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Pratylenchus thornei Associated with Reduced Wheat Yield in Oregon

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Abstract: *Pratylenchus thornei* reaches high population densities in non-irrigated annual cropping systems in low-rainfall regions of the Pacific Northwest. Two spring wheat varieties with different levels of tolerance and susceptibility to *P. thornei* were treated or not treated with aldicarb in three experiments. Grain yield was inversely correlated ($P < 0.05$) with pre-plant populations of *P. thornei* in soil and with *P. thornei* density in mature roots. As population of *P. thornei* increased, yield of the moderately tolerant/moderately susceptible variety Krichauff was generally more stable than for the intolerant/susceptible variety Machete. The reproductive factor (Pf/Pi) was generally lower ($P < 0.05$) for Krichauff than Machete. Aldicarb improved wheat yield ($P < 0.05$) in highly infested fields by an average of 67% for Krichauff and 113% for Machete. Aldicarb increased ($P < 0.05$) numbers of headed tillers, plant height, and grain test weight and kernel weight, and reduced ($P < 0.05$) the density of *P. thornei* in mature wheat roots, variability in height of heads, and leaf canopy temperature. Aldicarb did not improve yield in a soil with a low population of *P. thornei*. This is the first report that *P. thornei* causes economic damage to wheat in the Pacific Northwest.

Key words: aldicarb, crop loss, leaf canopy temperature, lesion nematode, *Pratylenchus thornei,* resistance, tolerance, *Triticum aestivum,* wheat.

Wheat (*Triticum aestivum* L.) in semiarid regions of the Pacific Northwest states of Oregon and Washington is produced mostly as a 2-year rotation of winter wheat and summer fallow. This is the most profitable production system for rain-fed fields that receive 250 to 400 mm annual precipitation, with little if any rain during the summer. Many wheat-fallow rotations are vulnerable to water erosion and also contribute to concerns regarding quality of air and water. Cereals are produced on about 1.5 million ha in Oregon and Washington, with 1.05 million ha in winter wheat and 0.43 million ha in spring wheat and spring barley (*Hordeum vulgare* L.). Interest in conservation tillage systems (Cook, 2001) has led to conversion of 77,000 ha of land formerly in winter wheat-summer fallow rotation to spring wheat or barley planted annually without tillage. Approximately 10% of spring grains in Oregon and Washington now are planted without tillage, with percentages of 20% to 34% in at least four major cereal-producing counties (Veseth, 1999). For economic reasons, most direct-seeded fields are planted annually to cereals rather than rotated among crop species. The effect of changes in production systems on nematode populations in the Pacific Northwest is unknown.

Gair et al. (1969) reported that populations of *Pratylenchus neglectus* (lesion nematode) increased dramatically when dryland fields were shifted to a higher intensity of cereal cropping. Riley and Kelly (2002) also reported a direct association between *Pratylenchus* population density and the frequency of cereal cropping. Clewett et al. (1993) stated that *P. thornei* could be reduced to populations non-damaging to wheat if wheat were grown no more frequently than once every 3 years in rotation with crops less suitable for multiplication of the nematode. Nombela et al. (1998) reported much lower populations of *Pratylenchus* following summer fallow compared to wheat or vetch. In the Pacific Northwest wheat belt, Smiley et al. (2004b) found much higher populations of *P. thornei* and *P. neglectus* in annually cropped fields than in winter wheat-summer fallow rotations. *Pratylenchus* species often occurred in populations considered potentially damaging in fields cropped more than 50% of the years, >300/g of fresh root in 40% of fields, and >2,500/kg of soil in 20% of fields.

Pratylenchus thornei is well recognized for damaging wheat in many regions of the world (Nicol, 2002; Rivoal and Cook, 1993). Pre-plant populations of *P. thornei* are often negatively correlated with wheat yield (Hollaway, 2001; Nicol et al., 1999). Economic damage thresholds for *P. thornei* on wheat vary greatly. Thresholds as low as 420 and 2,500 *P. thornei*/kg of soil have been reported from Mexico (Nicol and Ortiz-Monasterio, 2004; Van Gundy et al., 1974) and Queensland (Thompson, 1993), respectively. A threshold as high as 30,000 *P. thornei*/kg of soil was reported for an intolerant variety at a location in South Australia (Nicol et al., 1999), although populations as low as 4,000 *P. thornei*/kg of soil have caused severe damage to intolerant wheat at other locations in South Australia (Taylor et al., 1999). Yield constraint from root damage depends on the nematode species and numbers in roots; crop species, variety, growth stage, and rotation; tillage management; and soil temperature, moisture and texture. Wide divergences of economic threshold estimates for *P. thornei* indicate that high numbers do not necessarily equate to high potential for damage.

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The economic importance of *P. thornei* has not been studied under field conditions in the Pacific Northwest. In Washington, *P. thornei* reduced foliar growth of winter wheat in a greenhouse seedling assay using an initial inoculum density of approximately 6,700 nematodes/kg of soil, but there was no effect on growth when the initial density was about 670/kg (Mojtahedi et al., 1986). While Smiley et al. (2004b) reported high populations in many annually cropped fields, it is recognized that nematode population estimates often are poor predictors of potential damage by *Pratylenchus* (Riley and Kelly, 2002).

In this paper we report relationships between *P. thornei* and yield for annual no-till spring wheat in eastern Oregon. Procedures and wheat germplasm were selected to provide direct comparisons with research on *P. thornei* in Australia (S. Taylor, pers. comm.; V. Vanstone, pers. comm.).

