *P. neglectus* increased in plots with 0 to 4,000 nematode/kg of soil.

Where irrigation was terminated prematurely at the Cuthbert farm during 2003, grain yield was negatively correlated with canopy leaf temperature ($P < 0.0001$, $r^2 = 0.46$). The relationship was weaker but still

significant at the adequately watered Davis-1 ($P = 0.02$, $r^2 = 0.08$) and Davis-2 ($P = 0.004$, $r^2 = 0.23$) experiments. At the latter site, density of *P. neglectus* in roots was inversely correlated with test weight ($P = 0.003$, $r^2 = 0.24$), tiller height ($P = 0.04$, $r^2 = 0.12$), and canopy temperature ($P = 0.06$, $r^2 = 0.10$).

DISCUSSION

This is the first report that *P. neglectus* causes economic damage to spring wheat in the Pacific Northwest. High populations of *P. neglectus* in soil at planting were correlated with up to 71% reduction in grain yield. Damage was demonstrated in irrigated as well as dryland fields. Yields of a moderately tolerant cultivar were higher than those of intolerant cultivars in dryland fields, and the density of *P. neglectus* was higher in susceptible than in moderately resistant cultivars. In South Australia and Victoria, wheat yields in dryland fields are also inversely associated with the initial density of *P. neglectus* in soil (41,44). In the current experiments, specific associations between grain yield and initial populations of *P. neglectus* in soil were variable, making it impossible to suggest damage thresholds based on studies reported in this paper. However, it was clear that initial *P. neglectus* populations as low as 2,000 per kg of soil were capable of limiting grain yield in one dryland (Moro-1; Figs. 1A and 4) and one irrigated (Davis-1; Fig. 2B) experiment. Yield constraints from initial populations as low as 3,000 *P. neglectus*/kg of soil have been reported in Australia (44). *Pratylenchus* populations exceeding 2,500 per kg of soil in the surface 20 cm of the soil profile occur in 20% of the intensively cropped fields in the Pacific Northwest (34). Populations of *Pratylenchus* spp. at depths greater than 20 cm have not been investigated, possibly leading to important underestimations of percentages of fields having high populations (39). It is therefore important to recognize *P. neglectus* as another important constraint to yield in Pacific Northwest fields planted to cereals more frequently than once every 2 years.

Reviews of literature indicate that yield reductions by *P. thornei* are generally greater than by *P. neglectus* (20,44). Yield reductions up to 70 and 85% were associated with *P. thornei* in Israel and Australia, respectively. Yield reductions associated with *P. neglectus* were generally in the range of 16 to 40%. Yields have been suppressed as much as 74% in the presence of a mixed population of *P. thornei* and *P. neglectus* (44). *P. thornei* has been reported to reduce yield of intensively cropped spring wheat by as much as 40 to 60% in the Pacific Northwest (36). *P. neglectus* was generally associated with yield reductions of 8 to 36% for studies reported in this paper, although yield for one intolerant cultivar was suppressed 71% in a field also

Fig. 2. Relationships between initial population of *Pratylenchus neglectus* and yield of spring wheat cvs. Frame and Spear in control plots (not treated with aldicarb) at the A, Cuthbert and B, Davis-1 experiments during 2003.

Fig. 3. Relationship between density of *Pratylenchus neglectus* in roots (fresh-weight basis) and yield of spring wheat cv. Spear in aldicarb-treated soil at the Moro-2 experiment during 2003.

highly infested with *H. avenae*, *Pratylenchus* spp., and soilborne root-infecting fungi. The greater damage reported for *P. thornei* than for *P. neglectus* in the Pacific Northwest appears consistent with reports from other regions.

Accurate identification of *Pratylenchus* species is important because cultivars of wheat and other field crops differ in resistance and/or tolerance to *P. neglectus* and *P. thornei* (9,40,44). Rotations effective for reducing populations of *P. thornei* may not be effective for reducing populations of *P. neglectus*, and wheat cultivars with tolerance to *P. thornei* may be intolerant to *P. neglectus*. Differentiation between *P. neglectus* and *P. thornei* using standard microscopy can be challenging (11,14). Recent advances in molecular diagnostics (24,47) provide an opportunity to achieve a higher level of precision for identifying *Pratylenchus* species. The current study quantified the population of *Pratylenchus* in the traditional manner, by sending samples to a commercial diagnostic laboratory, and then also employing molecular diagnostics to identify and estimate proportions of individual *Pratylenchus* species in the extracts. Diagnostic services in Australia have advanced to a level permitting the quantification and identification processes to be combined (24), but that level of precision and calibration is not yet available in the Pacific Northwest.

