Crop Sequences for Managing Cereal Cyst Nematode and Fungal Pathogens of Winter Wheat

RICHARD W. SMILEY, Professor, Oregon State University, Columbia Basin Agricultural Research Center, P.O. Box 370, Pendleton 97801; RUSSELL E. INGHAM, Associate Professor, Oregon State University, Department of Botany and Plant Pathology, 2076 Cordley Hall, Corvallis 97331; WAKAR UDDIN, Former Faculty Research Assistant, Columbia Basin Agricultural Research Center, P.O. Box 370, Pendleton 97801; and GORDON H. COOK, Field Crops Specialist, Union County Extension Service, 10507 North McAlister Road, La Grande, OR 97850

ABSTRACT

Smiley, R. W., Ingham, R. E., Uddin, W., and Cook, G. H. 1994. Crop sequences for managing cereal cyst nematode and fungal pathogens of winter wheat. Plant Dis. 78:1142-1149.

In the Pacific Northwest, *Heterodera avenae* is spreading to soils infested with root-infecting fungal pathogens of wheat. A poorly drained, silty clay loam infested with multiple pathogens was used to examine productivity of winter wheat in 11 crop sequences. Breaks between wheat crops included summer fallow or crops of pea, barley, rape, alfalfa, or Kentucky bluegrass. In the fifth year, winter wheat was planted in all sequences, after one-half of each plot was treated with aldicarb. Yield of annual winter wheat was always 40–60% less than wheat alternated with fallow or any other crop, except alfalfa contaminated with grass weeds. Wheat yielded equally following 1- or 2-yr breaks from wheat. Effective breaks included summer fallow, pea, and weed-free alfalfa. *H. avenae* was the most important individual constraint to yield. Combined damage from *H. avenae* and *Gaeumannomyces graminis* var. *tritici* caused highest overall yield loss, whereas *H. avenae* and *Pythium* spp. had the greatest negative effect on number of roots. During the fifth year, where aldicarb was applied, root damage by *H. avenae* decreased but damage by *Rhizoctonia solani* and *Pythium* spp. increased, resulting in no yield improvement.

Additional keywords: *Brassica campestris*, dryland root rot, *Hordeum vulgare*, *Pisum sativum*, *Poa pratensis*, Pythium root rot, Rhizoctonia root rot, take-all, Temik, *Triticum aestivum*

Cereal cyst nematode (*Heterodera avenae* Wollenweber) was first reported in the United States, in Washington County, western Oregon, during 1974 (14). This nematode has now been identified in nine additional counties where wheat is a primary crop in southeast Washington, northeast Oregon, and southeast Idaho. During 1987, 67% of the cultivated fields surveyed in Union County, Oregon, were infested with *H. avenae* (*unpublished*). Although yields of winter and spring wheat were improved up to 29% by application of aldicarb (31,32), this is not an acceptable practice in infested fields with a shallow water table.

In the Pacific Northwest, host crops of *H. avenae* (29,36) include wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), grass seed crops (species of *Agrostis, Festuca, Lolium, Poa*, and others), corn (*Zea mays* L.), and oats (*Avena sativa* L.). These crops are also affected by Pythium root rot, caused by *Pythium* spp.; Rhizoctonia root rot, caused by *R. solani* Kühn; take-all, caused by *Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici* J. Walker; and dryland root rot, caused by a complex of *Fusarium graminearum* Schwabe, *Cochliobolus sativus* (Ito & Kuribayashi) Drechs. ex Dastur, *F. culmorum* (Wm.G. Sm.) Sacc., and *F. avenaceum* (Fr.:Fr.) Sacc.) (5,7).

Disease complexes resulting from *H. avenae* and soilborne fungi have been described (4,8,17,18,26,33,35). Meagher et al (17) reported that individual effects of *H. avenae* and *R. solani* on wheat were less damaging than when both pathogens were present. Rovira and Ridge (26) increased yield of wheat by a factor of six by fumigating soil infested with *H. avenae, R. solani*, and *G. g. tritici*. Other studies have demonstrated that *R. solani* (22) and *G. g. tritici* (4) reduce formation of *H. avenae* cysts by rotting roots and competing for root sites, thus reducing the nematode population. A mutual antagonism between *R. solani* and *G. g. tritici* has been described (22).

Crop rotations are used to reduce damage caused by the cereal cyst nematode (1,11-13,19,23,25,27) and fungal pathogens of wheat (3,5,7,34). However, management strategies for *H. avenae* and complex root diseases involving the nematode and fungal pathogens have not been developed in the semiarid Pacific Northwest. Winter wheat is the most profitable nonirrigated crop and can be produced in a 2-yr rotation with summer fallow, pea (*Pisum sativum* L.), or lentil (*Lens culinaris* Medik.); in a 3-yr rotation with fallow, then barley, lentil, pea, or rape (*Brassica campestris* L.); or in longer rotations that include grass seed crops (*Agrostis, Festuca, Lolium*, or *Poa* spp.). Some growers produce winter or spring wheat annually with inversion or minimum tillage. Rotations on irrigated fields may include winter wheat, barley, corn, grass seed, potato (*Solanum tuberosum* L.), alfalfa, mint (*Mentha arvensis* L.), pea, rape, and others.

The objective of this experiment was to examine plant growth, root damage, and yield of winter wheat produced with commercial management practices for 11 crop sequences in soil infested with cereal cyst nematode and multiple soilborne plant-pathogenic fungi.

MATERIALS AND METHODS

Experimental site. A 23-ha field infested with *H. avenae* was mapped into a 60 × 60 m grid. The field, 8 km northeast of La Grande, Oregon, had been managed as a 2-yr rotation of winter wheat and summer fallow for 6 yr. On 11 August 1987, 15 soil cores (2.5 cm in diameter and 20 cm deep) were collected within a 3-m radius around 27 intersects of the grid lines. Cysts of *H. avenae* were floated from air-dried soil (10), picked from the debris, and ground to liberate eggs and second-stage juveniles for enumeration (2). Numbers of eggs plus juveniles ranged from one to 21/g of soil in the 27 samples. Variability for population density was randomly distributed, and a plot was established on a level area containing the full range of *H. avenae* population densities. Seasonal dynamics for egg hatch were examined and population densities in each plot were determined annually during late summer. Effects of cropping sequences on population changes for *H. avenae* will be reported elsewhere.

The experimental area has a mean annual precipitation of 510 mm and an average daily temperature of −1 C during January and 18 C during July and August. Soil is a deep, poorly drained Conley silty clay loam (fine, montmorillonitic, mesic Xeric Argialbolls) that grades into clay at a depth of 0.3 m. The water table becomes perched at a depth of 0.5 m for up to 5 mo during winter and spring. Sprinkler irrigation is required during summer because few roots penetrate deeper than 0.6 m into the clay

Oregon Agricultural Experiment Station Paper No. 10177.

Accepted for publication 9 September 1994.

substratum. Surface soil has 30% clay, very slow infiltration, pH 7.9, and 4.4% organic matter.

