Increased Take-all of Wheat with Direct Drilling in the Pacific Northwest

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ABSTRACT

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Take-all, caused by *Gaeumannomyces graminis* var. *tritici*, occurred more frequently or more severely on consecutive wheat crops seeded directly (no-till) into the undisturbed stubble than on wheat seeded into plots that had been prepared by moldboard or disk plowing. Increased take-all with direct drilling was found at each of three locations in Washington (where climate, soil type, and management all were different), in two seasons, and in both spring and winter wheat. Differences in soil temperature and soil moisture between tilled and no-tilled plots could not account for the greater take-all with direct drilling. When soil cores (15 cm diam, 17 cm deep) from a no-tilled wheat plot (naturally infested with *G. graminis* var. *tritici*) were either left undisturbed or given simulated tillage, planted to wheat, and incubated under the same conditions, take-all was greatest in the undisturbed cores. Differences in nutrition of the host plant likewise could not explain the effect; fertilizing plots with a mixture of nitrogen, phosphorus, potassium, sulfur, and trace minerals suppressed take-all more than fertilizing with only nitrogen and sulfur, but suppression was similar in tilled and no-tilled plots. Several times more infested debris was recovered by sieving from no-tilled plots than from tilled plots just before sowing the next crop, and infested fragments from the no-tilled plots generally were larger. When plots were fumigated with methyl bromide and the take-all pathogen then introduced to provide the same amount of inoculum in all plots, disease severity was the same whether the plots were tilled or not. Disease with direct drilling apparently was increased because of more infested debris and because the inoculum source was ideally positioned for infection of the wheat crop.

Additional key words: conservation tillage, root disease, soilborne pathogen, *Triticum aestivum*.

Reduced or no tillage (conservation tillage) for soil erosion control has not been accepted by the majority of wheat farmers in the Pacific Northwest, in part because it often results in lower yields (4,17). The responsible factors are undoubtedly complex but may include increased damage caused by *Pythium* spp. (9), phytotoxins released from decomposing crop residues (4,10), and insect pests (1).

During the 1976–1977 growing season, we observed mild to severe take-all, caused by *Gaeumannomyces graminis* (Sacc.) v. Arx & Olivier var. *tritici* Walker, on spring and winter cereals (wheat and barley) in direct-drilled (no-tilled) fields near Pullman, WA. Take-all was not evident in neighboring fields where cereals had been sown into conventionally prepared (moldboard-plowed) seedbeds. Typically, take-all has occurred on irrigated wheat but has been rare on rainfed wheat near Pullman (7,8). Under field conditions in Europe, take-all either was less (3,13,16) or was not affected (15,20) by direct drilling. However, Ferraz (11) reported that under glasshouse conditions, the incidence of take-all was generally higher after simulated direct drilling than after simulated plowing. The apparent conflicting reports from other wheat-growing areas, and our preliminary observations indicating that direct drilling favors take-all, prompted this study on (i) the effect of no tillage (direct drilling) vs. moldboard or disk plowing on the incidence and severity of take-all of wheat (*Triticum aestivum* L.) in field plots and (ii) the basis for the difference, if any, in occurrence of take-all between the two systems of soil, residue, and crop management.

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MATERIALS AND METHODS

Location of field plots, tillage treatments, seeding, plot care, and harvest. Field plots were established with irrigated wheat at Lind and with rainfed (natural rainfall only) wheat at Puyallup (about 100 cm per year) and Pullman (about 50 cm per year). The Puyallup site, on Farm 5 of the Western Washington Research and Extension Center, has a humid, mild climate and take-all is commonly severe. The plot site, which had been used for many years to grow small fruits, was cropped to wheat in 1973, 1974, and 1975, prior to these experiments. The soil is a Pilchuck loamy fine sand, naturally acid (pH 4.5–5.0), and had been limed periodically in past years. The Lind site, on the Washington State University Experiment Station, is in the semiarid area of eastern Washington, and the plot site had been in continuous irrigated wheat for 9 yr. The soil is a Ritzville silt loam (pH 7.5). The Pullman site, on the Palouse Conservation Field Station, is in the subhumid annually cropped Palouse region of eastern Washington and had been rotated between winter wheat and peas for several years before our study. The soil is a Palouse silt loam (pH 6.0). These locations represent the diversity of soils, climate, topography, management, and cropping systems in which wheat is produced in the Pacific Northwest (8).