In nonirrigated soil infested with *P. neglectus*, the moderately tolerant cultivar Krichauff yielded more grain than the intolerant cultivars Machete and Spear. These intolerant cultivars also exhibited a lower capacity than Krichauff and another moderately tolerant cultivar, Frame, to maintain optimal yields in plots with higher soil populations of *P. neglectus* at dryland as well as irrigated sites in Oregon. The locally adapted cultivar Zak was shown to be intolerant of *P. neglectus*. While the Australian cultivars served an important need in this research, they are not well adapted to production systems in the Pacific Northwest. Genes for tolerance to *P. neglectus* must be crossed into high-yielding, locally adapted spring wheat cultivars intended for planting into annual cereal cropping systems in the Pacific Northwest. Cultivars and lines with levels of tolerance higher than for Krichauff have been identified (44) and should serve as the focus for breeding programs in the Pacific Northwest.

The multiplication factor (Pf/Pi) for *P. neglectus* in control plots at the irrigated Davis-2 experiment was lower for Krichauff (0.23) than for Machete (0.96). In South Australia, relative Pf/Pi ratings of 0 and 1.71 were reported (40) for Krichauff and Machete, respectively, leading to ranking these cultivars as resistant and susceptible, respectively. For control plots at the Davis-1 experiment, we did not observe a significant difference between

multiplication factors for Frame (0.44) and Spear (0.48). Both cultivars are susceptible to *P. neglectus* in Australia, where relative multiplication factors of 1.35 and 1.09 have been reported (40). Demonstrations that Krichauff had a higher level of relative resistance than Frame, Machete, and Spear in the current study is therefore consistent with previous reports for these cultivars and supports the conclusion that it will be possible to reduce *P. neglectus* population densities in soil by growing resistant cultivars. As with tolerance ratings, cultivars and lines with much higher resistance ratings than expressed by Krichauff are now recognized (6,49) and should be utilized in wheat breeding programs in the Pacific Northwest.

Multiplication factors (Pf/Pi) for *P. neglectus* were higher for two dryland sites than for two irrigated sites. Taylor et al. (40) also reported higher multiplication factors for *P. neglectus* in drier than in wetter regions. Initial populations of *P. neglectus* were higher at the irrigated than at dryland sites in the current study. Higher multiplication rates in soils with lowest initial populations are consistent with previous reports (30) and may have been responsible for the significantly lower multiplication rates in response to aldicarb treatment at the irrigated but not dryland sites in the current study.

Aldicarb typically reduced the density of *P. neglectus* in roots, increased plant height and tiller density, and reduced leaf canopy temperature and variation in tiller height. Also, aldicarb improved grain yield and quality where water was sufficient for plants to respond to protection from nematode damage, but did not improve yields when crops at these very dry locations were not irrigated. Grain quality tended to be reduced by application of aldicarb at the driest sites, presumably by increasing the amount of water extracted from soil by seedlings, thereby creating an earlier or

more intense shortage of water late in the growing season. Aldicarb had no effect on growth or yield of spring wheat in an Oregon field where populations of plant-parasitic nematodes were very low (36). While aldicarb proved useful for illustrating the negative impact of *P. neglectus* on growth and yield of spring wheat, this nematicide is not registered for this purpose in the United States.

Spring wheat in the Pacific Northwest receives little in-season rainfall, and generally depletes stored water in the soil profile before plant maturity. Plant canopy temperature is directly correlated with water stress in wheat (8,31), and has been used as an indicator of plant stress induced by plant-pathogenic fungi and plant-parasitic nematodes (21). Canopy temperature was as much as 4°C higher in control than in aldicarb-treated plots, indicating a higher level of plant water stress in soils with high populations of *P. neglectus*. Comparable canopy temperature differentials were detected for spring wheat grown in soils infested with *P. thornei* (36). For both *Pratylenchus* species, temperature differentials between aldicarb-treated and control plots were higher in magnitude than temperature differentials reported for soils infested with *H. avenae* in France (21). The greater temperature differential in nematode-damaged plants in the Pacific Northwest than in northern Europe was an indication that wheat plants are more sensitive to nematode damage in semiarid regions where stresses from root dysfunction and water depletion are considered to be additive. In studies reported here, populations as low as 20 *P. neglectus*/g of fresh root tissue (ca. 80 *P. neglectus*/g of dry tissue) were associated with reduced root weight and grain yield for the intolerant cultivar Spear at one low-rainfall site.