Crop management. Eleven crop sequences (Table 1) were established on 5 × 30 m plots replicated four times in a randomized complete block design. Crop cultivars included Stephens winter wheat, Steptoe spring barley, Tobin spring rape (a low-glucosinolate cultivar [20]), Moranda dry pea or Columbia green pea, Blazer alfalfa, and Baron Kentucky bluegrass. Unless stated otherwise, all residues were retained on each plot. Except for alfalfa, these crops were produced following commercial practices. Manual weeding of "weed-free" alfalfa (treatment 9, or T9) was performed repeatedly. Wheat and barley seed were treated with carboxin + thiram (0.54 + 0.54 g a.i./kg seed, as Vitavax 200F, 20% carboxin + 20% thiram). Fallow was maintained by periodic rod weeding at a depth of 6 cm through soil previously plowed and disked. The experimental area was sprinkler-irrigated.

1987–1988. On 21 September 1987, wheat stubble remaining from a commercial crop was incorporated into the soil by plowing to 30 cm deep and disking to 10 cm deep. Ammonium nitrate (90 kg/ha N) was broadcast and incorporated with a harrow. Wheat was planted (90 kg/ha, 40-cm row spacing) in seven treatments (T1, T2, T3, T6, T7, T9, and T10) on 16 October (Table 1). Nitrogen (34 kg/ha, as urea ammonium nitrate, [Uran]) was also banded 4 cm below the seed at planting. Rape (T8) and bluegrass seed (T11) were planted on 14 April 1988, and wheat was harvested on 23 August.

1988–1989. All treatments except minimum-till wheat (T2) and bluegrass (T11) were plowed and disked on 9 September 1988. Residue was burned from the minimum-till wheat plots on 15 September. The experimental area was fertilized on 28 September by broadcasting ammonium nitrate at 90 kg/ha N, except for minimum-till wheat, which received 135 kg/ha N to compensate for a lower level of mineralizable nitrogen where stubble was burned. Fertilizer was incorporated shallowly with a skew treader on all tilled plots and to 2 cm deep in minimum-till wheat plots. Wheat was planted (T1, T2, T4, T5, T7, and T8) on 5 October, and peas (T6) and alfalfa (T9 and T10) were planted on 12 May. Wheat was harvested on 12 July.

1989–1990. On 20 September, bluegrass (T11) and minimum-till wheat (T2) plots were burned, and all plots to be fallowed or planted to wheat (except minimum-till), barley, or pea were plowed and disked. On 27 September, the entire experimental area was fertilized (88 kg/ha N, as broadcasted ammonium nitrate) and wheat was planted (T1, T2, T3, and T6). Peas (T7) and barley (T5) were planted on 4 May, and wheat and barley were harvested on 15 August.

1990–1991. Minimum-till wheat (T2) residue was burned on 14 September 1990. On 11 October, all plots except alfalfa (T9 and T10), bluegrass (T11), and minimum-till wheat (T2) were plowed and disked. All plots except those designated as fallow (T3, T4, and T5) were fertilized with ammonium nitrate (55 kg/ha N). All tilled plots and the minimum-till wheat plot were tilled shallowly with a skew treader, and then wheat (T1 and T2) was planted. Rape (T8) and pea (T6 and T7) were planted on 14 June, and wheat was harvested on 21 August.

1991–1992. On 6 September 1991, soil samples (composites of 20 cores per plot, 2.5 cm in diameter and 20 cm deep) were collected from all plots for analysis of residual nitrogen. Residue of minimum-till wheat (T2) was burned on 12 September. All treatments except minimum-till wheat were plowed on 28 September, and all treatments were disked twice (6 cm deep on minimum-till wheat plots). On 30 September, each of the 44 plots was fertilized individually with ammonium nitrate to achieve a uniform target rate of 170 kg/ha N. Rates of application ranged from 0 to 124 kg/ha N, based on analyses of residual nitrogen and estimates of nitrogen to be released during mineralization of straw. All plots were planted to wheat on 9 October. Wheat was planted perpendicular to the long axis of each plot, using a double-disk minimum-till drill with 25-cm row spacings. Aldicarb (4 kg/ha, as Temik 15G, 15% a.i.) was banded with the wheat seed in one-half of each plot (5 × 15 m). Wheat establishment was uniform and in the two-leaf stage on 5 December. Aldicarb was reapplied on 26 March 1992, since effects of the autumn treatment were not apparent; 2.9 kg/ha was broadcast and immediately incorporated by rain. While this application is not a normal method for applying aldicarb, it was used in this experiment to ensure that nematode populations would be reduced in order to determine their impact in nontreated plots. Wheat was harvested on 14 August.

Diseases, plant growth, and yield. Wheat plants were collected for evaluation of growth, development, disease incidence and severity, and damage from *H. avenae* on 21 June 1988, 10 July 1989, 30 November 1989, 9 April 1990, 29 March 1991, 15 May 1991, 30 March 1992, and 4 May 1992. Barley was also sampled during the 1990 crop year. Nonhosts of *H. avenae* (e.g., alfalfa, pea, rape) and bluegrass were not monitored for diseases, growth, or yield.

Plants with intact root systems were dug from three randomly selected positions in each plot. Roots were rinsed to remove adhering soil, and 15 plants from each plot were evaluated visually for incidence and/or severity of all diseases and nematode damage. Periodic confirmatory isolations and/or microscopic observations were made from symptomatic roots. Root segments were washed under running water for 3 hr and then, without surface-disinfection, were placed onto 2% water agar (Bacto Agar, Difco) treated with 50 μg/ml of rifampicin. Emerging fungal isolates were transferred onto 1% potato-dextrose agar (PDA) medium (BBL grade) prepared by mixing equal quantities of PDA and water agar to achieve a 2% firm agar gel.

Cereal cyst nematode damage was assessed by the visual scale of Simon and Rovira (30). Dryland root rot was quantified as percentage of subcrown internodes affected by characteristic dark lesions. Take-all was rated as the percentage of seminal root main axes affected by characteristic blackening of the root cortex or vascular system.

Table 1. Sequences for crops[v] and summer fallow

Treatment	Year of harvest 1988	1989	1990	1991	1992
1[w]	Wheat	Wheat	Wheat	Wheat	Wheat
2[x]	Wheat	Wheat	Wheat	Wheat	Wheat
3	Wheat	Fallow	Wheat	Fallow	Wheat
4	Fallow	Wheat	Fallow	Fallow	Wheat
5	Fallow	Wheat	Barley	Fallow	Wheat
6	Wheat	Pea	Wheat	Pea	Wheat
7	Wheat	Wheat	Pea	Pea	Wheat
8	Rape	Wheat	Fallow	Rape	Wheat
9[y]	Wheat	Alfalfa	Alfalfa	Alfalfa	Wheat
10[z]	Wheat	Alfalfa	Alfalfa	Alfalfa	Wheat
11	Grass	Grass	Grass	Grass	Wheat

[v] Crops included Stephens winter wheat, Steptoe spring barley, Tobin spring rape, Moranda dry pea, Blazer alfalfa, and Baron Kentucky bluegrass. Tillage was performed on all treatments except No. 2, using a moldboard plow, disk, and spring-tooth harrow. Weed-free summer fallow was maintained with a rod-weeder.

