Journal of Nematology 37(3):297–307. 2005.
© The Society of Nematologists 2005.

Plant-Parasitic Nematodes Associated with Reduced Wheat Yield in Oregon: *Heterodera avenae.*

Richard W. Smiley,[1] Ruth G. Whittaker,[2] Jennifer A. Gourlie,[2] Sandra A. Easley,[2] and Russell E. Ingham[3]

Abstract: Heterodera avenae is widely distributed in the western United States, where most wheat is grown in non-irrigated winter wheat/summer fallow rotations in low rainfall regions. Economic and social pressures have motivated growers to pursue a transition from winter wheat/summer fallow rotation to no-till annual spring cereals. Annual cereals are also planted in some irrigated fields. The impact of *H. avenae* on spring wheat yield in the Pacific Northwest had been observed but not quantified. Spring wheat was planted with or without aldicarb to examine relationships between *H. avenae* and yield under dryland and irrigated conditions in moderately infested fields. Spring wheat yields were negatively correlated ($P < 0.05$) with initial populations of *H. avenae.* Aldicarb application improved spring wheat yield as much as 24%. The infective juvenile stage of *H. avenae* reached a peak density during mid-spring. Yield of irrigated annual winter wheat was also negatively correlated with initial density of *H. avenae.* Research priorities necessary to develop control strategies include a description of the pathotype, identification of sources for genetic resistance, and integrated practices designed to manage multiple yield-reducing pests.

Key words: aldicarb, cereal cyst nematode, *Heterodera avenae, Triticum aestivum,* wheat, yield loss.

The cereal cyst nematode, *Heterodera avenae* Woll., 1924, is distributed worldwide in temperate cereal-producing regions (Nicol, 2002; Nicol et al., 2003; Rivoal and Cook, 1993). This plant-parasitic species is present in more than half the fields in major cereal-producing regions of Europe (Rivoal and Cook, 1993). It was first reported from North America in the Province of Ontario, Canada (Chapman, 1938), and 30 years later was detectable in most counties of that province (Fushtey, 1966).

Heterodera avenae was first detected in the United States during 1974 (Jensen et al., 1975) and is now known to occur in many cereal-producing regions in the Pacific Northwest (PNW) states of Idaho, Oregon, and Washington (Hafez and Golden, 1984, 1985; Hafez et al., 1992; Smiley et al., 1994). During 1987, *H. avenae* was detected in two-thirds of all cultivated dryland and irrigated fields sampled in Union County, Oregon, and in 1990 this species was documented to have been disseminated from that geographically isolated county to dryland and irrigated fields in the primary wheat-producing region in eastern Oregon (Smiley et al., 1994). The known distribution now includes dryland fields from the highest to lowest precipitation zones in Oregon's "wheat belt" (Smiley et al., 2005a, 2005b).

Smiley et al. (1994) reported that *H. avenae* reduced yield as much as 50% when winter wheat and other hosts were planted annually into a heavily infested irrigated field in Union County. Damage was reduced and yield was comparable to noninfested fields when winter wheat was rotated with summer fallow or non-hosts of *H. avenae.* Summer fallow is not an economically acceptable alternative for irrigated fields. However, for dryland (rainfed) cereal crops in the region, which comprise up to 80% of the production area, the dominant cropping system has been a 2-year rotation of winter wheat (10 months) and summer fallow (14 months). The summer fallow system is highly conducive to soil erosion from water and wind, and recent socio-economic concerns regarding the declining quality and sustainability of soil and water have encouraged development of more conservation-oriented farming systems (Cook, 2001). Total wheat acreage has sustained a gradual reduction in winter wheat produced in a 2-year winter wheat-summer fallow rotation, and an increase in spring wheat and spring barley planted annually without tillage, and usually without rotation to a broadleaf nonhost crop.

These practices have resulted in an increase in damage from *H. avenae,* with some severely affected spring wheat crops in Union County, being plowed under without harvesting (Smiley, pers. obs.). Nevertheless, the economic impact from *H. avenae* on spring wheat in the PNW has not been quantitatively evaluated. Economic damage estimates under dryland as well as irrigated conditions are required to justify research for managing *H. avenae.*

This paper reports relationships between *H. avenae* population densities and grain yield in annual spring wheat on moderately infested dryland and irrigated fields, and in one heavily infested irrigated field planted to winter wheat annually or in 2-year rotations. Hatching dynamics of *H. avenae* during the spring are also reported.

Methods

Spring wheat experiments were conducted over a 3-year period (2001 to 2003) on annually cropped *H.*

Received for publication 12 July 2004.

[1] Professor and [2]Faculty Research Assistants, Oregon State University, Columbia Basin Agricultural Research Center, P.O. Box 370, Pendleton, OR 97801, and [3]Professor, Oregon State University, Department of Botany and Plant Pathology, 2076 Cordley Hall, Corvallis, OR 97331.

The authors thank John Cuthbert and Roger Davis (wheat producers) for hosting field experiments, and Kathy Merrifield, Nadine Wade, and Nick David (Oregon State University, Nematode Testing Service, Corvallis, OR) and Dr. Harry Kreeft (Western Laboratories, Parma, ID) for diagnostic services. The authors also thank Abby Burnett, John Collins, Jonathan Jackson, Nicole Kellogg, Joanna Skirvin, and Tina Zeckman for technical assistance. This research was funded by an OSU subcontract to the USDA-Agricultural Research Service; SCA#58-5348-9-100.

E-mail: richard.smiley@oregonstate.edu

This paper was edited by Deborah Neher.

avenae-infested fields at the Cuthbert and Davis farms near La Grande, in Union County. Additionally, relationships between *H. avenae* and winter wheat yield at the Cuthbert farm, and the dynamics of the juvenile (J2) population during the spring, are described for a crop-rotation and tillage management experiment partially reported earlier (Smiley et al., 1994).

Spring wheat experiments: One experiment was performed at the Cuthbert farm during 2001 using six varieties planted with or without a nematicide. A second experiment was initiated during 2002, using a single variety planted into plots treated or untreated with nematicide at two locations, the Cuthbert and Davis farms. The 2002 experimental areas at both farms were replanted during 2003 using four varieties treated or untreated with nematicide, with the nematicide applied to the same plots treated during 2002. Spring wheat was irrigated in all except the 2002 experiment at the Cuthbert farm.

Locations: The Cuthbert and Davis farms are located 10 km northeast and 13 km east-southeast of La Grande, respectively. Fields at both farms are near 825 m elevation, obtain 460 mm annual precipitation, and average daily air temperatures of −1 °C during January and 18 °C during July and August. Soil at the Cuthbert farm was a deep, well-drained Imbler fine sandy loam, a coarse-loamy, mixed, superactive, mesic Pachic Haploxerolls. Soil at the Davis farm was a well-drained Hoopal fine sandy loam, a coarse-loamy, mixed, superactive, mesic Typic Duraquolls.

Cuthbert farm—2001. The field had been planted to winter wheat during autumn 2000, after stubble of a perennial fine-leaf fescue crop was turned under with a moldboard plow and disked. Winter wheat in the experimental area was killed by herbicide, and fertilizer was applied uniformly using a rate based on soil tests and standard practices for the region. Six spring wheat varieties were planted on 16 April 2001, including two adapted to the Pacific Northwest (Alpowa and Penawawa) and four adapted to Australia (Frame, Krichauff, Molineux, and Spear). The locally adapted varieties are susceptible to the *H. avenae* population in eastern Oregon. Frame and Molineux carry the *Cre8* gene for resistance to *H. avenae* pathotype Ha13 in Australia and are considered resistant and moderately tolerant to that pathotype. Krichauff is susceptible but moderately tolerant to *H. avenae* pathotype Ha13. Spear is susceptible and intolerant to *H. avenae* in Australia. *Heterodera avenae* pathotype Ha13 was recently redescribed as *H. australis* (Subbotin et al., 2002).