At each location, the plot area was divided into three, four, or six replicates. Each of these was split longitudinally and used as adjacent split-blocks for tilled and no-tilled treatments. The dimensions of each split-block for each location, crop, and year were: Lind, winter wheat (1976–1977), 2.4 × 36.6 m; Lind, spring wheat (1977), 3.7 × 36.6 m; Pullman, spring wheat (1976), 5.0 × 26.2 m; Pullman, winter wheat (1976–1977), 5.0 × 26.2 m; and Puyallup, winter wheat (1976–1977), 3.1 × 36.6 m. Primary tillage of tilled split-blocks was completed as soon as possible after harvest. For winter and spring wheat at Lind, the soil was tilled twice about 15 cm deep with an offset disk. One week later, the soil was disked again and then rod-weeded (5). A skew treader (offset, passively driven spiked disks) was also used for the spring wheat plot at Lind 1 wk before seeding. At Puyallup, a tandem disk was used to a depth of 15 cm in August and again 2 wk before seeding. For spring wheat at Pullman, a moldboard plow was used to a depth of 16 cm in the fall of 1975. For winter wheat at Pullman, the tilled areas of the spring wheat experiment were disked four times to a depth of 12.5 cm and rolled 2 wk later. At all locations, a harrow was used on the tilled areas to smooth the soil surface just before seeding.

All plots were seeded with the same drill fitted with double-disk openers for 25-cm row spacings and equipped with fluted coulters for direct drilling into no-tilled soil (designed by R. Schirman, Agricultural Research Service, U.S. Department of Agriculture, Pullman). The varieties seeded and the dates and rates of seeding were: Lind, Nugaines winter wheat, 23 September 1976, 80 kg/ha; Lind, Fielder spring wheat, 21 March 1977, 90 kg/ha; Puyallup, Yamhill winter wheat, 22 September 1976, 75 kg/ha; Pullman, Fielder spring wheat, 11 May 1976, 67 kg/ha; and Pullman, Nugaines winter wheat, 3 November 1976, 75 kg/ha.

Nitrogen was applied in spring to the plots at Pullman as a 1:3 (w/w) mixture of $(NH_4)_2SO_4$ and NH_4NO_3 to provide N at 68 and 78 kg/ha for spring and winter wheat, respectively. The plots at Lind and Puyallup received special fertilizer treatments (described later). All fertilizers were surface-broadcast; for tilled areas, the fertilizers were mixed into the surface 10–12 cm of soil.

Glyphosate [N-(phosphonomethyl)glycine] herbicide was applied at 1 L/ha as necessary before seeding and also before emergence in some locations. Broadleaf weeds were controlled at Pullman and Lind with metribuzin [4-amino-6-tertbutyl-3(methylthio)-as-triazin-5(4H)-one] or 2,4-D (2,4-dichlorophenoxyacetic acid), applied in the spring, and at Puyallup with diuron [3-(3,4-dichlorophenyl)-1,1-dimethylurea], applied in the fall after the wheat had emerged. Grassy weeds were removed from the growing crop by hand, as necessary.

The plots were harvested either by hand (three rows 5 m long from the center of each plot) or machine (a swath at least 1.5 m wide from the center of each plot).

Effects of tillage on wheat in the absence of root diseases and weeds. Soil fumigation was used to compare the effects of tillage and no tillage on wheat growth without root diseases or weeds. At Lind, replicate blocks were divided in half at right angles to their long axis and alternate halves were fumigated, giving a checkerboard pattern of fumigated and nonfumigated areas. At Pullman, randomly assigned subplots (10 × 6.5 m) within replicate blocks were fumigated. Each area to be fumigated was covered with a sheet (4 mil) of polyethylene, the edges of which were buried in trenches. Methyl bromide was introduced under each sheet at the rate of 450 kg/ha. Covers were removed after 1–3 days and the plots were seeded 1–4 days later.