[w] Soil was plowed and disked before planting winter wheat annually (conventional tillage).

[x] Stubble was removed by burning and the soil surface was shallowly mixed by disk or skew treader before planting winter wheat annually (minimum-till).

[y] Alfalfa was continually rogued to eliminate grass weeds and volunteer cereals.

[z] Alfalfa was moderately contaminated by volunteer wheat, downy brome, and wild oats, and no effort was made to control these weeds.

Pythium root rot was quantified as the percentage of roots with light-brown, water-soaked lesions. Rhizoctonia root rot was evaluated on coronal root systems, based on percentages of main root axes with brown cortical rot or "spear tip" severance: 0 = none, 1 = <25%, 2 = 26–50%, 3 = 51–75%, and 4 = >76%.

Table 2. Yield (kg/ha) of winter wheat in 11 crop sequences near La Grande, Oregon

	Crop[s] and year					Year of harvest[t]				
Treatment	**1988**	**1989**	**1990**	**1991**	**1992**	**1988**	**1989**	**1990**	**1991**	**1992[u]**
1	W	W	W	W	W[v]	7,906	3,690 a	5,203 b	3,188	4,434 a
2	W	W	W	W	W[w]	8,717	7,080 b	4,252 a	2,821	4,143 a
3	W	F	W	F	W	8,694	...	6,580 c	...	6,557 c
4	F	W	F	F	W	...	7,782 b	...	...	7,036 c
5	F	W	B[x]	F	W	...	8,353 b	...	...	6,362 c
6	W	P	W	P	W	8,657	...	7,253 c	...	6,252 c
7	W	W	P	P	W	7,906	4,078 a	...	...	6,368 c
8	R	W	F	R	W	...	8,062 b	...	...	6,792 c
9	W	A	A	A	W[y]	8,301	...	...	...	6,328 c
10	W	A	A	A	W[z]	8,475	...	...	...	5,467 b
11	G	G	G	G	W					6,520 c
LSD ($P = 0.05$)						ns	1,418	550	ns	549

[s] W = winter wheat, B = spring barley, F = summer fallow, P = spring pea, R = spring rape, A = alfalfa, G = bluegrass. Years refer to year of harvest.
[t] Means followed by the same letter did not differ significantly (P = 0.05) according to the Student-Newman-Keuls test.
[u] Yields are pooled means of aldicarb-treated (mean yield of 6,059 kg/ha) and untreated (mean yield of 5,988 kg/ha) wheat; the aldicarb treatment was not significant (P = 0.54), and there was no crop × aldicarb interaction (P = 0.62).
[v] Soil was plowed and disked before planting winter wheat annually (conventional tillage).
[w] Stubble was removed by burning and the soil surface was shallowly mixed by disk or skew treader before planting winter wheat annually (minimum-till).
[x] Yield of spring barley was 5,898 kg/ha.
[y] Alfalfa was continally rogued to eliminate grass weeds and volunteer cereals.
[z] Alfalfa was moderately contaminated by volunteer wheat, downy brome, and wild oats, and no effort was made to control these weeds.

Table 3. Incidence and severity of cereal cyst nematode and root diseases on wheat roots during spring 1989

	Crop sequence[x]						LSD
Sampling parameter	**1**	**2**	**4**	**5**	**7**	**8**	**($P = 0.05$)**
Incidence (% plants)							
Cereal cyst nematode	98	97	80	78	90	80	6
Rhizoctonia root rot	38	60	53	52	27	75	17
Severity							
Cereal cyst nematode[y]	1.7	1.8	1.1	1.1	1.7	0.9	0.3
Rhizoctonia root rot[z]	0.9	0.9	0.8	0.8	0.6	1.2	0.3

[x] Wheat followed wheat in sequences 1, 2, and 7, fallow in sequences 4 and 5, and rape in sequence 8.
[y] Root damage index: 0 = no evidence of damage; 1 = 1–5 *Heterodera avenae* galls per root system, no reduction in root length; 2 = 6–25 galls and 20% reduction in root length; 3 = 26–50 galls and 40% reduction in root length; 4 = >50 galls, 60% reduction in root length and 25% reduction in plant height; and 5 = roots very knotted and reduced 80% in length and plant height reduced by 50%.
[z] Root rot index based on percentages of main axes with lesions: 0 = none, 1 = <25%, 2 = 26–50%, 3 = 51–75%, and 4 = >76%.

Table 4. Wheat plant development and damage by cereal cyst nematode and root diseases during autumn and spring 1990

	Crop sequence[x]				LSD
Sampling parameter	**1**	**2**	**3**	**6**	**($P = 0.05$)**
Severity, 30 Nov. 1989					
Cereal cyst nematode[y]	1.0	1.0	0.3	0.2	0.2
Pythium root rot[z]	2.9	1.0	0.2	0.2	1.4
Incidence (% plants), 9 Apr. 1990					
Cereal cyst nematode	59	49	13	11	18

[x] Wheat followed wheat in sequences 1 and 2, fallow in sequence 3, and peas in sequence 6.
[y] Root damage index: 0 = no evidence of damage; 1 = 1–5 *Heterodera avenae* galls per root system, no reduction in root length; 2 = 6–25 galls and 20% reduction in root length; 3 = 26–50 galls and 40% reduction in root length; 4 = >50 galls, 60% reduction in root length and 25% reduction in plant height; and 5 = roots very knotted and reduced 80% in length and plant height reduced by 50%.
[z] Percentage of roots with symptoms of Pythium root rot.

Data from individual plants were also used to determine percentages of plants affected by each disease.

Plant growth and development characteristics were determined on the same seedlings evaluated for diseases. The Haun development stage (7,15) for each wheat and barley plant was estimated (e.g., Haun 2.8 = three leaves are present on the main stem, with the third leaf 80% as long as the second). The length of the longest main stem leaf was measured, and the presence or absence of tillers was recorded for each tiller position (15), e.g., T_0 = coleoptilar tiller, T_1 = tiller in the axil of the first leaf of the main stem, and so on. Seminal and coronal roots crossing a horizontal plane 3 and 5 cm below the caryopsis were counted by floating washed root systems in water over a white background. Shoots were then cut at the soil surface position, dried in an oven, and weighed. Grain yields and test weights were measured at maturation by threshing plants in 1 × 30 m or 2 × 30 m segments of each plot, using a plot combine.

Statistical treatment. Data for each parameter (growth, development, yield, disease, and root damage) and sampling date were subjected to analysis of variance. Least-significant differences were used to separate treatment means for parameters having significant F values. The Student-Newman-Keuls test was also used to compare grain yields. All significant differences are reported at $P < 0.05$ unless otherwise indicated. Correlation coefficients (r) were used to explore relationships among parameters. Data were pooled for crop sequences having 0-, 1-, or 2-yr breaks between crops of winter wheat or grass weeds (e.g., Poaceae hosts for cereal cyst nematode). This process was performed to evaluate the length of rotation necessary to achieve yield improvement over sequences that include a host every year.