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, and wheat was seed-treated with fungicides (tebuconazole plus mefenoxam) to suppress seed rot and seedling damping-off. Aldicarb (Temik 15G) was mixed with the seed in the seed cone while planting 24 of the 48 plots in the experiment. Aldicarb was dispensed at 4.2 kg a.i./ha to suppress damage and reproduction by nematodes (Brown, 1987; Hague and Gowen, 1987; Taylor et al., 1999). The experiment consisted of 1.5 × 6-m plots with wheat variety and aldicarb treatments arranged in randomized complete blocks replicated four times. Weeds were controlled by hand weeding. Soil sampling and *H. avenae* extractions are described in a later section. Grain was harvested during mid-August with a plot combine.

Cuthbert and Davis farms—2002. An experiment at the Cuthbert farm was placed in a field adjacent to that used for the 2001 experiment. Following a perennial mint crop, the Cuthbert field was plowed, disked, and planted to winter wheat during October, 2001. The experiment at the Davis farm followed two successive spring wheat crops planted without tillage.

Winter wheat at the Cuthbert farm and volunteer spring wheat and grass weeds at the Davis farm were killed by herbicide during mid-March 2002. On April 14, spring wheat was planted without tillage using a double-disk plot drill equipped with a cone-seeder and five openers at 30-cm row spacing. A single variety of spring wheat (Zak) was planted in 36 plots (3.3 × 9 m), half of which were treated with aldicarb mixed with the seed at the time of planting. The field at the Cuthbert farm was managed without irrigation, and the field at the Davis farm was irrigated as needed. Sampling methods were as described for the 2001 experiment.

Cuthbert and Davis farms—2003. Following the 2002 harvest, the field at the Cuthbert farm was fertilized, plowed, disked, and planted to winter wheat during mid-October. The location of the 2002 experiment site was preserved by installing metal cables vertically into soil before plowing. The site at the Davis farm was not tilled or planted to an over-winter crop following the 2002 harvest. Planted and (or) volunteer vegetation at both sites was killed by herbicide during mid-March, 1 month before planting during 2003. Fertilizer was also applied as a surface broadcast at the Davis farm. On April 14, spring wheat was planted directly into killed winter wheat at the Cuthbert farm and into stubble from the 2002 harvest at the Davis farm.

Plot width at both sites in 2003 was reduced by half compared to that in 2002, resulting in 72 plots (1.5 × 9 m). Wheat was planted with the drill described earlier. Four varieties were planted with or without aldicarb (2.9 kg a.i./ha) treatment, with the aldicarb treatments applied to the same plots treated during 2002. The experimental design during 2003 was a randomized complete block with nine replicates of each combination of variety and aldicarb. Varieties included Frame, Molineux, Ouyen, and Spear. Ouyen is also an Australian variety that carries the *Cre1* gene for resistance to *H. avenae* and is resistant but moderately intolerant to the Australian population of *H. avenae*.

Both fields were irrigated during 2003. Soil samples

were collected before planting, following harvest, and in spring 2004 (Davis farm only). During early summer, when plants were nearing anthesis, wheat roots were dug from selected plots, washed, and rated for damage by *H. avenae* using a five-point scale (Simon and Rovira, 1982). Grain was harvested in mid-August with a plot combine.

Soil sampling and H. avenae extraction: Soil samples were collected within 2 days before planting to assess *H. avenae* populations in individual plots. Samples consisted of 15 to 20 cores (2.5-cm diam × 10-cm deep) composited for each 9-m^2 plot. Samples were placed on ice in the field and stored at 4 °C for 1 week before being transported to the Oregon State University Nematode Testing Service at Corvallis during 2001 and 2002, and to Western Laboratories, Parma, Idaho, during 2003.

Extractions were from a single 200-g subsample from the composite sample for each plot. Vermiform stages in the soil were extracted by a modified wet-sieving and density-centrifugation technique. Cysts were extracted from air-dried soil with a modified Fenwick can and were further separated from debris by ethanol-glycerin flotation (Caswell et al., 1985; Ingham, 1994). Cysts were picked from the remaining debris and crushed to determine numbers of eggs and J2. Numbers were adjusted to reflect density per kilogram of oven-dry soil.

Winter wheat experiment: A 5-year crop rotation experiment involving 11 crop sequences was performed on a field at the Cuthbert farm. Soil on the field used for the winter wheat experiment was heavier than the sandy loam at the spring wheat site and is described as a poorly drained Conley silty clay loam, a fine, montmorillonitic, mesic Xeric Argialbolls. The clay loam surface graded into a clay at 30-cm depth. Few roots penetrate deeper than 60 cm into the soil profile.

Crop sequences and management have been described (Smiley et al., 1994). Briefly, a field infested with *H. avenae* had been managed as a winter wheat/summer fallow rotation for 6 years. During the spring following the 1986 harvest, wheat stubble was incorporated into soil by moldboard plowing to 30-cm depth and disking to 10-cm depth. During mid-August 1987 the field was grid-sampled and eggs and J2 from cysts were determined as described above. Spatial variability of the initial *H. avenae* distribution was random among proposed treatments, ranging from 1,000 to 21,000 eggs plus J2/kg.

Treatments were established in 5 × 30-m plots replicated four times in a randomized complete block design. The experiment commenced during autumn 1987 and terminated with wheat harvest in August 1992. Treatments discussed in this paper included: (i) annual winter wheat with seedbed prepared by deep plowing and disking, (ii) annual winter wheat with stubble removed by burning and seedbed preparation by shallow mixing to about 2- to 4-cm depth with a skew treader or light disk, (iii) winter wheat/summer fallow rotation with seedbed preparation by deep plowing and disking, and (iv) winter wheat/field pea rotation with seedbed preparation by deep plowing and disking. Data presented here represent the third successive wheat crop for the two annual wheat treatments and the second wheat crop for the two rotation treatments that, in practice, were a continuation of the 2-year rotation on the field during the previous 12 years.

Nematodes were sampled and extracted as described above during late August each year. Wheat roots were washed in a water spray and rated for damage by *H. avenae* during April. Additional plant growth and disease measurements were described in Smiley et al. (1994).

J2 population dynamics: Population densities of *H. avenae* J2 were monitored from a winter wheat/summer fallow rotation at the Cuthbert farm during the spring of the first crop year (1988). Soil was sampled at biweekly intervals from February to July 1988 as described above and extracted with a modified Baermann funnel procedure (Ingham, 1994). Average weekly air temperatures were calculated from data at a nearby weather station.

Statistical analysis: Nematode populations in each experiment were described by calculating means and standard deviations among plots. All nematode, plant growth, and yield variables among variety x aldicarb treatment combinations were also analyzed by analysis of variance for the randomized complete block model using Co-Stat Statistical Software version 6.101 (CoHort Software, Monterey, CA). When treatment effects were significant at $P < 0.10$, 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 or polynomial regression.