Intolerant plants with roots heavily damaged by *P. thornei* may exhibit stunting, poor vigor, reduced tillering, and pre-

Fig. 4. Relationship between initial density of *Pratylenchus neglectus* in soil and yield of spring wheat cv. Zak at the Moro-1 experiment during 2004. Zak was planted uniformly over plots in which a gradient in *P. neglectus* density was created during 2003 by planting plots with spring wheat cvs. Krichauff or Machete, each with or without aldicarb treatment.

mature wilt at the onset of moisture stress (7,25,43). It is presumed that parasitism of roots by *P. neglectus* causes similar symptoms. However, these foliar symptoms are similar to those caused by other abiotic and biotic stresses and are therefore not diagnostic for invasion of wheat roots by *Pratylenchus* spp. Without benefit of systematic soil testing for enumeration and identification of plant-parasitic nematodes, the symptoms described above are likely to be ascribed to plant stresses caused by inadequate availability of soil nutrients, impedance to root penetration, low or high temperature, insufficient water for plant growth and maturation, or infection of roots by soilborne plant-pathogenic fungi. The current demonstration that *Pratylenchus* species are a contributing cause for poor wheat growth and yield in the Pacific Northwest, together with economic constraints to intensive and/or frequent sampling programs to detect plant-parasitic nematode populations in large acreages of dryland field with irregular terrain, indicates that development of resistant and tolerant germ plasm will be the most cost-effective strategy for improving wheat yields in fields heavily infested with *Pratylenchus* species. Since *P. neglectus* and *P. thornei* initially invade roots of resistant as well as susceptible plants, they may cause damage to roots of resistant-intolerant as well as susceptible-intolerant hosts. Genetic tolerance therefore may improve performance of the current crop, and resistance may reduce the magnitude of threat to subsequent crops. Both tolerance and resistance are needed for annual wheat in the Pacific Northwest.

Variability in height of headed tillers was reduced by the aldicarb treatment within experiments, and was considered an important quantitative indicator of relative damage by *P. neglectus*. A similar relationship was reported for *P. thornei* (36). Variability in head height appears useful for ranking wheat tolerance reactions in fields highly infested with *P. neglectus* and *P. thornei*.

Interactions among nematodes and fungal pathogens are well known (1,15,38). Observations at the Davis farm indicated a negative association between take-all and a browning root-rot complex composed mostly of damage by *P. neglectus*, *R. solani*, and *Pythium* species. Positive associations also occurred between severity of the root rot complex and initial population of *P. neglectus* and density of *P. neglectus* in roots. Interactions of *R. solani* and *P. neglectus* have been reported for winter wheat (2). The fungal pathogen was considered most important, but *P. neglectus* apparently enhanced the development of root rot. Multiplication rates of *P. neglectus* were amplified when the nematode entered root tissue already breached by the fungal pathogen. However, when *R. solani* and *G. graminis* var. *tritici* (take-all) both

occupied the same root tissue, the combination of fungal pathogens caused a strong reduction in nematode reproduction (2). 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. Likewise, the density of *P. neglectus* in wheat roots has been amplified by the presence of *R. solani*, *Bipolaris sorokiniana*, *Pythium irregulare*, *G. graminis* var. *tritici*, *Microdochium bolleyi*, or *Fusarium equiseti* (38). A combination of *R. solani* and *G. graminis* var. *tritici* reduced multiplication rates for *P. neglectus*. Severity of root rot was increased by various combinations of *P. neglectus* and fungal pathogens. A similar inverse relationship has also been reported for *P. neglectus* and *H. avenae* (18). The first species to colonize root tissue caused a subsequent reduction in reproductive capacity for the later-arriving parasite. However, a negative interaction between *P. neglectus* and *H. avenae* was not detected in the present study. Interactions among plant-parasitic nematodes and soilborne fungal pathogens are clearly complex and must be considered as fully as possible when interpreting results of field trials.