RESULTS

1987–1988. Wheat in all treatments (T1, T2, T3, T6, T7, T9, and T10) during the first year was preceded by a single year of summer fallow. No treatment differences were measured for growth of foliage or roots during the spring and summer (*data not shown*). Incidence and severity of damage from cereal cyst nematode, take-all, Rhizoctonia root rot, Pythium root rot, and dryland root rot were minimal (*data not shown*). Grain yields also did not differ (Table 2).

1988–1989. On 10 July, damage from cereal cyst nematode was present on most plants in all sequences (Table 3) and was slightly more prevalent in wheat following wheat (T1, T2, and T7) than fallow (T4 and T5) or rape (T8). Damage ratings were also higher for wheat following wheat than for wheat following fallow or rape. Nematode damage to bluegrass roots (T11) was minimal (rating 0.3; *data not shown*). Rhizoctonia root rot in second-year wheat in plowed plots (T1 and T7) affected fewer plants than in minimum-till (T2) and where wheat followed fallow (T4 and T5) or rape (T8). Damage ratings on affected plants were also higher for wheat following rape (T8) than for wheat following wheat (T1, T2, and T7) or fallow (T4 and T5). Take-all, Pythium root rot, and dryland root rot were present in trace amounts and did not differ among treatments (*data not shown*). Yield of wheat following wheat in plowed soil (T1 and T7) was 55–62% less ($P < 0.001$) than wheat following fallow (T4 and T5) or rape (T8) (Table 2). Yield of annual wheat was significantly greater in minimum-till (T2) than in plowed (T1) soil.

1989–1990. On 30 November 1989, cereal cyst nematode damage ratings and Pythium root rot incidence were higher for annual wheat (T1 and T2) than for wheat following fallow (T3) or peas (T6) (Table 4). Compared with annual wheat plants, wheat following fallow or peas was taller (12 vs. 14 cm; $P < 0.001$, LSD = 1) and phenologically more developed (Haun 2.8 vs. 3.3; $P < 0.001$, LSD = 0.1). Wheat following fallow or peas also had higher percentages of tillers than annual wheat: T_0 on 3–28% vs. 0–1% of plants, T_1 on 77–92% vs. 6–34% of plants, and T_2 on 16–17% vs. 0% of plants. Numbers of roots were equivalent for

Table 5. Incidence and severity of cereal cyst nematode damage to winter wheat roots in soil treated or not treated with aldicarb in 11 crop sequences during the 1991–1992 crop year

	Crop[s] and year					Root damage severity rating[t]			Percentage of plants damaged		
						29 Mar.	4 May		29 Mar.	4 May	
Treatment	**1988**	**1989**	**1990**	**1991**	**1992**		**−Ald[u]**	**+Ald**		**−Ald**	**+Ald**
1	W	W	W	W	W[v]	0.5	4.4	0.5	49	100	40
2	W	W	W	W	W[w]	0.5	3.6	0.8	48	100	65
3	W	F	W	F	W	0.2	1.9	0.4	26	94	40
4	F	W	F	F	W	0.1	0.6	0.4	16	52	42
5	F	W	B	F	W	0.4	2.5	0.5	38	100	52
6	W	P	W	P	W	0	1.1	0.3	5	65	25
7	W	W	P	P	W	0	0.3	0.1	1	31	8
8	R	W	F	R	W	0	0.5	0.1	0	42	8
9	W	A	A	A	W[x]	0	0.1	0.1	1	13	10
10	W	A	A	A	W[y]	0.2	0.9	0.4	19	65	40
11	G	G	G	G	W	0.5	0.7	0.4	50	54	31
$P > F$[z] for:											
Crop						<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Aldicarb						0.92	<0.001		0.79	<0.001	
Crop × aldicarb						0.56	<0.001		0.61	0.01	
LSD ($P = 0.05$) for:											
Crop						0.2	0.7	0.2	19	25	20
Aldicarb						ns	0.2		ns	7	

[s] W = winter wheat, B = spring barley, F = summer fallow, P = spring pea, R = spring rape, A = alfalfa, G = blugrass. Years refer to year of harvest.
[t] Root damage index: 0 = no evidence of damage; 1 = 1–5 *Heterodera avenae* galls per root system, no reduction in root length; 2 = 6–25 galls and 20% reduction in root length; 3 = 26–50 galls and 40% reduction in root length; 4 = >50 galls, 60% reduction in root length and 25% reduction in plant height; and 5 = roots very knotted and reduced 80% in length and plant height reduced by 50%.
[u] Aldicarb applied as in-row band (4 kg/ha) at planting on 11 Oct. 1991 and again as surface broadcast (2.9 kg/ha) on 26 Mar. 1992. Data were pooled for the 29 Mar. sampling because there was no effect of aldicarb treatment or crop × aldicarb interaction.
[v] Soil was plowed and disked before planting winter wheat annually (conventional tillage).
[w] Stubble was removed by burning and the soil surface was shallowly mixed by disk or skew treader before planting winter wheat annually (minimum-till).
[x] Alfalfa was continually rogued to eliminate grass weeds and volunteer cereals.
[y] Alfalfa was moderately contaminated by volunteer wheat, downy brome, and wild oats, and no effort was made to control these weeds.
[z] Probability of obtaining a larger value of F for the effect of crop rotation in an analysis of variance.

Table 6. Root disease incidence (percent plants affected) and severity on 4 May 1992 in winter wheat treated or not treated with aldicarb in 11 crop sequences

	Aldicarb[x]	Crop sequence[y]											LSD
Sampling parameter	**(+ or −)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**($P = 0.05$)**
Incidence (% plants)													
Rhizoctonia root rot	−	2	2	15	11	13	9	6	2	2	4	10	ns
	+	13	4	21	10	16	27	15	11	8	6	11	13
Pythium root rot	−	6	44	38	36	27	46	44	27	27	34	19	22
	+	44	54	52	40	27	60	50	48	38	38	23	24
Take-all	Pooled	13	21	0	1	2	3	0	0	0	13	1	10
Dryland root rot	Pooled	34	4	18	15	13	10	9	11	4	8	10	14
Severity[z]													
Rhizoctonia root rot	−	0	0	0.2	0.1	0.2	0.1	0.1	0	0	0	0.1	ns
	+	0.2	0	0.3	0.2	0.2	0.4	0.2	0.2	0.1	0.1	0.2	0.2
Pythium root rot	Pooled	2.0	4.8	3.9	2.7	2.3	5.3	3.6	3.1	2.7	2.4	1.4	1.5
Take-all	Pooled	1.6	3.2	0	0	0.1	0.2	0	0	0	1.9	0	1.4

[x] Data from aldicarb-treated and untreated plots were pooled when the treatment effect and crop × aldicarb interaction did not differ significantly at $P = 0.05$.
[y] See Table 1 for description of crop sequences in the 11 treatments.
[z] Percent affected roots for Pythium root rot and take-all and root rot index for Rhizoctonia root rot based on percentages of main axes with lesions: 0 = none, 1 = <25%, 2 = 26–50%, 3 = 51–75%, and 4 = >76%.

plants from all four treatments (*data not shown*).

Incidence of cereal cyst nematode on 9 April 1990 was higher ($P < 0.001$) for wheat following wheat (T1 and T2) than for wheat following fallow (T3) or peas (T6), but damage ratings did not differ among treatments (Table 4). Estimates of fungal pathogen incidence and damage also did not differ among treatments (*data not shown*).