Results

Population of *H. avenae.* Spatial heterogeneity for initial populations of *H. avenae* was high when each spring wheat experiment was first established (Table 1). However, there were no differences ($P < 0.05$) in populations among plot areas designated to be differentiated into specific varieties or aldicarb treatments (data not presented).

Heterodera avenae J2 extracted directly from soil in the spring represented 18% (range of 0% to 59%, std. dev. = 13) of the total (eggs plus J2) population at the Cuthbert farm during 2002 (Table 1). The proportion of eggs that hatched before samples were collected was higher at the Cuthbert farm during 2002 than during 2001 (Table 1). Hatching (determined by J2 in the soil) was not detected before planting at the Davis farm during 3 years of sampling. Eggs and J2 were present in cysts extracted from soils at both farms for each sam-

TABLE 1. Population means and ranges (number/kg dry soil) of *Heterodera avenae* during early April before planting spring wheat at the Cuthbert and Davis farms in Union County, Oregon.

Population	Farm	Year	Mean	Range	Std. Dev.	Plots (n)[a]
J2 from soil	Cuthbert	2001	202	0–4,840	711	48
		2002	2,366	0–8,570	1,715	36
		2003	0	—	—	72
	Davis	2002	0	—	—	36
		2003	0	—	—	72
		2004	0	—	—	72
Eggs plus J2 from cysts	Cuthbert	2001	2,606	0–12,190	2,930	48
		2002	7	0–98	19	36
		2003	7	0–160	28	72
	Davis	2002	92,269	10,022–321,380	69,997	36
		2003	1,690	100–8,020	1,512	72
		2004	1,279	0–4,400	1,052	72

[a] Samples were composed of 15 to 20 soil cores composited for each of *n* plots that were arranged in adjacent blocks of 12 columns × 3 rows ($n = 36$), 4 rows ($n = 48$), or 6 rows ($n = 72$).

pling period. The *H. avenae* population declined dramatically in experimental areas at both farms between the times that pre-plant samples were collected in 2002 and 2003. This was particularly notable for pre-plant populations at the Cuthbert farm.

Averaged over all varieties, initial 2003 *H. avenae* populations of eggs and J2 from cysts at the Davis farm were 55% lower for plots that had been treated with aldicarb in 2002 (1,055 nematodes/kg) than in control plots (2,325 nematodes/kg); $lsd_{0.05} = 633$ (Table 2).

TABLE 2. Population densities of *Heterodera avenae,* from cysts (eggs + J2/kg of soil), in soils at the Davis farm near La Grande, Oregon, following aldicarb treatment in 2002 and production of spring wheat varieties treated or untreated with aldicarb during 2003.

		2003[b]		2004[c]
Variety	Nematicide[a]	April	September	April
Frame	control	2,489	5,469	1,873
	aldicarb	1,071	1,084	784
Molineux	control	2,536	3,451	1,296
	aldicarb	1,113	1,112	711
Ouyen	control	2,682	2,944	1,082
	aldicarb	884	496	660
Spear	control	2,593	5,273	2,073
	aldicarb	1,151	2,504	1,756
$lsd_{(0.05)}$				
variety		ns	ns	598
nematicide		633	1,434	422
P>F				
variety		0.53	0.07	<0.01
nematicide		<0.001	<0.001	<0.01
var. × nema.		0.86	0.62	0.58

[a] Spring wheat cv Zak was planted into 36 plots (3.3 × 9 m) during 2002, with 18 plots treated with aldicarb (4.2 kg a.i./ha) at the time of planting, and 18 control plots not treated with aldicarb. During 2003, initial density of *H. avenae,* from cysts, averaged 92,269 eggs plus J2/kg of soil, without any significant diference ($P = 0.27$) among aldicarb treatments applied during 2002. The range of population densities for the 36 plots was 10,022 to 321,380/kg of soil, with a standard deviation of 69,997. During 2003, the plots were split lengthwise for a total of 72 plots (1.5 × 9 m). All 2003 aldicarb treatments (2.9 kg a.i./ha) were placed in plots also treated during 2002, and all controls were in plots not treated with aldicarb during 2002.

[b] Degrees of freedom for the 36-plot design were nematicide (1), error (34), total (35).

[c] Degrees for the 72-plot design were nematicide (1), variety (3), nematicide × variety (3), error (55), total (70).

This pattern was repeated for samples collected during 2004, when average populations in aldicarb-treated areas were 38% lower (978 nematodes/kg) than in the controls (1,518 nematodes/kg); $lsd_{0.05} = 423$. Post-harvest samples collected during 2003 and spring samples collected during 2004 from treated and untreated plots each suggested that there were significant population differences ($P < 0.10$) following production of different wheat varieties. However, for both sample periods there was no indication of varietal differences when control plots were analyzed separately.

Grain yield. Grain yields were not different among varieties in any year or location. Averaged over all varieties, aldicarb increased yield by 15% at the Cuthbert farm in 2001 (Table 3). During 2002, yield of Zak was increased by application of aldicarb in the irrigated experiment at the Davis farm but not in the dryland experiment at the Cuthbert farm. Aldicarb improved grain yield by 11% at the Cuthbert farm and by 24% at the Davis farm in 2003.

Nematodes and spring wheat yield. Overall yield for the six varieties at the Cuthbert farm during 2001 was not closely associated with pre-plant populations of *H. avenae* J2 in soil or with eggs and J2 from cysts ($P = 0.42$). However, negative correlations with regression coefficients (r^2) greater than 0.50 occurred for 6 of the 12 varieties by aldicarb treatment combinations. Regressions were significant ($P < 0.10$) for three of the coefficients. For instance, Molineux in untreated soil was highly negatively correlated with the pre-plant density of *H. avenae* eggs and J2 from cysts ($P = 0.04$, $r^2 = 0.93$, $n = 4$).

At the Cuthbert farm during 2002, grain filling was adversely affected by drought stress as well as by a late freeze during anthesis. Nevertheless, yield of Zak from all plots was negatively correlated with the population of *H. avenae* J2 extracted directly from soil ($P = 0.03$, $r^2 = 0.15$, $n = 36$). When control plots were analyzed separately, yield was negatively correlated with the total population of *H. avenae,* including J2 in soil plus eggs

TABLE 3. Grain yield (kg/ha) of spring wheat varieties treated or untreated with aldicarb at the Cuthbert and Davis farms near La Grande, Oregon, during 2001–2003.

		2001[a]	2002[b]		2003[c]	
Variety	Nematicide	Cuthbert	Cuthbert	Davis	Cuthbert	Davis
Alpowa	control	3,734				
	aldicarb	4,084				
Frame	control	3,748			2,767	1,451
	aldicarb	4,072			3,191	1,822
Krichauff	control	3,489				
	aldicarb	4,753				
Molineux	control	3,149			2,915	1,491
	aldicarb	4,271			3,258	1,792
Ouyen	control				2,827	1,669
	aldicarb				3,060	1,924
Penawawa	control	3,788				
	aldicarb	4,144				
Spear	control	4,189			3,084	1,440
	aldicarb	4,617			3,370	1,952
Zak	control		981	1,809		
	aldicarb		980	2,786		
Mean for all varieties						
	control	3,683	981	1,809	2,898	1,513
	aldicarb	4,224	980	2,786	3,220	1,873
$lsd_{(0.05)}$						
variety		ns	—	—	ns	ns
nematicide		258	ns	314	212	140
P>F						
variety		0.07	—	—	0.24	0.34
nematicide		<0.001	0.99	<0.001	<0.01	<0.001
var. × nema.		0.11	—	—	0.92	0.59

[a] Degrees of freedom for the 48-plot design were nematicide (1), variety (5), nematicide × variety (5), error (33), total (47).
[b] Degrees of freedom for the 36-plot design were nematicide (1), error (34), total (35).
[c] Degrees of freedom for the 72-plot design were nematicide (1), variety (3), nematicide × variety (3), error (55), total (70.)

and J2 from cysts (Fig. 1) In contrast, at the Davis farm during 2002 there was no correlation between *H. avenae* density and grain yield for all plots or for only untreated plots.