Materials and Methods

Locations and crop management: Three field experiments were performed during 2003 at two locations in northeast Oregon. Experiments were performed on the Hill Farm, 13 km southeast of Pendleton, and at the Oregon State University Columbia Basin Agricultural Research Center (CBARC), 15 km northeast of Pendleton. Annual precipitation averages 400 and 442 mm at the Hill Farm and CBARC, respectively. Soils at both locations were silt loams. Each field had a recent history of annual cropping without tillage and was naturally infested with *P. thornei.*

Spring wheat was planted as a direct-seeded (no-till) annual crop at each location. Experiments were planted at the Hill Farm and CBARC on 11 and 9 April 2003, respectively. Seed was planted using a drill equipped with a cone-seeder and four openers at 36-cm row spacing. Starter fertilizer was applied by banding below the seed at the time of planting. 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. The crop prior to establishing each experiment was canola (*Brassica napus* 'Hyola 401') at the Hill Farm, spring wheat (cv. 'Zak') for one experiment at CBARC (CBARC-1), and chickpea (*Cicer arietinum* 'Sinaloa') for a second experiment at CBARC (CBARC-2).

The experimental design at each location was a two-way randomized complete block with variables of wheat variety and aldicarb treatment. The four treatment combinations (two varieties with and without aldicarb) were replicated nine times in 1.7-×-6.1-m plots.

Wheat varieties were Krichauff and Machete, each of which is an Australian variety characterized for tolerance and resistance to *P. thornei.* Tolerance is defined as the ability of the plant to withstand nematode infection (Roberts, 2002). In wheat, tolerance 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 (Roberts, 2002). Machete, released in 1985, has been characterized as susceptible and intolerant to *P. thornei* in South Australia (Vanstone et al., 1998; Wheeler and Wurst, 2003). Krichauff, released in 1997, is a higher-yielding variety than Machete (Wheeler and Wurst, 2003) and has been characterized in South Australia as moderately resistant and moderately tolerant (Vanstone et. al., 1998), or as moderately susceptible and moderately intolerant (Wheeler and Wurst, 2003). In Queensland, Krichauff is ranked as tolerant to *P. thornei,* Machete has not been rated for tolerance, and both varieties are ranked as moderately susceptible (J. G. Sheedy, pers. comm.). While minor differences in reaction to *P. thornei* have been reported, Krichauff is generally considered more tolerant and less susceptible than Machete.

Aldicarb (Temik 15G) was mixed with the seed in the seed cone while planting 18 of the 36 plots in each experiment. Aldicarb was dispensed at 4.2 kg a.i./ha to suppress damage and reproduction by *Pratylenchus* spp. (Taylor et al., 1999).

Data for each plot included pre-plant populations of nematodes in soil, density of *Pratylenchus* in mature roots, and incidence and severity of diseases caused by root-infecting fungi. Plant growth and development data included seedling emergence; plant height; variability in head height; density of headed tillers; and grain yield, test weight, and kernel weight. Variability in head height was calculated by dividing the standard deviation by mean head height. 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 (Ehrler et al., 1978; Nicolas et al., 1991) during mid-afternoon on hot days in July, using a Rayinger ST noncontact thermometer (Raytek Corp., Santa Cruz, CA).

Corner locations for all experiments were preserved by burying woven-wire cables vertically into the four corners of each experimental area. Soil samples were collected during late February 2004 to evaluate residual influences, if any, of the variety and aldicarb treatments applied during 2003. Reproductive factors (Pf/Pi) for *P. thornei* in each plot were calculated by comparing populations during 2003 (Pi) and 2004 (Pf). Experimental areas at CBARC were then re-planted uniformly to 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. thornei* populations prior to planting.

Soil sampling and nematode extraction: Soil was collected to assess *Pratylenchus* populations in individual plots for all experiments. Initial samples were collected while moist during early April 2003, 2 days prior to planting. Samples consisted of 15 to 20 cores (2.5-cm-diam. × 10-cm-deep) composited for each 10-m^2 plot. Final sampling in 2004 occurred while soil was still cold (February) and moist after the soil had over-wintered. To account for vertical distribution of *Pratylenchus* (Taylor and Evans, 1998; Thompson and Clewett, 2004), 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.

A modified elutriation method (Ingham, 1994) was used to extract all soil-dwelling nematodes from 250-g subsamples (H. Kreeft, pers. comm.). Using an Oosterbrink elutriator, coarse material was collected on a 500-µm-pore sieve, cysts on a 125-µm-pore sieve, and free-living nematodes on a stack of two 38-µm-pore and two 32-µm-pore 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 at 3,200 rpm for 5 minutes. Water was discarded, replaced by magnesium sulfate solution at specific gravity 1.80, mixed by spatula, and centrifuged again for 4 minutes. The supernatant solution containing nematodes was passed over a 20-µm-pore sieve, transferred to another 50-ml tube, and allowed to settle for at least 2 hours 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 seconds, 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 (Filho and Huang, 1989; Handoo and Golden, 1989). Numbers were reported as nematodes per kg of oven-dry soil. All numeric data presented in tables and figures were from these routine extraction procedures.