Wheat yields (Table 2) were significantly lower in annual wheat (T1 and T2) than in wheat-fallow (T3) or wheat-pea (T6) sequences. Wheat in plowed soil (T1) yielded more than wheat in minimum-till soil (T2). Yield was directly correlated with numbers of roots on plants during the spring ($P = 0.05$, $r = 0.50$) and negatively correlated with damage from cereal cyst nematode ($P = 0.02$, $r = -0.57$). Backward multiple regression indicated that the strongest determinant of yield was combined damage from cereal cyst nematode and take-all ($P = 0.02$, $r = -0.57$).

1990–1991. On 29 March, none of the disease parameters differed significantly among the two annual wheat treatments (T1 and T2) (*data not shown*). Wheat in plowed soil (T1) was 1.4 cm taller than that in minimum-till soil (T2) and was phenologically more advanced (0.3 Haun), but numbers of roots did not differ significantly among treatments.

Damage from cereal cyst nematode on 15 May was moderately severe and was more damaging in plowed (T1) than in minimum-till (T2) plots (Haun 3.6 vs. 2.3; LSD = 0.2). Pythium root rot (5 vs. 12% roots infected; LSD = 4) and Rhizoctonia root rot (Haun 0.4 vs. 1.3; LSD = 0.6) were less prevalent and damaging in plowed than in minimum-till plots. Take-all (1–2% of roots) and dryland root rot (40–50% of plants) did not differ among treatments. Plants in plowed soil had 20% more roots (15 vs. 12 roots at 3-cm depth) and were taller (35 vs. 24 cm) than plants in minimum-till soil on 15 May. Tillering was variable (*data not shown*) and grain yields (Table 2) did not differ among tillage treatments.

1991–1992. *Crop sequences without aldicarb.* Root damage ratings from *H. avenae* on 4 May (Table 5) were high in annual wheat treatments (T1 and T2) and intermediate in the wheat-fallow (T3), wheat-pea (T6), and wheat-barley-fallow (T5) sequences. Damage ratings were lowest in treatments where hosts had not been present for 2 yr or longer (T4, T7, T8, and T9). Grass weeds in alfalfa (T10) contributed to an increase in damage to the following wheat crop (13 and 65% damaged plants from weed-free [T9] and weedy [T10] alfalfa, respectively). These relationships among crop sequences for percentages of plants affected by *H. avenae* were comparable to those for root damage ratings by this nematode. An exception occurred in the bluegrass-wheat (T11) sequence, where the incidence of plants affected by *H. avenae* was intermediate but the severity of damage was consistently low.

Take-all was more prevalent and severe ($P < 0.05$) in annual wheat (T1 and T22) and wheat following weedy alfalfa (T10) than in wheat following host-free (T3, T4, T5, T6, T7, T8, and T9) or bluegrass (T11) sequences (Table 6). Dryland root rot was more prevalent ($P = 0.01$) in annual wheat in plowed soil (T1) than in all other treatments. Although treatment differences for Pythium and Rhizoctonia root rots were significant, no patterns of disease incidence or severity relative to crop sequences were apparent.

H. avenae damage and Rhizoctonia root rot were negatively correlated ($P = 0.01$, $r = -0.37$) during early spring (29 March) but were not correlated ($P = 0.27$) during late spring (4 May). Pythium root rot was negatively correlated with *H. avenae* during both sampling dates (early spring $P = 0.02$, $r = -0.35$; late spring $P < 0.001$, $r = -0.50$). A positive correlation between Rhizoctonia root rot and Pythium root rot occurred at both sampling dates (early spring $P = 0.005$, $r = 0.41$; late spring $P = 0.01$, $r = 0.38$).

All growth and development parameters examined were affected by crop sequence (Table 7). Fewest roots occurred in annual wheat (T1 and T2), wheat following bluegrass (T11), and wheat following barley and fallow (T5). Plant height, development (Haun growth stage), and tillering were also less for annual wheat (T1 and T2) and wheat following bluegrass (T11) than for other treatments.

Annual wheat (T1 and T2) produced less grain than wheat in all other sequences (Table 2). Plowing or minimum-till soil prior to planting annual wheat had no effect on yield. Yield of wheat following 3 yr of alfalfa was higher when alfalfa was weed-free (T9) than when it was contaminated by grasses (T10). Wheat following fallow (T3, T4, and T5), peas (T6 and T7), rape (T8), or bluegrass (T11) resulted in highest yields.

Wheat yield was negatively correlated with percentage of plants affected by *H. avenae* during early spring ($P = 0.002$, $r = -0.45$) and late spring ($P = 0.02$, $r = -0.33$) and by take-all during late spring ($P < 0.001$, $r = -0.48$). Similar negative relationships with yield were present for *H. avenae* damage ratings in early spring ($P < 0.001$, $r = -0.45$) and late spring ($P < 0.001$, $r = -0.54$) and by take-all in late spring ($P < 0.001$, $r = -0.54$). Multiple regression indicated that the strongest determinant of yield was combined damage from cereal cyst nematode and take-all ($P < 0.001$, $r = -0.55$).

Yield was positively correlated with all plant growth parameters ($P < 0.002$, r

Table 7. Winter wheat growth and development in 11 crop sequences during 1992

Sampling date Parameter	Aldicarb[y] (+ or −)	Crop sequence[z] 1	2	3	4	5	6	7	8	9	10	11	LSD ($P = 0.05$)
29 March													
Plant height (cm)	Pooled	18.9	18.7	24.6	26.2	25.1	24.5	25.7	26.1	27.0	24.0	20.0	2.5
Haun growth stage	Pooled	4.6	4.4	5.3	5.4	5.4	5.4	5.4	5.5	5.3	5.2	4.8	0.3
Percent plants with tiller													
T_1	−	0	6	15	50	29	56	44	48	42	33	25	26
	+	25	10	30	58	38	46	31	67	48	54	25	33
T_2	−	33	71	92	98	92	92	100	100	98	83	75	20
	+	81	71	94	98	90	96	98	100	98	100	77	18
T_3	−	44	33	100	100	100	98	100	100	100	85	63	28
	+	85	54	100	100	96	98	100	100	98	98	65	24
T_4	Pooled	1	1	9	16	10	11	11	13	4	9	3	ns
Root axes at 3-cm depth	−	8.6	11.3	12.8	18.0	12.1	15.5	17.2	17.0	16.0	14.8	12.8	4.1
	+	9.4	12.5	12.1	14.8	12.0	12.6	13.9	17.2	15.8	15.9	11.0	3.7
Root axes at 5-cm depth	−	4.8	7.0	7.5	11.5	6.6	10.1	11.7	12.0	11.2	9.2	7.4	2.8
	+	5.8	8.7	7.1	9.6	7.4	8.3	8.6	10.3	9.6	10.6	6.3	2.0
4 May													
Tillers/plant	Pooled	2.8	2.1	4.0	4.0	3.8	4.5	5.0	4.4	4.6	4.4	4.4	0.6

[y] Data from aldicarb-treated and untreated plots were pooled when the treatment effect and crop × aldicarb interaction did not differ significantly at $P = 0.05$.