During 2003 at the Davis farm, yields across all varieties in the 36 control plots were negatively correlated with pre-plant population densities of *H. avenae* (Fig. 2) and the relationship between *H. avenae* density and yield was similar to that for the Cuthbert farm in 2002 (Fig. 1). The population of *H. avenae* was low at the

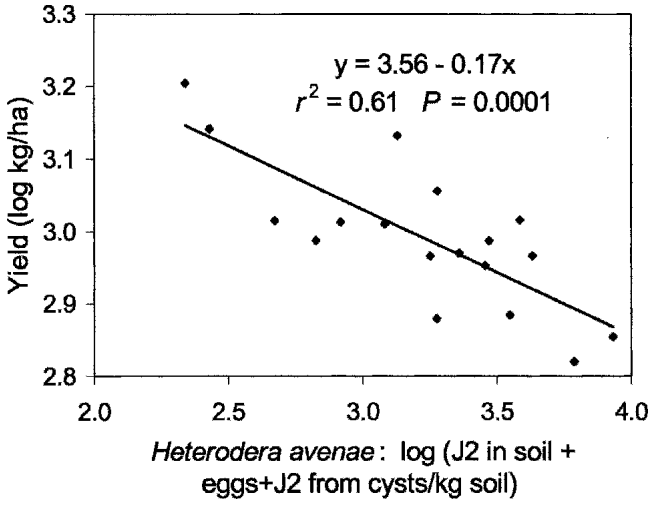

FIG. 1. Relationship between yield of dryland spring wheat and total population of *Heterodera avenae* before planting at the Cuthbert farm during 2002. Data are from control plots not treated with aldicarb and include both J2 in soil plus eggs and J2 from cysts.

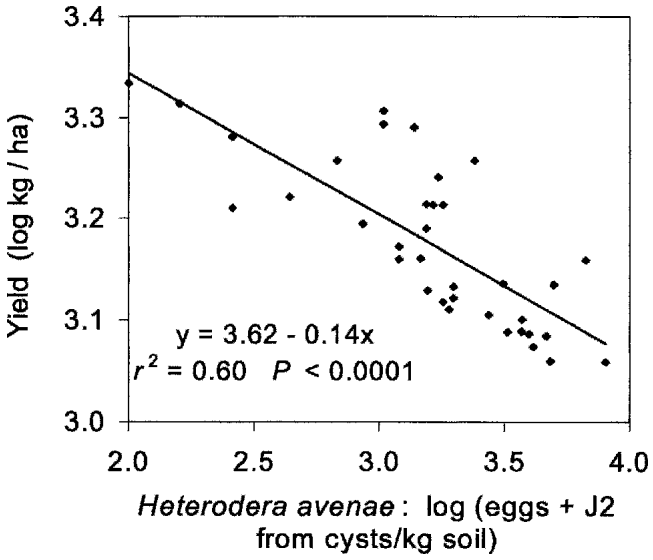

FIG. 2. Relationship between yield of irrigated spring wheat and the number of *Heterodera avenae* eggs and J2, from cysts, before planting at the Davis farm during 2003. Data are from control plots not treated with aldicarb.

Cuthbert farm during 2003, and associations between *H. avenae* and yield could not be detected. Witches' brooms symptoms on roots, caused by *H. avenae,* were also minor at the Cuthbert farm (mean severity rating of 0.2 on 16% plants) compared to those at the Davis farm (mean severity rating of 1.8 on 72% plants).

Nematodes and winter wheat yield: Details of disease ratings, plant growth, and yield were published (Smiley et al., 1994). Briefly, damage ratings from *H. avenae* on seedling roots during autumn 1989 were higher for annual winter wheat (1.0) than for wheat following fallow or peas (0.2 to 0.3); $lsd_{0.05}$ = 0.3. Damage ratings did not differ among individual treatments during spring 1990, but percentages of symptomatic plants were higher in annual wheat (49% to 59%) than in the rotations (11% to 13%); $lsd_{0.05}$ = 18. Compared to annual wheat, the plants in plots following the rotations were taller, more physiologically advanced in growth stage, and had higher percentages of tillering. Wheat yields were lower for annual wheat than for wheat in the rotations; 4,252 to 5,203 vs. 6,580 to 7,253 kg/ha, $lsd_{0.05}$ = 550. We reported previously (Smiley et al., 1994) that wheat yields for the 16 plots (four replicates of four treatments) were negatively correlated with witch's broom symptom ratings (P = 0.02, r^2 = 0.32) and with post-harvest populations of *H. avenae* (P = 0.04, r^2 = 0.86). In this paper we report that wheat yield was also negatively correlated with densities of *H. avenae* eggs and J2 from cysts before planting (Fig. 3).

Populations dynamics for *H. avenae:* Soil sampling at approximately weekly intervals began when average weekly temperature during February was less than 0 °C (Fig. 4). By late February the soil profile had thawed after a 2-month frozen period during winter, but shallow freeze-thaw cycles continued at the surface until early April. Populations of *H. avenae* J2 in soil increased rapidly 2 weeks after average weekly air temperature stabilized between 2 °C and 5 °C. Peak populations occurred following a spike in weekly average temperature to 15 °C. Temperature declined to 10 °C to 15 °C in April and then increased to 22 °C by late June but J2 declined in May to barely detectable levels by June 1. Adult males were first detected on June 1.

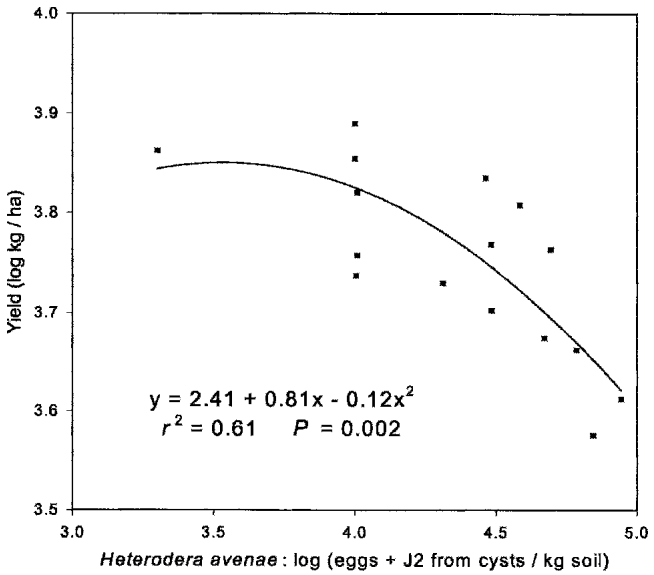

FIG. 3. Relationship between yield of annual irrigated winter wheat (in 1990) and the number of *Heterodera avenae* eggs and J2, from cysts, before planting at the Cuthbert farm in autumn 1989.