Pratylenchus species for each experiment were further identified to species level based on DNA profiles in a composite of extractions from each plot for each location. 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 (Ophel-Keller and McKay, 2001). Results, in picograms DNA per g of soil, were converted through calibrations into estimates for numbers of each *Pratylenchus* species per kg soil. The numerical estimates were used to determine proportions of each species in each experimental area. During 2004, *Pratylenchus* species were identified in our laboratory using procedures described by Waeyenberge et al. (2000). Extracts returned from Western Laboratories were used to extract DNA from plots with high numbers of *Pratylenchus*. Results of DNA analyses in our laboratory were based on intensity, or presence vs. absence, of banding patterns for each *Pratylenchus* species, and these tests were not calibrated with numbers of *Pratylenchus* species in soil in Oregon.

Plant sampling, nematode extraction, and disease and insect assessment: Root systems for 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 sub-sampling 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 (Ingham, 1994) with samples misted for 60 seconds every 5 minutes. 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 g of fresh root tissue and of oven-dry root tissue.

Plants were also collected separately to assess incidence and severity of diseases caused by soilborne plant-pathogenic fungi and Hessian fly (*Mayetiola destructor*). Because there were no treatment effects in comparable experiments during 2001 and 2002 (unreported data), 25 plants with intact roots to 10-cm depth were collected arbitrarily across each experimental area to assess the general incidence and severity of diseases and Hessian fly during June 2003 (heading stage). Roots were scored visually for incidence and severity of disease (Smiley et al., 1996) and for incidence of Hessian fly (Smiley et al., 2004b).

Statistical analysis: Nematode populations were described by calculating means and standard deviations among plots. All plant growth, disease, and nematode variables among variety-x-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 and, where required, log-transformations.

RESULTS

Populations and identities of nematodes in soil: Pre-plant populations of *Pratylenchus* were highly variable among the 36 plots in each experiment (Table 1). Replication of treatments effectively minimized the high level of spatial heterogeneity within experiments, as indicated by an absence of difference ($P < 0.05$; data not shown) in initial *Pratylenchus* population for each of the four treatments (two varieties with and without aldicarb) in each experiment.

TABLE 1. *Pratylenchus* population and species identity in soils of 36 individual 1.5-×-6-m plots in three experiments; samples were collected during April 2003 and February 2004, before planting spring wheat at Hill Farm and Columbia Basin Agriculture Research Center (CBARC).

			Pratylenchus population[c]		
Location[a]	Year	Species[b]	Mean	Range	Std. dev.
			no./kg	*no./kg*	
Hill Farm	2003	6:1 ratio of Pt/Pn	1,355	20–7,740	1,691
	2004	Pt	4,635	140–15,740	3,884
CBARC-1	2003	Pt	2,118	160–4,980	1,387
	2004	Pt	6,614	780–16,280	4,351
CBARC-2	2003	nd	1,091	20–9,720	1,673
	2004	Pt	6,210	1,120–20,800	5,076

[a] Two spring wheat experiments at CBARC were differentiated as CBARC-1 (following spring wheat) or CBARC-2 (following chickpea).

[b] Pn = *P. neglectus;* Pt = *P. thornei.* Species were extracted and identified to genus level by a commercial nematode diagnostic laboratory. During 2003, proportions of species were determined by DNA extraction from a single soil sample from each experiment; the sample was a composite of soil from all plots in the experiment. Where indicated by nd, species were not determined. During 2004, DNA extractions from plots with highest numbers of *Pratylenchus* indicated a strong presence of *P. thornei* and an inability to detect *P. neglectus.*

[c] Mean, range, and standard deviations for *Pratylenchus* populations for 36 samples, each of which was composed of a composite of 15-20 soil cores collected from each of 36 plots in each experiment.

DNA extracts analyzed in Australia during 2003 indicated a strong dominance of *P. thornei* over *P. neglectus* at Hill Farm (6,000 vs. 1,000/kg soil) and at CBARC-1 (12,000 vs. <1,000/kg). The lower limit for detection by the procedure was 1,000/kg, indicating the possibility that the population at CBARC-1 was entirely *P. thornei.* DNA analyses at our laboratory during 2004 also indicated a strong presence of *P. thornei* and an inability to detect *P. neglectus* at all three locations.

Samples collected during February 2004 indicated lower ($P < 0.05$) reproductive (Pf/Pi) factors (Table 2) for Krichauff than for Machete in two experiments, both of which had initial populations half that for the experiment where a varietal response was not observed (Table 1). Reproductive factors were also lower ($P < 0.05$) for *P. thornei* in aldicarb-treated plots compared to control plots in two of three experiments (Table 2). There was no variety-x-aldicarb interaction in any of the experiments.

Tylenchorhynchus clarus was detected in soil each year at both locations (data not presented). During 2003 the range in numbers for individual plots varied from 0 to 1,620/kg (mean = 172) at Hill Farm and from 0 to 500/kg (mean = 141) at CBARC. Low populations (0 to 60/kg, means <2/kg) of *Heterodera avenae* and *Xiphinema* were also detected at these locations.

Pratylenchus density in roots: Aldicarb reduced ($P < 0.05$) *P. thornei* densities in roots for two experiments and for the overall mean for three experiments (Table 3). The density of *P. thornei* in mature roots did not differ for Machete and Krichauff in individual experiments but did differ for the three-experiment mean (Table 3). The variety-x-aldicarb interaction was significant at $P = 0.08$. When data for control plots (not treated with aldicarb) were analyzed separately, the varietal difference was significant at $P < 0.001$. Relative *P. thornei* densities were comparable when evaluated on the basis of either fresh- or dry-root weights (Table 3).