[z] See Table 1 for description of crop sequences in the 11 treatments.

= 0.45–0.69). Among the plant growth and development parameters measured, yield was most correlated ($P < 0.001$, $r = -0.71$) with combined influences of root numbers 3 cm below the caryopsis during seedling growth and numbers of tillers on mature plants. Numbers of seedling roots were most negatively correlated ($P < 0.001$, $r = -0.63$) with combined damage from *H. avenae* and Pythium root rot. Numbers of tillers with heads were most negatively correlated ($P < 0.001$, $r = -0.66$) with combined damage from *H. avenae* and take-all.

Aldicarb. On 29 March 1992, root damage severity ratings for *H. avenae* were minimal and did not differ among aldicarb treatments (Table 5). The nematicide also did not reduce the incidence of damaged plants. However, aldicarb significantly reduced both the incidence and the severity of *H. avenae* damage in assessments made on 4 May (i.e., after aldicarb reapplication in March). The beneficial effect of aldicarb was most apparent in treatments where hosts of *H. avenae* had been present within the previous 2 yr (e.g., annual wheat [T1], grass-contaminated alfalfa [T10], and wheat-fallow [T3], wheat-pea [T6], and wheat-barley-fallow [T5] sequences).

Aldicarb did not affect the incidence or severity of Rhizoctonia root rot, Pythium root rot, or take-all during the early spring (*data not shown*). In contrast, percentages of roots and plants affected by each fungal disease were nearly always higher in aldicarb-treated than in untreated soil on 4 May, and differences were significant ($P < 0.05$) for incidence of Rhizoctonia and Pythium root rots and for severity of Rhizoctonia root rot (Table 6). Crop sequence × aldicarb interactions were not significant ($P < 0.05$) for any disease parameter measured. Collectively for the 11 crop sequences, the incidence of all diseases was higher in aldicarb-treated plots than in comparable plots without aldicarb. The increase in incidence was 87% ($P = 0.01$), 36% ($P = 0.02$), 54% ($P = 0.86$), and 83% ($P = 0.57$), respectively, for Rhizoctonia root rot, Pythium root rot, take-all, and dryland root rot.

Plant tiller and root numbers, but not plant development stage or height, were increased by treatment of soil with aldicarb (Table 7). Grain yield was not improved by aldicarb (Table 2).

Influence of break crops or fallow on root damage and yield. Crop sequences following wheat or grass-contaminated alfalfa were grouped by years of breaks from a Poaceae host of cereal cyst nematode and fungal root pathogens. Bluegrass (T11) was not included in this assessment because it did not serve as an adequate host for the nematode. Incidence and severity of damage from cereal cyst nematode decreased with increasing years of breaks (Table 8). Rhizoctonia root rot occurred more frequently on wheat following 1- or 2-yr breaks from wheat than on wheat following wheat during 1989, 1990, and 1992. A similar trend occurred for Pythium root rot but not for take-all or dryland root rot. Severity ratings for all fungal diseases were not affected by break periods. Although yield of grain was always increased by a break between wheat and previous Poaceae plants, the response did not appear related to length of the break.

Relationship of nematode population to wheat yield. In the 1990 wheat treatments, the number of *H. avenae* eggs plus juveniles from cysts following harvest was higher in minimum-till annual wheat (T2) than in the three other treatments (T1, T3, and T6). Nematode numbers were correlated positively with nematode damage ratings during the spring ($P = 0.03$, $r = 0.74$) and negatively with grain yield ($P = 0.04$, $r = -0.96$; Fig. 1).

DISCUSSION

Winter wheat was more healthy and productive in all sequences containing a break between winter wheat crops than with wheat produced annually. This observation in soil infested with *H. avenae* and multiple pathogenic fungi supports concepts developed independently for each of these pests (1,7,11,12,19, 25,27). Rivoal and Saar (25) determined that yield constraints from *H. avenae* could be minimized by rotations that included winter wheat less than 50 and 25% of the time on loams and sands, respectively. In this study, yields were acceptably stable when winter wheat was produced during alternate years on a poorly drained silty clay loam. Based on yields from 1992, a 1-yr break from a grass host was as adequate as a 3-yr break for maintaining winter wheat yields, although a 2 yr or longer break was necessary to reduce nematode damage. The length of break may be more critical in a sandier soil or with spring-planted cereals (23).

In view of the crop sequence effect demonstrated in this study, severe damage from *H. avenae* alone or in combination with other pathogens is not likely to become widespread on nonirrigated fields of winter wheat in the Pacific Northwest because most wheat is produced on loams and very little is produced as an annual crop. Chronic damage from *H. avenae* and other pathogens will continue in most infested fields. Our study demonstrated that when present, *H. avenae* will suppress yields further whenever wheat is grown annually. This is of concern because efforts to reduce soil erosion are contributing to an increasing production of spring wheat annually, and spring cereals are damaged more than winter cereals by *H. avenae*.

Agricultural equipment, cattle, plant products (seed potatoes, mint rootstock, ornamentals), and other products with

Table 8. Root damage and grain yield for winter wheat produced after a 0-, 1-, 2-, or 3-yr break from Poaceae hosts of cereal cyst nematode and fungal root pathogens

Disease and yield parameters	1989			1990			1991	1992				
	0	2	LSD ($P = 0.05$)	0	1	LSD ($P = 0.05$)	0	0	1	2	3	LSD ($P = 0.05$)
Incidence (% plants)												
Cereal cyst nematode	95	79	10	54	12	16	83	88	86	42	13	17
Rhizoctonia root rot	42	60	13	47	66	11	0	3	12	6	2	8
Pythium root rot	...	...	...	19	29	7	42	28	37	36	27	ns
Dryland root rot	...	...	...	4	3	ns	27	14	9	8	2	ns
Take-all	...	...	...	1	0	ns	6	11	2	0	0	9
Severity[z]												
Cereal cyst nematode	1.7	1.0	0.3	0.7	0.1	0.4	3.0	3.0	1.8	0.5	0.1	0.9
Rhizoctonia root rot	0.8	0.9	ns	0.9	0.5	ns	0	0	0.2	0.1	0	ns
Pythium root rot	...	...	...	5.2	3.8	ns	8.5	2.5	3.4	2.7	2.9	ns
Dryland root rot	...	...	...	2.5	1.3	ns	43.8	...	...	...	...	...
Take-all	...	...	...	1.6	0	ns	1.7	1.6	0.1	0	0	1.4
Grain yield												
kg/ha	4,950	8,066	1,275	4,738	6,894	799	3,005	4,623	6,608	6,730	6,352	538
Percent increase over annual wheat		63			46				43	46	37	

[z] See Tables 3 and 6 for rating systems.

adhering soil are regularly transported long distances from highly infested soils in Oregon (Union and Washington counties) to production fields in Washington, Oregon, and Idaho. Trees and ornamental plants are distributed nationally from regions in Oregon known to contain *H. avenae*. Thus, the potential exists for *H. avenae* to be spread throughout the Pacific Northwest and nation. For instance, we recovered cysts of *H. avenae* from tare soil in a Union County potato storage building and from tare soil and seed potatoes being discharged from a truck into a Morrow County field 160 km from where the potatoes had been grown and stored over winter. We also collected *H. avenae* from soil dislodged into a Umatilla County field by a wheat seed drill used previously in Union County. There had been no previous reports of *H. avenae* being present in Morrow or Umatilla counties. On irrigated fields, soil erosion from wind is sometimes reduced by planting wheat as a windrow (rows 1 m apart) during the autumn and then potatoes or onions during the spring. The cereal crop is allowed to mature. *H. avenae* hosts such as wheat and corn are then rotated with potatoes, onions, or alfalfa on these fields, thereby shortening the effective rotation of nonhosts for *H. avenae*. Soil is also moved by wind from irrigated to adjacent nonirrigated wheat fields, providing another avenue (23) for disseminating cyst nematodes through the region.