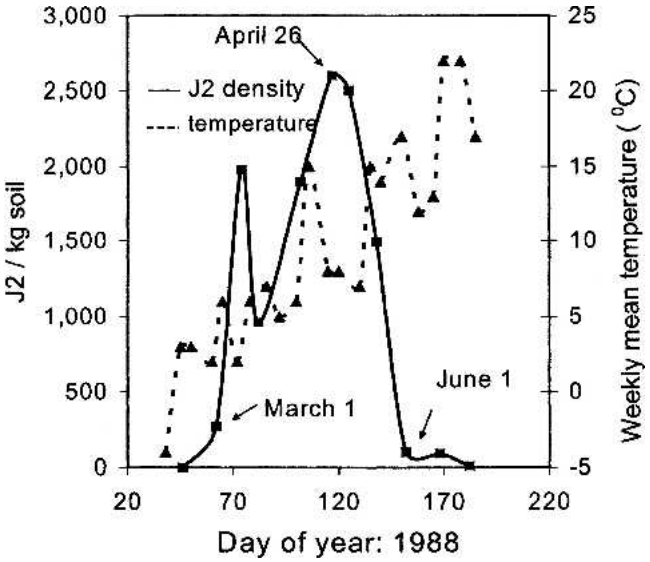

FIG. 4. Average weekly air temperature and number of *Heterodera avenae* J2 in soil at approximately weekly intervals under winter wheat in a winter wheat/summer fallow rotation during spring 1988 at the Cuthbert farm.

DISCUSSION

This paper reports the first quantifiable evidence for yield reduction by *H. avenae* in both dryland and irrigated spring wheat in the PNW. Documentation of a negative correlation between *H. avenae* density and yield of spring wheat under dryland conditions is particularly important because it demonstrates that yields can be responsive to *H. avenae* even under drought or other stresses that greatly restrict yields. These stresses are common in low-rainfall areas of the PNW where *H. avenae* occurs (Smiley et al., 2005a, 2005b). The impact of *H. avenae* in these low-rainfall environments was comparable to that observed in Australia (Brown, 1987).

Application of aldicarb improved spring wheat yield as much as 24% in moderately infested fields and often reduced the post-harvest population of *H. avenae* in soil. These results were comparable to benefits of aldicarb reported previously (Brown, 1987; King et al., 1982; Meagher et al., 1978; Rovira et al., 1981; Smiley et al., 1994). However, aldicarb is not registered for application to wheat in the United States so management of damage by *H. avenae* in the United States must be accomplished through other practices such as crop rotation, green manures, resistant varieties, seed treat-

ments, or biocontrol. Each of these management strategies has improved yields in other regions, but only crop rotation has been evaluated in the PNW. Rotation of wheat with non-hosts is a well-established practice for reducing damage from *H. avenae* (Brown, 1985, 1987; Garrett, 1934; Rivoal and Saar, 1987; Rovira and Simon, 1982; Smiley et al., 1994). However, effective crop rotations for producing dryland spring wheat in semiarid regions of the PNW have not been economical (Juergens et al., 2003).

Varieties carrying the *Cre1* or *Cre8* genes for resistance are effective for controlling damage from the Australian population of *H. avenae* pathotype Ha13 (= *H. australis*), but each of the varieties with these genes (Frame, Molineux, and Ouyen) failed to exhibit resistance or tolerance to the population of *H. avenae* in Union County. Likewise, varieties that are moderately tolerant to the Australian population (Frame and Molineux) were not more productive in Oregon than varieties that are moderately intolerant (Ouyen) or intolerant (Spear) to the Australian population.

Hatching of *H. avenae* in eastern Oregon was high during early spring, conforming with characteristics of the northern ecotype described by Rivoal (1986). However, the possibility for an additional or partial hatching cycle during autumn has not been studied in the PNW. The greatest damage from *H. avenae* occurs when the nematode invades roots during the early seedling stage (Brown, 1972; King et al., 1982). Therefore, the high magnitude of hatching during the spring, described in this paper, is likely to pose greater risk to newly planted spring wheat than to more physiologically advanced plantings of winter wheat. Spring wheat has been totally destroyed in some commercial fields, but winter wheat has never been more than moderately affected by patches of stunted plants and reduced yield (Smiley, pers. obs.). These observations of relative susceptibilities for spring and winter wheat in commercial fields have not been supported by experiments performed thus far. In this paper we report yield reductions up to 24% for spring wheat. We previously reported yield reductions up to 50% for winter wheat (Smiley et al., 1994).

Populations of *H. avenae* at both farms declined dramatically between pre-plant samplings in 2002 and 2003. The reasons for this decline are unknown, but possible explanations include the following. During spring 2002, when experiments were first established, the population of J2 and eggs was very high at each farm. Winter wheat and (or) volunteer wheat plus weed grasses in both experimental areas were sprayed with herbicide 1 month before planting and may have served as trap plants, effectively removing a large proportion of active *H. avenae* J2 during the transition to spring wheat. The decline was particularly acute at the Cuthbert farm, where (i) the sprayed-out winter wheat vegetation was more abundant than vegetation at the Davis farm, and (ii) the spring wheat produced during the previous year was not irrigated and yield was exceptionally low. The greater population decline at the Cuthbert farm, compared to the Davis farm, may have been in response to the relative paucity of root mass on the drought-affected crop at the Cuthbert farm, and in response to more trapping by the existing host vegetation. It is also possible that the reproductive efficiency (Rivoal et al., 2001) of *H. avenae* may have been low on the wheat variety planted at both farms during 2002. The ancestry for Zak includes a wild-wheat relative (*Aegilops umbellulata;* goatgrass) as a source for resistance to leaf rust. Wild-wheat relatives in many *Aegilops* species have been important sources of genes for resistance to *H. avenae* (Delibes et al., 2001; Jahier et al., 2001; Nicol, 2002) and other insects, nematodes, and fungal pathogens of cereals (Zaharieva et al., 2001). The reproductive efficiency for *H. avenae* on wheat cultivars adapted to the PNW, including Zak, has not been investigated.

Presence of J2 in soil indicated that *H. avenae* had started hatching at the Cuthbert farm before soil samples were collected during mid-April. Allowing for minor deviations associated with annual variability in weather, this would suggest that the hatching period was similar to that observed in the 1988 study of hatching dynamics, where hatching commenced in early March, peaked in late April, and was completed by late May. The field at the Cuthbert farm studied in 2001–03 was adjacent to the field studied in 1988. Hatching was not detectable during this same period at two other sites (Davis Farm, 2002, and Wallender Farm, 2001, unpubl. data). Differences in hatching at these sites may have been related to differences in slope aspect. The Cuthbert field had a south-facing slope of 3% to 5%, and fields at the other farms had no slope. It is possible that the soil warmed earlier at the Cuthbert site than at the other sites, although this was not apparent when soil temperatures at planting depth were measured at the time the experiments reported in this paper were established (unpubl. data). Potential variability in the timing of the hatch at various locations requires additional study.

Nematicidal seed treatments have been intensively investigated on winter wheat in the PNW but have not been studied on spring wheat. Smiley et al. (1992) reported that the insecticide aldoxycarb improved winter wheat yield by 10% in *H. avenae*-infested soil in Union County during 1988. Winter wheat yield was not improved by treating seed with methamidophos or by in-furrow application of carbofuran, ethoprop, or aldicarb. Benefits from seed treatment or in-furrow application of aldicarb, carbofuran, ethylene dibromide, furathiocarb, oxamyl, and terbufos have been reported from Australia and Israel (Brown, 1973; King et al., 1982; McLeod et al., 1986; Orion and Shlevin, 1989; Rovira and Simon, 1982). None of these pesticides had been evaluated on spring wheat in the PNW until the

current study evaluated aldicarb. Since aldicarb and other effective chemicals are either not registered or not economically feasible for application to dryland wheat in the United States, investigations of other potentially useful chemicals or other practices are needed to manage *H. avenae* damage on spring cereals.