Plant growth and development: Seedling establishment did not differ between varieties (data not presented). However, stand density was higher in control than in aldicarb-treated plots in all three experiments: 92 vs. 60 plants/m ($LSD_{0.05}$ = 14) at Hill Farm, 105 vs. 85 plants/m ($LSD_{0.05}$ = 9) at CBARC-1, and 113 vs. 82 plants/m ($LSD_{0.05}$ = 11) at CBARC-2. In all three experiments, aldicarb treatment increased ($P < 0.001$) the height of mature plants and reduced variability in head height (Table 4). Numbers of headed tillers were in-

TABLE 2. Reproduction factors (Pf/Pi) for *Pratylenchus thornei* in response to cultivar and aldicarb variables in experiments at Hill Farm and Columbia Basin Agricultural Research Center [CBARC]) during 2003.[a]

	Krichauff		Machete		Significance[b] ($P > F$)		
Location	Control	Aldicarb	Control	Aldicarb	Variety	Aldicarb	V × A
		Reproduction factor					
Hill	3.6	2.1	7.7	5.1	<0.01**	0.02*	0.63
CBARC-1	3.7	2.1	3.8	2.1	0.61	0.05*	0.91
CBARC-2	3.9	3.7	9.2	7.3	0.01*	0.84	0.33
Mean	3.7	2.6	6.9	4.8	<0.01**	0.05*	0.68

[a] Reproduction factor was derived from the number of nematodes per kg soil before planting and application of aldicarb during April 2003 (Pi) and re-sampling 1 year later (Pf). Plots were not tilled or cropped between harvest (August 2003) and collection of Pf samples (March 2004).

[b] Degrees of freedom for the 36-plot experimental design were nematicide (1), variety (1), nematicide × variety (1), error (24), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*) or 99% (**).

TABLE 3. Density of *Pratylenchus* in mature roots in aldicarb-treated and untreated plantings of Krichauff and Machete spring wheat at Hill Farm and Columbia Basin Agricultural Research Center (CBARC) during 2003.[a]

	Krichauff		Machete		Significance[b] ($P > F$)		
Location	Control	Aldicarb	Control	Aldicarb	Variety	Aldicarb	V × A
		Nematodes/g fresh root tissue[c]					
Hill	151	7	644	85	0.13	0.07	0.26
CBARC-1	281	10	406	2	0.36	<0.001***	0.35
CBARC-2	31	4	187	2	0.07	0.02*	0.07
Mean	154	7	412	30	0.03*	<0.001***	0.08
		Nematodes/g oven-dry root tissue[d]					
Hill	1,010	43	4,660	635	0.12	0.07	0.26
CBARC-1	1,506	55	2,149	47	0.31	<0.001***	0.33
CBARC-2	186	20	1,197	10	0.07	0.02*	0.06
Mean	901	39	2,669	231	0.04*	<0.001***	0.10

[a] Samples were collected during June, between anthesis and grain-filling stages of growth.

[b] Degrees of freedom for the 36-plot experimental design were nematicide (1), variety (1), nematicide × variety (1), error (24), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*), 99% (**), or 99.9% (***).

[c] Fresh root weights did not differ ($P < 0.05$) for treatments or locations. Overall means were 13.3, 12.9, 13.1, and 11.6 g of fresh root tissue extracted for Krichauff plus aldicarb, Krichauff control, Machete plus aldicarb, and Machete control, respectively.

[d] Dry root weights differed ($P = 0.05$) for aldicarb treatments but not for varieties or locations. Overall means were 2.4, 2.2, 2.2, and 1.9 g of dry root tissue extracted for Krichauff plus aldicarb, Krichauff control, Machete plus aldicarb, and Machete control, respectively.

creased by aldicarb in two of the three experiments ($P < 0.01$). Canopy leaf temperature was also reduced by aldicarb treatment in two of the three experiments ($P < 0.05$), coinciding with the two locations where the density of *Pratylenchus* in roots was highest (Table 1). Temperature of the plant canopy was as much as 4 °C cooler in aldicarb-treated compared with control plots.

Diseases and insects: Rhizoctonia root rot (*Rhizoctonia solani* AG-8 and *R. oryzae*) and take-all (*Gaeumannomyces graminis* var. *tritici*) were present at low levels of incidence and severity. Fusarium crown rot (*Fusarium pseudograminearum*) also was present at low incidence and severity at CBARC and was not detected at Hill Farm. Hessian fly puparia were present on <0.5% tillers, a level of incidence that had little or no effect on plant growth and development. Foliar diseases did not occur in these experiments.

Grain yield: Krichauff had a higher ($P < 0.001$) yield than Machete in each experiment (Table 5). Averaged across experimental variables and locations, Krichauff yields were 78% greater than for Machete in control soils that had not been treated with aldicarb. Yields also were improved by aldicarb in each experiment ($P < 0.001$). Averaged across locations, aldicarb increased yield by 67% for Krichauff and 113% for Machete. The variety-x-aldicarb interaction was significant only at Hill Farm, indicating that the yield response to aldicarb treatment was less for Krichauff (118%) than for Machete (147%) at that location.

During 2004, yield of Zak was higher ($P < 0.001$) in the CBARC-1 than the CBARC-2 experiment (5,239 vs. 4,703 kg/ha, $\text{LSD}_{0.05} = 211$). There was no residual response to variety or aldicarb variables studied during 2003.

Grain quality: Test weights were higher ($P < 0.05$) for Krichauff than for Machete in each experiment (data not presented). Test weights averaged over the three locations were 756 and 714 kg/m^3 ($\text{LSD}_{0.05} = 15$) for

TABLE 4. Plant growth, development, and physiology in aldicarb-treated and untreated plantings of Krichauff and Machete spring wheat at two locations (Hill Farm and Columbia Basin Agricultural Research Center [CBARC]) during 2003.