Wheat yields during 1990 and 1992 were negatively correlated with damage by *H. avenae* and take-all. Sources of resistance against the nematode are known (9,21,24), but not against *G. g. tritici* (28). Chemical and cultural control strategies are not adequate for either pathogen in the United States. Biological controls for each pathogen are known (6) but are not commercially available, and information about the efficiency of biological controls is lacking for plants affected simultaneously by two or more pathogens. Therefore, at this time it appears that wheat affected by combinations of these pathogens will be controlled most effectively by rotating wheat with nonhost crops or fallow.

Yield was not enhanced by application of aldicarb during 1992. A similar response occurred in a satellite study conducted on second-year annual wheat at the experimental site during 1988 (31). In contrast, aldicarb treatment increased yield of spring and winter wheat by 29 and 25%, respectively, during 1987 at a location 20 km from the site of this experiment (32). Several differences in these responses were noted. Severity of Pythium and Rhizoctonia root rots increased as damage from *H. avenae* was reduced in the present and earlier experiment at the site used for this study. Thus, the lack of an aldicarb effect on wheat yield appeared to be a response to disease trading. In contrast, take-all was the only fungal root pathogen observed at the other site (32) and its incidence in the earlier and present studies was not significantly affected by application of aldicarb. The increase in wheat yield at the other site appeared to be a response to reduced damage from *H. avenae* without compensatory increase in damage from fungal pathogens.

In view of large differences in the incidence and damage ratings from *H. avenae* during 1992, it was surprising that wheat yields were equivalent in all sequences involving a 1-, 2-, or 3-yr break from wheat. Barley was included in a cropping sequence because it is less susceptible than wheat to *H. avenae* (16). An earlier investigation at a nearby location indicated that yields of winter and spring barley were not improved by application of aldicarb, whereas winter and spring wheats were highly responsive to this nematicide (32). However, the barley-fallow sequence caused as much nematode damage to the subsequent wheat crop as the wheat-fallow sequence. Since barley is a host for *H. avenae*, it may perpetuate the potential for damage as well as wheat. Thus, a fallow or nonhost break between barley and wheat appears necessary. Inserting a nonhost such as rape, peas, or alfalfa between wheat crops was as effective as fallow in reducing *H. avenae* damage to wheat roots and increasing yield. Inadequate control of grassy weeds in a nonhost crop (alfalfa) reduced some of the benefit of growing a nonhost crop and contributed to an intermediate level of root damage and yield loss. Surprisingly, bluegrass did not sustain populations of *H. avenae* (*data not shown*), and while some minor damage was observed on wheat roots, yields were equivalent to preceding wheat with fallow or a non-Poaceae crop. Further evaluations are required to determine the host range and reproductive efficiencies for *H. avenae* on various hosts in Oregon. The identity of the pathotype and host specificity for *H. avenae* in eastern Oregon are unknown.

Many interactions were evident among root diseases caused by soilborne fungi and by *H. avenae*. Pythium root rot was often more prevalent and damaging in rotations than in annual wheat or in wheat following bluegrass or weedy alfalfa. The opposite effect occurred with *H. avenae*.

All annual wheat plants were affected by *H. avenae* but the severity of root damage was greater in minimum-till than in plowed soil, an effect opposite that reported from Australia (27). Wheat roots were also more heavily damaged by take-all and Pythium root rot in minimum-till than in plowed soil, but the reverse was true for dryland root rot. Resultant yields in the two tillage treatments were equivalent, reflecting the compensatory responses of root parasites and pathogens present in this soil. The complexity of interactions in soils infested with multiple pathogens or parasites suggests that it will be difficult to develop predictive guidelines for specific crop rotations unless disease potential is known.

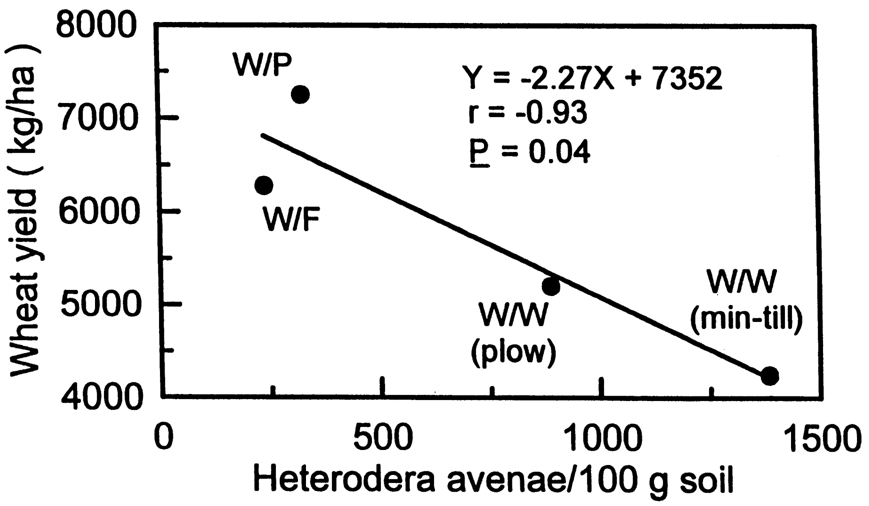

Fig. 1. Relationship between 1990 winter wheat yield and *Heterodera avenae* density (eggs and juveniles from cysts) after harvesting wheat following wheat (W/W, annual wheat) in plowed or minimum-till soil or wheat following summer fallow (W/F) or peas (W/P) in plowed soil.

ACKNOWLEDGMENTS

We thank John Cuthbert for donating land, equipment, and assistance for this experiment; Oregon State University staff for support services; and the Oregon Wheat Commission and USDA-CSRS-Pacific Northwest Regional STEEP Research Program for financial assistance.