During the course of this research many cysts were observed to be colonized by several morphologically distinct fungi. Although not identified or studied further, the proportion of parasitized cysts appeared to increase with increasing time in situ in the field and with incubation at moderate temperatures in the laboratory (Ruth Whittaker and Sandra Easley, pers. obs.). Nematotrophic fungi such as *Verticillium chlamydosporium* and *Nematophthora gynophila* are widespread and recognized for their ability to reduce viability of eggs within cysts (Irving and Kerry, 1987; Kerry, 1987). However, even under experimental conditions, these fungi typically fail to colonize and impair more than half the eggs. *Paecilomyces carneus* and *Cylindrosporium destructans* also have been suggested as important fungal parasites of *H. avenae* (Boag and Lopez-Llorca, 1989). While fungal parasites clearly do not suppress *H. avenae* populations to non-damaging levels in all fields in Union County, it is possible that they may suppress populations to smaller densities than may occur in the absence of the fungus. Additional study will be required to elucidate the importance of natural biocontrol systems as components of an integrated management strategy for *H. avenae* in Oregon.

This report supplements results of a previous study of *H. avenae* on irrigated winter wheat (Smiley et al., 1994). However, irrigated wheat fields in Union County are often managed very differently than the vast areas of irrigated agriculture where potato and other higher-value crops are produced on the Columbia Plateau in north-central Oregon and south-central Washington. Most fields in Union County are not treated for the specific purpose of suppressing damage by plant-parasitic nematodes. In contrast, fields in which higher-value crops are produced in the Columbia Plateau are mostly treated with one or more fumigant and non-fumigant chemicals that have nematicide activity such as aldicarb, chloropicrin, 1,3-dichloropropene, ethoprop, metam-sodium, or oxamyl. These treatments are used to suppress economic damage by plant-parasitic nematodes, fungal pathogens favored by root injuries caused by a nematode, and viral diseases in which the pathogen is vectored by a nematode (Pscheidt and Ocamb, 2005). Fields treated by these chemicals are likely to have lower populations of plant-parasitic nematodes than are reported for Union County, or are likely to have a dominance of species that are not known to cause damage to wheat in the long rotations used on most irrigated fields on the Columbia Plateau. Results of research reported here are therefore not necessarily applicable to most irrigated fields in which crops with higher value than wheat are produced in the PNW.

Fields used for this research were infested with more than one species of plant-parasitic nematode (Smiley, 2005a, 2005b). In view of the complexity and potential interactions among plant-parasitic nematode species in Union County, it may be difficult to demonstrate advantages of varieties with resistance to only one species if other species are also capable of reducing yield. Thus, there is a need to develop wheat varieties that have resistance to more than one species. Highest priorities for plant-parasitic nematodes in Union County include *H. avenae* and *Pratylenchus neglectus*. This line of investigation could be initiated after the *H. avenae* pathotype in eastern Oregon has been identified, following the progress currently being made through introgression of dual resistances to *H. avenae* pathotype Hal3 and *P. thornei* at the International Maize and Wheat Improvement Center (Julie Nicol, pers. comm.).

Heterodera avenae is capable of being disseminated rapidly and widely (Rivoal and Cook, 1993; Fushtey, 1966). This is clearly evident in the western United States, where *H. avenae* was first detected on oats in a high-rainfall (1,000 mm) region of western Oregon (Washington County) during 1974 (Jensen et al., 1975). The Cascade Mountains form a geographical barrier between Washington County and the primary PNW wheat belt east of these mountains. *H. avenae* was next identified in a wheat field in Whitman County, Washington, during 1983 (Hafez and Golden, 1984), representing the high-precipitation (600 mm/year) edge of the primary wheat belt in the PNW. During 1984, *H. avenae* was reported from irrigated barley fields in Parker and Fremont countries in southeast Idaho (Hafez and and Golden, 1985). *Heterodera avenae* was also detected on oats in an irrigated field in Union County during 1984 (Gordon Cook, pers. comm.) and, by 1987, *H. avenae* was detected in two-thirds of all cultivated dryland and irrigated fields sampled in that county (Smiley et al., 1994). In 1990, dissemination of *H. avenae* from Union County to irrigated fields in Morrow County, Oregon, was documented from cysts in soil transported with seed potatoes grown in rotation with wheat on fields infested with *H. avenae* (Smiley et al., 1994). The known distribution in the PNW was extended in 1992 to include irrigated wheat fields in three additional countries in southeast Idaho and one additional county in eastern Oregon (Hafez et al., 1992). *Heterodera avenae* has also been detected in soil samples from irrigated fields in western Idaho, southern Oregon (Klamath County), northern California (Modoc/Siskiyou County), the irrigated Columbia Basin counties of central Washington and north-central Oregon, and, in particularly high population densities in the western Great Plains, such as in south-central Colorado (Harry Kreeft, Western Laboratories, pers. comm.). All of the *H. avenae* infestations reported above are

thought to have been in irrigated fields or in dryland fields in areas with 600 to 1,000 mm annual precipitation.

Sixty percent of the wheat produced in Oregon and Washington is on dryland fields in areas receiving 250 to 400 mm annual precipitation. *Heterodera avenae* was detected in a dryland wheat field in the 400-mm zone, in Umatilla County, Oregon (Smiley et al., 1994). The introduction was traced to soil that had been transported as a contaminant on a grain drill used previously in Union County. Smiley et al. (2005a, 2005b) reported low population densities of *H. avenae* on dryland wheat in countries representing the lowest range of precipitation for wheat production in the PNW. Since nematodes in general, and cyst nematodes in particular, are rarely sampled from dryland fields in the PNW, the extent of *H. avenae* infestation in dryland fields remains unknown.

It is clear that *H. avenae* is now distributed across many or most principal small-grain producing regions in the western United States. There is little or no effort to prevent further dissemination. Rivoal et al. (2003) reported that *H. avenae* is widely distributed "in Western Europe [and] Australia, but scarcely in Northern America." The perception of scarcity for this species in the United States appears to be due only to limited investigation and reporting. However, the misconception that *H. avenae* is not widespread has caused North American populations to be omitted or of minor interest in recent investigations on the biology of the worldwide *H. avenae* group complex (Andrés et al., 2001; Rivoal et al., 2003; Subbotin et al., 1999, 2003).