		Krichauff		Machete		Significance ($P > F$)		
Plant parameter	Location	Control	Aldicarb	Control	Aldicarb	Variety	Aldicarb	V × A
Mature plant height (cm)	Hill	29	43	27	36	<0.001***	<0.001***	0.01*
	CBARC-1	35	44	28	37	<0.001***	<0.001***	0.78
	CBARC-2	39	49	32	43	<0.001***	<0.001***	0.65
Variability in head height (std. dev./mean)	Hill	0.28	0.22	0.26	0.23	0.87	<0.001***	0.12
	CBARC-1	0.26	0.19	0.33	0.22	<0.001***	<0.001***	0.08
	CBARC-2	0.26	0.19	0.32	0.22	<0.001***	<0.001***	<0.01**
Headed tillers/m row	Hill	89	99	85	80	<0.01**	0.57	0.06
	CBARC-1	90	102	71	91	<0.01**	<0.01**	0.32
	CBARC-2	110	115	98	120	0.35	<0.01**	0.04*
Leaf temperature at soft dough stage (°C)	Hill	46.1	41.5	47.5	42.8	0.32	<0.01**	0.96
	CBARC-1	46.1	43.4	47.0	46.0	0.08	0.05*	0.36
	CBARC-2	35.1	34.4	37.5	36.0	0.03*	0.19	0.63

Degrees of freedom for the 36-plot experimental design were nematicide (1), variety (1), nematicide × variety (1), error (24), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*), 99% (**), or 99.9% (***).

TABLE 5. Grain yield (kg/ha) for Krichauff and Machete spring wheat grown in aldicarb-treated and untreated soil at Hill Farm and Columbia Basin Agricultural Research Center (CBARC) during 2003.

Location	Krichauff		Machete		Significance ($P > F$)		
	Control	Aldicarb	Control	Aldicarb	Variety	Aldicarb	V × A
Hill	699	1,527	362	895	<0.01***	<0.01***	0.05*
CBARC-1	1,072	1,654	524	1,165	<0.01***	<0.01***	0.46
CBARC-2	1,499	2,294	950	1,858	<0.01***	<0.01***	0.22
Mean	1,090	1,825	612	1,306	<0.01***	<0.01***	0.90

Degrees of freedom for the 36-plot experimental design were nematicide (1), variety (1), nematicide × variety (1), error (24), total (35). Comparisons were accepted as significant at confidence intervals of 95% (*), 99% (**), or 99.9% (***).

Krichauff and Machete, respectively. Aldicarb also improved test weight ($P < 0.05$) in each experiment. Test weights averaged across locations were 749 and 721 kg/m^3 ($LSD_{0.05} = 12$) for aldicarb and control treatments, respectively. Grain kernel weights were higher for Machete than Krichauff in each experiment and also were improved by aldicarb. When averaged over the three experiments, kernel weights were 24.8 and 26.9 mg ($LSD_{0.05} = 1.4$) for Krichauff and Machete, respectively, and 27.7 and 24.1 mg ($LSD_{0.05} = 1.4$) for aldicarb and control treatments, respectively.

Association between Pratylenchus and grain yield: Yield for Machete was negatively associated with pre-plant populations of *Pratylenchus* at Hill Farm during 2003 (Fig. 1), and there was no association between yield of Krichauff and population of *Pratylenchus.* Regression slopes differed ($P = 0.01$) for the two varieties. Yield of Machete was reduced by approximately 60% as the population complex of *P. thornei* and *P. neglectus* (6:1 ratio) increased at Hill Farm. Grain yields were not correlated with the initial population of *P. thornei* in soil at CBARC-1 and CBARC-2 during 2003. However, when each experiment was planted uniformly to a single variety (Zak) during 2004, yields in both experiments were negatively correlated ($P < 0.05$) with the initial population of *P. thornei* (Fig. 2). Slopes of the regression lines differed ($P < 0.01$), indicating a greater impact of *P. thornei* on the higher-yielding CBARC-1 experiment than on the lower-yielding CBARC-2 experiment.

During 2003, the density of *P. thornei* in mature roots was negatively correlated ($P < 0.05$) with grain yield for each variety at each location (Fig. 3). At CBARC-1, a significant difference ($P = 0.01$) between regression slopes indicated that Machete was more intolerant than Krichauff to increasing density of *P. thornei* in roots.

DISCUSSION

We report the first field-derived evidence that *P. thornei* causes economic damage to wheat in the Pacific Northwest. Evidence in soils with high populations of *P. thornei* included greater yield and yield stability for a moderately tolerant variety (Krichauff) than for an intolerant variety (Machete), and responses to application of aldicarb that included a reduction in late-season plant stress and improvement in yield, test weight, and kernel weight.