LITERATURE CITED

1. Brown, R. H. 1985. The selection of management strategies for controlling nematodes in cereals. Agric. Ecosyst. Environ. 12:381-388.
2. Caswell, E. P., Thomason, I. J., and McKinney, H. E. 1985. Extraction of cysts and eggs of *Heterodera schactii* from soil with an assessment of extraction efficiency. J. Nematol. 17:337-340.
3. Christen, O., Sieling, K., and Hanus, H. 1992. The effect of different preceding crops on the development, growth and yield of winter wheat. Eur. J. Agron. 1:21-28.
4. Cook, R. 1975. Invasion and development of the cereal cyst nematode *Heterodera avenae* in

roots of barley infected by the take-all fungus *Gaeumannomyces graminis*. Ann. Appl. Biol. 81:349-357.
5. Cook, R. J. 1990. Diseases caused by root-infecting pathogens in dryland agriculture. Adv. Soil Sci. 13:215-239.
6. Cook, R. J., and Baker, K. F. 1983. The Nature and Practice of Biological Control of Plant Pathogens. American Phytopathological Society, St. Paul, MN.
7. Cook, R. J., and Veseth, R. J. 1991. Wheat Health Management. American Phytopathological Society, St. Paul, MN.
8. DeBoer, R. F., Kollmorgen, J. F., Macauley, B. J., and Franz, P. R. 1991. Effects of cultivation on Rhizoctonia root rot, cereal cyst nematode, common root rot and yield of wheat in the Victorian Mallee. Aust. J. Exp. Agric. 31:367-372.
9. Eastwood, R. F., Lagudah, E. S., Appels, R., Hannah, M., and Kollmorgen, J. F. 1991. *Triticum tauschii*: A novel source of resistance to cereal cyst nematode (*Heterodera avenae*). Aust. J. Agric. Res. 42:69-77.
10. Fenwick, D. W. 1940. Methods for the recovery and counting of cysts of *Heterodera schactii* from soil. J. Helminthol. 18:155-172.
11. Fisher, J. M., and Hancock, T. W. 1991. Population dynamics of *Heterodera avenae* Woll. in South Australia. Aust. J. Agric. Res. 42:53-68.
12. Gair, R., Mathias, P. L., and Harvey, P. N. 1969. Studies of cereal nematode populations and cereal yields under continuous or intensive culture. Ann. Appl. Biol. 63:503-512.
13. Garrett, S. D. 1934. Effect of crop rotation on the eelworm (*Heterodera schachtii*) disease of cereals. J. Dep. Agric. South Aust. 37:984-987.
14. Jensen, H. J., Eshtiaghi, H., Koepsell, P. A., and Goetze, N. 1975. The oat cyst nematode, *Heterodera avenae*, occurs in oats in Oregon. Plant Dis. Rep. 59:1-3.
15. Klepper, B., Rickman, R. W., and Peterson, C. M. 1982. Quantitative characterization of vegetative development in small cereal grains. Agron. J. 74:789-792.
16. Meagher, J. W. 1972. Cereal cyst nematode (*Heterodera avenae* Woll.). Studies on ecology and content in Victoria. Victoria Dep. Agric. Tech. Bull. 24.
17. Meagher, J. W., Brown, R. H., and Rovira, A. D. 1978. The effects of cereal cyst nematode *Heterodera avenae* and *Rhizoctonia solani* on the growth and yield of wheat. Aust. J. Agric. Res. 29:1127-1137.
18. Meagher, J. W., and Chambers, S. C. 1971. Pathogenic effects of *Heterodera avenae* and *Rhizoctonia solani* and their interaction on wheat. Aust. J. Agric. Res. 22:189-194.
19. Meagher, J. W., and Rooney, D. 1966. The effect of crop rotations in the Victorian Wimmera on the cereal cyst nematode (*Heterodera avenae*), nitrogen fertility and wheat yield. Aust. J. Exp. Agric. Anim. Husb. 6:425-431.
20. Mojtahedi, H., Santo, G. S., Hang, A. N., and Wilson, J. H. 1991. Suppression of root-knot nematode populations with selected rapeseed cultivars as green manure. J. Nematol. 23:170-174.
21. O'Brien, P. C., and Fisher, J. M. 1974. Resistance within wheat, barley and oat cultivars to *Heterodera avenae* in South Australia. Aust. J. Exp. Agric. Anim. Husb. 14:399-404.
22. Patel, B. K. 1983. Interrelationships between soil-borne pathogens on *Triticum aestivum*. Ph.D. thesis. University of Adelaide, South Australia.
23. Rivoal, R., and Cook, R. 1993. Nematode pests of cereals. Pages 259-303 in: Plant Parasitic Nematodes in Temperate Agriculture. K. Evans, D. L. Trudgill, and J. M. Webster, eds. CAB International, Wallingford, England.
24. Rivoal, R., Doussinault, G., and Hulle, M. 1990. Influence of *Heterodera avenae* on winter wheat in France: Experiments with resistant and susceptible varieties. Ann. Appl. Biol. 116:537-548.
25. Rivoal, R., and Saar, E. 1987. Field experiments on *Heterodera avenae* in France and implications for winter wheat performance. Nematologica 33:460-479.
26. Rovira, A. D., and Ridge, E. H. 1979. The effect of methyl bromide and chloropicrin on some chemical and biological properties of soil and on the growth and nutrition of wheat. Pages 231-250 in: Soil Disinfestation. D. Mulder, ed. Elsevier, Amsterdam.
27. Rovira, A. D., and Simon, A. 1982. Integrated control of *Heterodera avenae*. EPPO Bull. 12:517-523.
28. Scott, P. R. 1981. Variation in host susceptibility. Pages 219-236 in: Biology and Control of Take-all. M. J. C. Asher and P. J. Shipton, eds. Academic Press, London.
29. Shahina, F., and Maqbool. 1990. Host range studies of *Heterodera zeae* and *H. avenae*. Pak. J. Nematol. 8:79-85.
30. Simon, A., and Rovira, A. D. 1982. The relation between wheat yield and early damage of roots by cereal cyst nematode. Aust. J. Exp. Agric. Anim. Husb. 22:201-208.
31. Smiley, R. W., Biddle, J. A., Ott, S., and Cook, G. H. 1992. Control of cereal cyst nematode with Temik. Fungic. Nematicide Tests 47:168.
32. Smiley, R. W., Ingham, R. E., and Cook, G. H. 1992. Control of cereal cyst nematode with in-furrow and seed treatments. Fungic. Nematicide Tests 47:167.
33. Steinbrenner, K., Hoflich, G., and Sachse, B. 1984. Influence of cereal concentrations in the crop rotation on the crop yield and the infestation of the cereal plants with *Pseudocercosporella herpotrichoides* (Fron) Deighton and *Gaeumannomyces graminis* (Sacc.) Arx et Olivier and the contamination of soil with *Heterodera avenae* Woll. as demonstrated by the results of the international crop rotation trial at Dewitz. Arch. Acker. Pflanzenbau Bodenkd. 28:553-559.
34. Vyn, T. J., Sutton, J. C., and Raimbault, B. A. 1991. Crop sequence and tillage effects on winter wheat development and yield. Can. J. Plant Sci. 71:669-676.
35. Williams, T. D., and Salt, G. A. 1970. The effects of soil sterilants on the cereal cyst nematode (*Heterodera avenae* Woll.), take-all (*O. graminis* Sacc.) and yield of spring wheat and barley. Ann. Appl. Biol. 66:329-338.
36. Winslow, R. D. 1954. Provisional list of host plants of some root eelworms (*Heterodera* spp.). Ann. Appl. Biol. 41:591-605.