It is becoming increasingly unreliable to identify *Heterodera* species on the basis of small morphological characters (Handoo, 2002; Subbotin et al., 2003). Populations of *H. avenae* in the PNW clearly require further examination in view of recent advances in technologies that can be applied to critically differentiate species and ecotypes (Bekal et al., 1997; Subbotin et al., 1999). For example, it is important to determine if all cereal cyst populations in the PNW are in fact *H. avenae,* or whether the populations include other species in the "*H. avenae* complex," such as *H. filipjevi, H. latipons,* or *H. zeae.* Only two reports have applied modern technologies to PNW populations. Ferris et al. (1994) reported that 2-D PAGE protein patterns differed between single isolates tested from eastern Oregon and southeast Idaho, but that both isolates exhibited protein patterns consistent with the species concept for *H. avenae.* The biological importance of differences in protein patterns remains unknown for these populations that occur in regions differing in climate, elevation, soils, and 500-km aerial distance. Likewise, based on limited source material and without presentation of data, Subbotin et al. (2003) stated that molecular characteristics of populations from western Oregon and southeast Idaho clustered with those of European *H. avenae* populations. Using PCR-RFLP procedures with multiple restriction enzymes (Bekal et al., 1997; Rivoal et al., 2003), and guidance and interpretive assistance from Roger Rivoal and colleagues (INRA, LeRheu, France), the population at the Davis farm in the current study was confirmed to have a banding pattern descriptive of *H. avenae* (unpubl. data). Populations from three Union County farms (Davis, Cuthbert, and Wallender) also have been determined to be *H. avenae* based on unpublished results from DNA extracted from samples of soil and cysts sent to the Root Disease Testing Service, South Australian Research and Development Institute, Adelaide, Australia (Ophel-Keller and McKay, 2001).

The identity of the pathotype(s) in the PNW is unknown and must be determined before appropriate resistance genes can be acquired and screened efficiently (Al-Hazmi et al., 2001; Rivoal and Cook, 1993). This is particularly true in that fields with high populations that are also infested with a complex of root-infecting fungi (Smiley et al., 1994) and other plant-parasitic nematodes including *Pratylenchus neglectus* (Smiley et al., 2005b), *P. thornei* (Smiley et al., 2005a), *Tylenchorhynchus clarus* (Smiley et al., 2005a, 2005b), *Geocenamus brevidens* (Smiley et al., 2004c), and species of *Meloidogyne* and *Paratylenchus* (Smiley et al., 2004, 2005a, 2005b). This complex will preclude effective screening for resistance to *H. avenae* using standard small experimental plots in Union County because the presence of other pests may influence reproduction by *H. avenae.* While the pathotype in the PNW has not been determined, it was suggested (Holdeman and Watson, 1977) that the eastern Oregon/southeast Idaho population may be "similar to Dutch type C (Britain type 2)." Additional evidence is required because mixtures of pathotypes commonly occur when cereals are planted repeatedly over long time intervals (Swarup and Sosa Moss, 1990).

Much research is required to identify and describe the biology of cereal cyst nematodes in the western United States. These investigations must be completed before meaningful management practices other than crop rotation can be implemented.

Literature Cited

Al-Hazmi, A. S., R. Cook, and A. A. M. Ibrahim. 2001. Pathotype characterization of the cereal cyst nematode, *Heterodera avenae,* in Saudi Arabia. Nematology 3:379–382.

Andrés, M. F., M. D. Romero, M. J. Montes, and A. Delibes. 2001. Genetic relationships and isozyme variability in the *Heterodera avenae* complex determined by isoelectrofocusing. Plant Pathology 50:270–279.

Bekal, S., J. P. Gauthier, and R. Rivoal. 1997. Genetic diversity among a complex of cereal cyst nematodes inferred from RFLP analysis of the ribosomal internal transcribed spacer region. Genome 40: 479–486.

Boag, B., and L. V. Lopez-Llorca. 1989. Nematodes and nematophagous fungi associated with cereal fields and permanent pasture in eastern Scotland. Crop Research 29:1–10.

Brown, R. H. 1972. Chemical control of the cereal cyst nematode (*Heterodera avenae*) in Victoria. A comparison of systemic and contact nematicides. Australian Journal of Experimental Agriculture and Animal Husbandry 12:662–667.

Brown, R. H. 1973. Chemical control of the cereal cyst nematode (*Heterodera avenae*)—a comparison of methods and rates of application of two systemic nematicides. Australian Journal of Experimental Agriculture and Animal Husbandry 13:587–592.

Brown, R. H. 1985. The selection of management strategies for controlling nematodes in cereals. Agricultural and Ecosystem Environments 12:381–388.

Brown, R. H. 1987. Control strategies in low-value crops. Pp. 351–387 *in* R. H. Brown and B. R. Kerry, eds. Principles and practice of nematode control in crops. Sydney: Academic Press.

Caswell, E. P., I. J. Thomason, and H. E. McKinney. 1985. Extraction of cysts and eggs of *Heterodera schachtii* from soil with an assessment of extraction efficiency. Journal of Nematology 17:337–340.

Chapman, L. J. 1938. Oat nematodes on winter wheat. Scientific Agriculture 18:527–528.

Cook, R. J. 2001. Retooling Agriculture: A report on direct-seed cropping systems research in the Pacific Northwest. Washington State University PNW Extension Publication.

Delibes, A., I. López Braña, M. J. Montes, M. Gómez-Colmenarejo, M. D. Romero, M. F. Andrés, J. A. Martin-Sánchéz, E. Sin, C. Martínez, A. Michelena, J. del Moral, and A. Mejías. 2001. Transfer of resistance genes to Hessian fly and cereal cyst nematode from *Aegilops triuncialis* to hexaploid wheat and its use in breeding programs. Annual Wheat Newsletter 47:198–200.

Ferris, V. R., J. Faghihi, A. Ireholm, and J. M. Ferris. 1994. Comparisons of isolates of *Heterodera avenae* using 2-D PAGE protein patterns and ribosomal DNA. Journal of Nematology 26:144–151.

Fushtey, S. G. 1966. The oat nematode. Ontario Department of Agriculture Publication 453.

Garrett, S. D. 1934. Effect of crop rotation on the eelworm (*Heterodera schachtii*) disease of cereals. Journal of the Department of Agriculture of South Australia 37:984–987.

Hafez, S. L., and A. M. Golden. 1984. First report of oat cyst nematode in eastern Washington. Plant Disease 68:351.

Hafez, S. L., and A. M. Golden. 1985. First report of oat cyst nematode (*Heterodera avenae*) on barley in Idaho. Plant Disease 69:360.

Hafez, S. L., A. M. Golden, F. Rashid, and Z. Handoo. 1992. Plant-parasitic nematodes associated with crops in Idaho and eastern Oregon. Nematropica 22:193–204.

Hague, N. G. M., and S. G. Gowen. 1987. Chemical control of nematodes. Pp. 131–178 *in* R. H. Brown and B. R. Kerry, eds. Principles and practice of nematode control in crops. Sydney: Academic Press.

Handoo, Z. A. 2002. A key and compendium to species of the *Heterodera avenae* group (Nematoda: Heteroderidae). Journal of Nematology 34:250–262.

Holdeman, Q. L., and T. R. Watson. 1977. The oat cyst nematode *Heterodera avenae* Wollenweber, 1924: A root parasite of cereal crops and other grasses. State of California Department of Food and Agriculture, Sacramento, CA.

Ingham, R. E. 1994. Nematodes. Pp. 459–490 *in* R. W. Weaver, ed. Methods of soil analysis, part 2. Microbiological and biochemical properties. Madison, WI: American Society of Agronomy.

Irving, F., and B. R. Kerry. 1987. Variations between strains of the nematophagous fungus, *Verticillium chlamydosporium* Goddard. II. Factors affecting parasitism of cyst nematode eggs. Nematologica 32:475–485.

Jahier, J., P. Abelard, A. M. Tanguy, F. Dedryver, R. Rivoal, S. Khatkar, and H. S. Bariana. 2001. The *Aegilops ventricosa* segment on chromosome 2AS of the wheat cultivar VPM1 carries the cereal cyst nematode gene Cre5. Plant Breeding 120:125–128.