When produced at three locations in annual cropping systems where *P. thornei* populations exceeded 1,000/kg of soil, Krichauff yielded an average of 78% more grain than Machete in soil that had not been treated with aldicarb. For comparison, we also monitored yields for these varieties in two seed-increase blocks at CBARC. The fields had been fallowed (free from crops or weeds) for 8 months before the seed-increase blocks were planted, and soils in the fields had less than 100 *P. thornei* per kg of soil (Smiley, unpubl. data). The average yield for Krichauff (2,272 kg/ha)

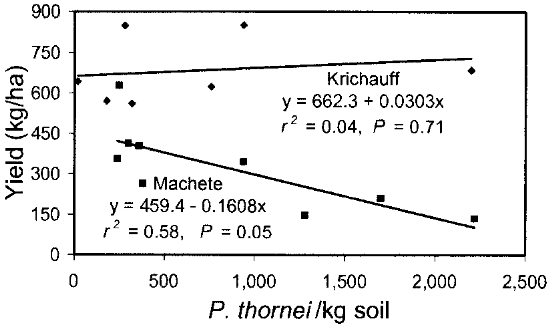

FIG. 1. Relationship between pre-plant numbers of a mixed (6:1 ratio) population of *Pratylenchus thornei* and *P. neglectus,* and yield of Krichauff and Machete spring wheat in control plots (not treated with aldicarb) at Hill Farm during 2003; slopes differed at $P = 0.01$.

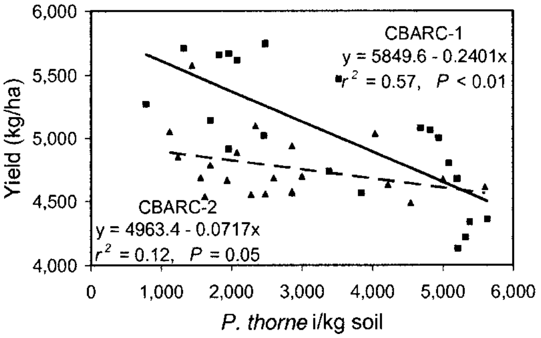

FIG. 2. Relationship between pre-plant numbers of *Pratylenchus thornei* and yield of Zak spring wheat planted uniformly in the CBARC-1 and CBARC-2 experiments in which two wheat cultivars (Krichauff and Machete) were planted with and without aldicarb during 2003; slopes differed at $P = 0.01$.

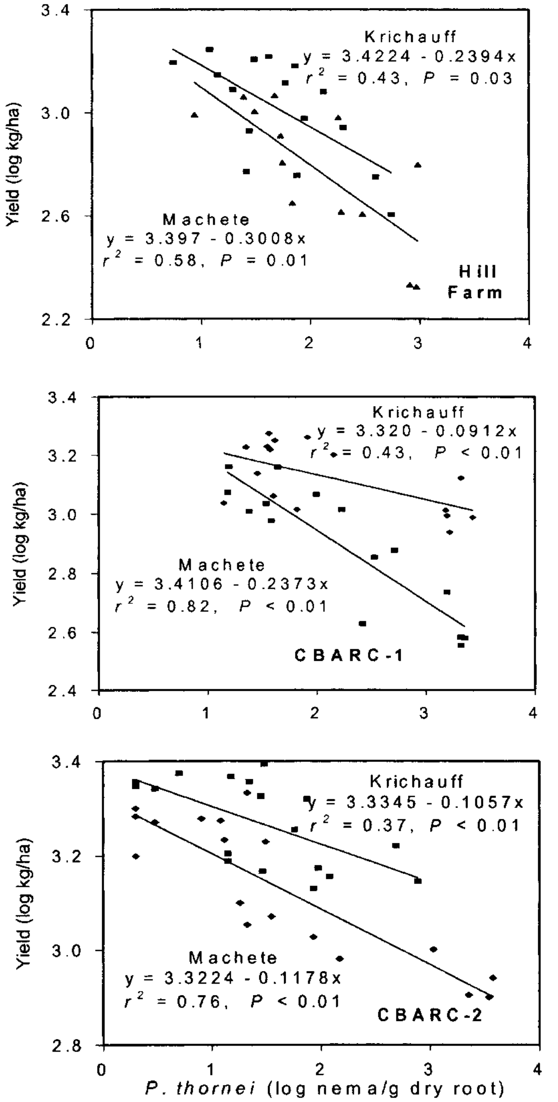

FIG. 3. Relationship between numbers of *Pratylenchus thornei* in mature roots and yield of Krichauff and Machete spring wheat during 2003 at Hill Farm and at two locations at the Columbia Basin Agricultural Research Center; slopes differed at CBARC-1 ($P = 0.01$) but not at Hill Farm ($P = 0.67$) or at CBARC-2 ($P = 0.22$).

was 19% higher than the yield for Machete (1,915 kg/ha) in the seed-increase blocks. In South Australia during 7 years of testing at 28 locations, yields of Krichauff exceeded those for Machete by 8% to 19%, depending on production district (Wheeler and Wurst, 2003). The 19% differential between Krichauff and Machete during a single season in Oregon was therefore interpreted to represent the greater genetic yield potential for Krichauff, an improved variety released 11 years later than Machete (Wheeler and Wurst, 2003). The higher yield differential between Krichauff and Machete in soils highly infested by *P. thornei* (78%) than in soils with low *P. thornei* populations (19%) was considered an approximation of the difference in tolerance of these varieties, resulting in a net 59% higher productivity for the more tolerant variety in soils heavily infested with *P. thornei*. A significant difference in regression slope for yield vs. initial *P. thornei* density in soil was also observed for the two varieties at Hill Farm during 2003, where Krichauff had a higher ability than Machete to maintain yield potential in fields infested with a high population of *P. thornei*. In the CBARC-1 experiment there was also a significant variety difference for the regression of yield vs. *P. thornei* density in mature roots. While varietal differences did not occur at all locations, these observations are important because they indicated that, if differences did occur, the performance of Krichauff was greater than for Machete in highly infested fields. This is consistent with Australian reports for these varieties (Vanstone et al., 1998; Wheeler and Wurst, 2003). It appears possible, therefore, to select varieties with greater tolerance to *P. thornei* to improve grain yields in fields planted annually in the Pacific Northwest.