Many growers who adopt direct-drill systems in the Pacific Northwest plant cereals annually because rotational opportunities are limited for economic and climatic reasons. In Australian soils heavily infested with *P. neglectus*, growers attempt to minimize damage by rotating crops. Although crop rotation is a preferred management practice (27), limiting damage by *P. neglectus* through rotation in the Pacific Northwest will be challenging because this species infests a wide range of field crop species (40) and broadleaf and grass weeds (45,46). In general, most commercial wheat and chickpea (*Cicer arietinum* L.) cultivars are considered good hosts for multiplication of *P. neglectus*. Poor hosts include field pea (*Pisum sativum* L.) and triticale (*X Triticosecale* Wittmack). Acreages of field pea and triticale are currently very limited in the Pacific Northwest small grain production region. Efforts to expand numbers and types of profitable crops for rotations have not been successful in the Pacific Northwest. Under current economic conditions, significant progress in limiting damage from *P. neglectus* is therefore likely to occur through wheat breeding rather than from further efforts to develop profitable crop rotations. Fortunately, much progress and promise exists for breeding wheat cultivars with sufficiently high tolerance and/or resistance to stabilize yields and reduce the multiplication efficiency for *P. neglectus* (6,49, 50,51).

Other plant-parasitic nematode genera and species were detected in soil during the course of these experiments. Populations of *Tylenchorhynchus*, *Geocenamus*,

Meloidogyne, and *Criconemoides* were each low and unlikely to have imposed any significant growth constraint on spring wheat (17,23,29). A high population of *Paratylenchus* was present at the two irrigated farms, and the impact of *Paratylenchus* on wheat growth has not been determined. High populations of *Paratylenchus* in some Pacific Northwest field crops were previously reported (13,34).

Populations of *H. avenae* were high in experiments at the Davis farm. Grain yield for control plots (not treated with aldicarb) in the Davis-1 experiment was negatively ($P < 0.05$) associated with the initial population of *P. neglectus* (Fig. 2B). However, Frame is classified as tolerant to moderately tolerant to the Australian population of *H. avenae* as well as *P. neglectus* (48), and Spear is classified as intolerant to moderately intolerant to both plant-parasitic species in Australia. The current study generally found that tolerance reactions for Australian wheat cultivars challenged with strains of *P. neglectus* in Oregon were comparable to published tolerance ratings for these cultivars in Australia. In contrast, Frame and other cultivars with enhanced tolerance to the Australian population of *H. avenae* were reported to be no better than intolerant cultivars when grown in soils infested with the Oregon population of *H. avenae* (37). In affiliated studies, Frame and Spear were considered equally intolerant of the *H. avenae* population at the Davis farm (37). In the present experiment, significant negative correlations occurred between the initial *P. neglectus* population and yield for both cultivars. It therefore appears that the previously reported negative association between four spring wheat cultivars and the population of *H. avenae* at the Davis farm (37) represented a general response to all cultivars in that experiment, and that grain yields for Frame and Spear were instead more closely associated with damage from the *P. neglectus* population than the *H. avenae* population. This conclusion is supported by associated results reported from the Davis farm in this paper, namely that, in addition to grain yield, there also were significant ($P < 0.05$) negative correlations between *P. neglectus* populations in roots and leaf canopy temperature, tiller height, and test weight. However, it was also apparent that the 71% yield suppression for an intolerant cultivar in the presence of *H. avenae*, *Paratylenchus* spp., *P. neglectus*, and fungal pathogens at the Davis-2 experiment greatly exceeded the general range (8 to 36%) for yield suppression by *P. neglectus* alone.

In summary, plots with higher populations of *P. neglectus* in soil were correlated with reduction in spring wheat yield in the Pacific Northwest. Damage by *P. neglectus* was demonstrated in irrigated and dryland fields. Invasion of spring wheat by *P. neglectus* also increased late-season stress

(higher canopy temperature) and reduced plant biomass production (plant height, root weight, and tillering) and grain quality (test weight and kernel weight). As with *P. thornei* (36), *P. neglectus* must be included on the lists of pathogens known to limit productivity of spring wheat in annual-crop systems in the Pacific Northwest (26,32). This is important because economics and air and soil quality issues are causing increasing numbers of growers to plant fields annually to spring cereals rather than to the traditional 2-year winter wheat–summer fallow rotation. *Pratylenchus* species pose a higher level of risk to annual cereals than to wheat rotated with summer fallow (34).

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