Jensen, H. J., H. Eshtiaghi, P. A. Koepsell, and N. Goetze. 1975. The oat cyst nematode, *Heterodera avenae,* occurs on oats in Oregon. Plant Disease Reporter 59:1–3.

Juergens, L. A., D. L. Young, H. R. Hinman, and W. F. Schillinger. 2003. Economics of alternative no-till spring crop rotations in Washington's wheat-fallow region. Pacific Northwest Conservation Tillage Handbook Series No. 19. Washington State University, Pullman, WA.

Kerry, B. R. 1987. Biological control. Pp. 233–263 *in* R. H. Brown and B. R. Kerry, eds. Principles and practice of nematode control in crops. Sydney: Academic Press.

King, P. M., A. D. Rovira, P. G. Brisbane, A. Simon, and R. H. Brown. 1982. Population estimates of cereal cyst nematode and response of wheat to granular nematicides. Australian Journal of Experimental Agriculture and Animal Husbandry 22:209–220.

McLeod, R. W., P. T. W. Wong, and R. J. Southwell. 1986. Biology and control of cereal cyst nematode in northern New South Wales. Australian Journal for Experimental Agriculture 26:375–381.

Meagher, J. W., R. H. Brown, and A. D. Rovira. 1978. The effects of cereal cyst nematode (*Heterodera avenae*) and *Rhizoctonia solani* on the growth and yield of wheat. Australian Journal of Agricultural Research 29:1127–1137.

Nicol, J. M. 2002. Important nematode pests of cereals. Pp. 345–366 *in* B.C. Curtis, ed. Bread wheat: Improvement and production. Rome, Italy: FAO Plant Production and Protection Series.

Nicol, J., R. Rivoal, S. Taylor, and M. Zaharieva. 2003. Global importance of cyst (*Heterodera* spp.) and lesion nematodes (*Pratylenchus* spp.) on cereals: Yield loss, population dynamics, use of host resistance, and integration of molecular tools. Nematology Monographs and Perspectives 2:1–19.

Ophel-Keller, K., and A. McKay. 2001. Root disease testing service: Delivery and commercialization. Pp. 17–18 *in* I. J. Porter, ed. Proceedings of the Second Australasian Soilborne Diseases Symposium. Victoria, Australia: Department of Natural Resources & Environment.

Orion, D., and E. Shlevin. 1989. Nematicide seed dressing for cyst and lesion nematode control in wheat. Supplement to Journal of Nematology 21:629–631.

Pscheidt, J. W., and C. M. Ocamb, eds. 2005. Pacific northwest plant disease management handbook. Corvallis, OR: Oregon State University.

Rivoal, R. 1986. Biology of *Heterodera avenae* Wollenweber in France. IV. Comparative study of the hatching cycles of two ecotypes after their transfer to different climatic conditions. Revue de Nématologie 9:405–410.

Rivoal, R., S. Bekal, S. Valette, J.-P. Gauthier, M. Bel Hadj Fradj, A. Mokabli, J. Jahier, J. Nicol, and A. Yahyaoui. 2001. Variation in reproductive capacity and virulence on different genotypes and resistance genes of Triticeae, in the cereal cyst nematode species complex. Nematology 3:581–592.

Rivoal, R., and R. Cook. 1993. Nematode pests of cereals. Pp. 259–303 *in* K. Evans, D. L. Trudgill, and J. M. Webster, eds. Plant parasitic nematodes in temperate agriculture. Wallingford, UK: CAB International.

Rivoal, R., and E. Saar. 1987. Field experiments on *Heterodera avenae* in France and implications for winter wheat performance. Nematologica 33:460–479.

Rivoal, R., S. Valette, S. Bekal, J.-P. Gauthier, and A. Yahyaoui. 2003. Genetic and phenotypic diversity in the graminaceous cyst nematode complex, inferred from PCR-RFLP of ribosomal DNA and morphometric analysis. European Journal of Plant Pathology 109: 227–241.

Rovira, A. D., P. G. Brisbane, A. Simon, D. G. Whitehead, and R. L. Correll. 1981. Influence of cereal cyst nematode (*Heterodera avenae*) on wheat yields in South Australia. Australian Journal of Experimental Agriculture and Animal Husbandry 21:516–523.

Rovira, A. D., and A. Simon. 1982. Integrated control of *Heterodera avenae.* European Plant Protection Organization Bulletin 12:517–523.

Simon, A., and A. D. Rovira. 1982. The relation between wheat yield and early damage of roots by cereal cyst nematode. Australian Journal of Experimental Agriculture and Animal Husbandry 22:201–208.

Smiley, R. W., R. E. Ingham, and G. H. Cook. 1992. Control of cereal cyst nematode with infurrow and seed treatments. Fungicide and Nematicide Tests 47:167.

Smiley, R. W., R. E. Ingham, W. Uddin, and G. H. Cook. 1994. Crop sequences for winter wheat in soil infested with cereal cyst nematode and fungal pathogens. Plant Disease 78:1142–1149.

Smiley, R. W., K. Merrifield, L.-M. Patterson, R. G. Whittaker, J. A. Gourlie, and S. A. Easley. 2004. Nematodes in dryland field crops in the semiarid Pacific Northwest USA. Journal of Nematology 36:54–68.

Smiley, R. W., R. G. Whittaker, J. A. Gourlie, and S. A. Easley. 2005a. *Pratylenchus thornei* associated with reduced wheat yield in Oregon. Journal of Nematology 37:45–54.

Smiley, R. W., R. G. Whittaker, J. A. Gourlie, and S. A. Easley. 2005b. Suppression of wheat growth and yield by *Pratylenchus neglectus* in the Pacific Northwest. Plant Disease 89:958–968.

Subbotin, S. A., D. Sturhan, H. J. Rumpenhorst, and M. Moens. 2002. Description of Australian cereal cyst nematode *Heterodera australis* sp. n. (Tylenchida: Heteroderidae). Russian Journal of Nematology 10:139–148.

Subbotin, S. A., D. Sturhan, H. J. Rumpenhorst, and M. Moens. 2003. Molecular and morphological characterization of the *Heterodera avenae* species complex (Tylenchida: Heteroderidae). Nematology 5: 515–538.

Subbotin, S. A., L. Waeyenberge, I. A. Molokanova, and M. Moens. 1999. Indentification of *Heterodera avenae* group species by morphometrics and rDNA-RFLPs. Nematology 1:195–207.

Swarup, G., and C. Sosa Moss. 1990. Nematode parasites of cereals. Pp. 109–136 *in* M. Luc, R. A. Sikora, and J. Bridge, eds. Plant parasitic nematodes in subtropical and tropical agriculture. Wallingford, UK: CAB International.

Taylor, S. P., V. A. Vanstone, A. H. Ware, A. C. McKay, D. Szot, and M. H. Russ. 1999. Measuring yield loss in cereals caused by root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) with and without nematicides. Australian Journal of Agricultural Research 50:617–622.

Zaharieva, M., P. Monneveux, M. Henry, R. Rivoal, J. Valkoun, and M. M. Nachit. 2001. Evaluation of a collection of wild wheat relative *Aegilops geniculata* Roth and identification of potential sources for useful traits. Pp. 739–746 *in* Z. Bedö and L. Láng, eds. Wheat in a global environment. The Netherlands: Kluwer Academic Publishers.