Reproductive factors (Pf/Pi) for *P. thornei* were approximately 50% lower for Krichauff than for Machete. Differences were significant ($P < 0.01$) at the two locations where the density of *P. thornei* was lowest. During the following year there was no residual influence of variety and aldicarb treatments on yield of Zak, but there was a significant negative association between initial population of *P. thornei* and yield of Zak in each experiment. Varieties with higher levels of resistance than Krichauff need to be examined in the Pacific Northwest to determine if populations of *P. thornei* can be suppressed to levels that may lead to higher yields for subsequent plantings of intolerant varieties, as was reported previously in Australia (Nicol et al., 1999; Taylor et al., 1999; Vanstone et al., 1998).

Observations of yield differences due to varietal tolerance and resistance to *P. thornei* in the Pacific Northwest are important because they indicate a potential for improving yields of locally adapted varieties by incorporating parental lines with improved tolerance and resistance to *P. thornei* into the breeding programs. However, while Krichauff served an important need in this research, yields for this variety are considerably lower in the Oregon environment than in the Australian environment, indicating that Krichauff is not well adapted to production systems in the Pacific Northwest. Moreover, Krichauff does not exhibit the highest level of tolerance and resistance currently available for *P. thornei* (Nicol et al., 2003) and did not result in improved yield for an intolerant variety planted the following year. Varieties and lines with greater tolerance and resistance to *P. thornei* (Zwart et al., 2004) must be tested and, if proven superior to Krichauff when tested against the *P. thornei* population in the Pacific Northwest, the appropriate genetic attributes must be crossed into locally adapted spring wheat varieties.

Compared to non-treated controls, aldicarb treatments at three locations improved yields by an average of 67% for Krichauff and 113% for Machete, or 90% overall. These responses are much higher than reported by Taylor et al. (1999). To determine whether aldicarb increases wheat yields in the absence of *P. thornei,* we measured yields for the variety Zak in 12 replicates of aldicarb-treated and control plots in the wheat-summer fallow rotation field with a low *P. thornei* population at CBARC (unreported data). Aldicarb and control treatments had uniform yield (3,154 and 3,169 kg/ha), test weight, and density of headed tillers. Improved yield in response to aldicarb in annually cropped experimental sites heavily infested with *P. thornei* was therefore interpreted as a response to suppressed invasion and reproduction of *P. thornei* in roots.

Spring wheat varieties currently available in Oregon and Washington are all likely to be intolerant of *P. thornei.* Highly variable terrain and localized climate differences will make it difficult or impossible to establish precise estimates for suppression of spring wheat yields by *P. thornei* in annually cropped fields in the Pacific Northwest. Using tolerance levels currently available in Krichauff, and adjusting for differences in yield potential for Krichauff and Machete, we established that yields of spring wheat could be improved 59% over that of the intolerant variety Machete in soil that was not treated with aldicarb. Nevertheless, the yield of Krichauff, the most tolerant of the varieties in our experiments, were improved 67% by treating the soil with aldicarb, illustrating that the level of genetic tolerance in Krichauff is far from optimal for achieving maximum production efficiency in soils highly infested with *P. thornei.* Yields for the intolerant variety could be improved 113% with aldicarb application. Yield suppression by *P. thornei* in Oregon and Washington is therefore likely to be in the range of 40% to 60% for intolerant locally adapted varieties in fields containing high populations of *P. thornei.* For comparison, Nicol et al. (2003) reviewed literature showing yield reductions due to *P. thornei* ranging from 38% to 85% in Australia, 12% to 37% in Mexico, and 70% in Israel. Estimates for yield suppression by *P. thornei* in the Pacific Northwest appear to be within the range for estimates from other regions.

In our experiments, average pre-plant populations of *P. thornei* ranged from 1,355 to 6,614/kg of soil. Reports of economic damage thresholds from field experiments in other regions have included 420 *P. thornei*/kg of soil in Mexico (Nicol and Ortiz-Monasterio, 2004; Van Gundy et al., 1974), 1,000/kg in Western Australia (Riley and Kelly, 2002), and 2,500/kg in Queensland (Thompson, 1993). Populations of *P. thornei* in Oregon clearly exceed those shown to be capable of damaging wheat in several other regions.

We also found that yield of Machete and Zak in Oregon declined by 1% to 4% for each increase of 1 *P. thornei*/g of soil. The rate of yield decline for Machete in South Australia has been reported at 3% (Taylor et al., 1999) and 8% (Nicol et al. [1999] for each increase of 1 *P. thornei*/g of soil. Yields of intolerant wheat varieties in other regions have been shown to decline by 0.5% in Victoria (Hollaway, 2001), 1% in Mexico (Nicol and Ortiz-Monasterio, 2004), and 16% in Colorado (Armstrong et al., 1993). Our results appear comparable to earlier reports from other regions. However, while negative associations between grain yield and *P. thornei* populations in soil and *P. thornei* density in roots was clearly defined in our experiments, the data are insufficient for establishing economic damage thresholds for *P. thornei* in the Pacific Northwest.

Invasion of roots by *P. thornei* generally does not cause diagnostic symptoms to occur in the foliar canopy. Plants with heavily damaged roots may exhibit stunting, poor vigor, reduced tillering, and premature wilt at the onset of moisture stress (Doyle et al., 1987; Orion et al., 1984; Van Gundy et al., 1974). In studies reported here, for treatments within an experiment, variability in height of headed tillers was considered an important quantitative indicator of relative damage by *P. thornei.* Variability of head height was reduced by application of aldicarb in all three experiments. In two of three experiments, variability was also greater in the intolerant variety, Machete, than in the moderately tolerant variety, Krichauff.

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 (Ehrler et al., 1978; Siddique et al., 2000) and has been used as an indicator of plant stress induced by plant-pathogenic fungi and plant-parasitic nematodes (Nicolas et al., 1991). We demonstrated that canopy temperature was as much as 4 °C higher in control compared with aldicarb-treated plots, corresponding with higher populations of *P. thornei* in roots. Nicolas et al. (1991) previously demonstrated more modest differentials in wheat canopy temperature with varying levels of invasion by *H. avenae.*

Availability of water has an important influence on the ability of *P. thornei* to restrict yield. This nematode is more damaging to crops in drier than wetter soils and regions (Castillo et al., 1995; Nicol and Ortiz-Monasterio, 2004; Orion et al., 1984). *Pratylenchus thornei* also reduces the ability of wheat roots to extract soil water (Thompson et al., 1995). As a result, wheat plants damaged by *P. thornei* wilt earlier than unaffected plants when water approaches pressures that limit plant growth (Van Gundy et al., 1984). Water in the Pacific Northwest typically becomes limiting to wheat growth soon after soil temperatures become elevated above 20 °C. Castillo et al. (1996) determined that the reproductive rate for *P. thornei* in chickpea roots increases as soil temperature increases from 15 °C to 20 °C. *Pratylenchus thornei* appears to be well adapted for suppressing root growth much sooner in warm, dry soils typical of Pacific Northwest dryland production systems than in cool, moist soils typical of areas with in-season rainfall or with irrigation.

Many growers who adopt direct-drill systems in the

Pacific Northwest plant cereals annually because rotational opportunities are limited for economic and climatic reasons. Growers in most other regions infested with *P. thornei* attempt to minimize damage by rotating crops that are adapted to regions with adequate in-season rainfall. Although crop rotation is a preferred management practice, limiting damage by *P. thornei* through rotation is a continuing challenge because this species infests a wide range of host plant species (Hollaway et al., 2000; Talavera and Vanstone, 2001; Thompson et al., 1999; Vanstone and Russ, 2001a, 2001b). In general, most commercial wheat and chickpea varieties are considered good hosts for *P. thornei.* Poor hosts include many varieties of barley, durum wheat, canola, safflower, lupin, lentil, field pea, and flax. Of the listed crops, only barley is adapted to the Pacific Northwest small grain-production region, where precipitation has a winter-dominant pattern, winter temperatures are very low, and summers are hot and dry. Assessment of barley as a potential break crop is required. Likewise, much progress and promise exist for breeding wheat varieties with sufficiently high tolerance and(or) resistance to stabilize yields and reduce the reproductive efficiency for *P. thornei* (Nicol et al., 2003). Numerous sources of improved genetic resistance to *P. thornei* were recently identified in wheat and closely related species (Hollaway et al., 2000; Nicol and Rivoal, 2001; Nicol et al., 1999, 2001; Nombela and Romero, 1999; Sheedy, 2005; Thompson et al., 1999; Zwart et al., 2004a,b). Of particular interest are lines, such as GS50A and AUS4930, that convey high levels of tolerance as well as resistance to *P. thornei* (Hollaway et al., 2000; Nicol et al., 1999).

Accurate identification of *Pratylenchus* species is important because some wheat and other field crop varieties differ in resistance and(or) tolerance to *P. neglectus* or *P. thornei,* the two species most prevalent in the Pacific Northwest cereal-production region. Differentiation between these species can be challenging and is not a service offered by most commercial diagnostic laboratories. Morphological differences between *P. neglectus* and *P. thornei* depend mostly on numbers of annules on the lip region and on a minor difference in the vulval position relative to body length (Filho and Huang, 1989; Handoo and Golden, 1989), both of which are difficult to visually differentiate. We found it particularly useful to apply traditional quantification procedures (Ingham, 1994) for determining populations of *Pratylenchus* in soils and roots, and to then apply molecular procedures to differentiate *Pratylenchus* species (Ophel-Keller and McKay, 2001; Waeyenberge et al., 2000).

In summary, we previously reported that *P. thornei* occurs in high numbers in many annually cropped dryland fields in the Pacific Northwest (Smiley et al., 2004b). This paper reports evidence that root injury by *P. thornei* increases late-season plant stress (higher canopy temperature), reduces plant biomass production (plant height and tillering), and reduces grain yield and quality (test weight and kernel weight). By using aldicarb to suppress damage by *P. thornei,* we found that yield for an intolerant wheat variety could be more than doubled in an annual no-till cropping system. In contrast, yield improvement from aldicarb treatment was only half that magnitude for a moderately tolerant variety. Yields for an intolerant variety adapted to the Pacific Northwest were negatively correlated with *P. thornei* populations in soil at the time of planting. This is the first report that *P. thornei* causes economic damage to annual dryland wheat in the Pacific Northwest. Development of tolerant, locally adapted varieties is essential for limiting damage by *P. thornei.* Lists of pathogens and pests known to limit productivity of spring wheat in annual-crop, direct-drill agricultural systems in the Pacific Northwest (Paulitz et al., 2002; Smiley, 1996; Smiley et al., 2004a) must also be expanded to include *P. thornei.*

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