Separation of direct effects of tillage on *G. graminis* var. *tritici* from effects on the environment occupied by the pathogen. Field and greenhouse trials were conducted to determine whether the effects of no tillage on take-all related to the physical environment of soil managed by a no-till system. In the trials at Lind in both 1976–1977 and 1977 and at Pullman in 1976–1977, the take-all fungus was introduced at seeding into half of each fumigated and nonfumigated area by drilling oat kernels infested with *G. graminis* var. *tritici* into the seed furrow (6). This provided subplots with native inoculum, native inoculum plus introduced inoculum, "no inoculum" (fumigated plots), and introduced inoculum (fumigated/reinfested plots). If take-all is favored by the physical environment of no-tilled soil, then it should be more severe in no-tilled than in tilled subplots that are fumigated, then reinfested.

For the greenhouse experiment, 60 soil cores were collected in June 1977 from Farm 5, Puyallup, from a site where take-all had been severe in the previous winter wheat crop. The site had not been tilled at the time the cores were taken. Each core was collected by placing a cylindrical can (15 cm i.d., 17 cm long) over the undisturbed stubble of several naturally infected wheat plants, forcing the open top of the can downward into the soil, then removing the can and its contents. The bottom of each can was then removed to expose the original soil surface. Twenty cores were left undisturbed, 20 were sawed in half and the top inverted over the undisturbed bottom half, and 20 were removed from their containers, stirred for several minutes, then placed in paper bags. All cores, including those in the bags, were placed in an outdoor sheltered area (lathhouse constructed from 5-cm-wide laths spaced 5 cm apart) and watered to maintain moisture. After 4 wk, the contents of each bag were mixed for 1 min in a twin-shell blender, placed in a new can, and returned to the lathhouse. All cans of soil were then seeded with 10 seeds of Yamhill winter wheat and thinned to five plants per can 2 wk after emergence. The cans were arranged in a completely randomized design during incubation. The soil was watered once with full-strength Hoagland's solution and thereafter weekly with tap water.

Recovery of infested debris from soil. The amount of inoculum (residue infested with *G. graminis* var. *tritici*) was determined by sieving debris from a given volume of soil taken from three areas (each about 2–3 m^2 × 15 cm deep) in tilled and three corresponding areas in adjacent no-tilled sites of the 1976–1977 Lind winter wheat experiment where take-all had been severe. The tilled plots had been rotovated 10 cm deep on 5 August, 27 August, and 21 September 1977. The debris was recovered 7 October 1977 by passing the top 15 cm of soil from each tilled and corresponding no-tilled subplot through a screen 1.25 × 1.25 cm and then through a screen 0.63 × 0.63 cm. Debris not obviously of wheat origin (eg, weed fragments) was removed by hand. Wheat crowns (including attached roots when present) from each screening were weighed. Random crown fragments were also bioassayed for the presence of *G. graminis* var. *tritici* by placing one crown with root end up into a Conetainer (Ray Leach Container Co., Canby, OR) that had been filled three-quarters with acid-washed sand, then covering the crown with 15 g of sand. Two seeds of Nugaines wheat were placed on top of the sand in each tube and covered with more sand. Control tubes were filled with sand only. All tubes were watered initially with full-strength Hoagland's solution and incubated in a greenhouse at 10–15 C. They were watered to saturation every 3 days with deionized water and allowed to drain freely. After 30 days, the seedlings were removed and examined for infection by *G. graminis* var. *tritici*.

Effect of host nutrition on development of take-all. Interactions between host nutrition (18) and tillage in the development of take-all were examined at Lind and Puyallup. For winter wheat at Lind, each tilled and no-tilled split-block within each fumigated and nonfumigated area was further divided into subplots that received either nitrogen and sulfur only (check), provided by $(NH_4)_2SO_4$, NH_4NO_3 (1:3, w/w), or a "complete" treatment, ie, nitrogen and sulfur plus $ZnSO_4$, KCl, Na_2MoO_4, boreated $CaSO_4$, and 11:55:0 (N:P:K) to supply 11.2 kg of Zn/ha, 78.5 kg of K_2O/ha, 0.5 kg of Mo/ha, 0.1 kg of B/ha, and 67.3 kg of P_2O_5/ha. The fertilizer treatments were applied at the rates of 170 kg of N/ha and 120 kg of S/ha. One-third of each treatment was applied before planting and the remainder in the spring.

For the spring wheat trial at Lind (1977), each fumigated and nonfumigated area (including both tilled and no-tilled plots) was divided into three 7.3 × 6.1 m subplots that received, at random, the same fertilizer treatments applied to the winter wheat plot except that the rate of N was 160 kg/ha. For winter wheat at Puyallup (1976–1977), the entire plot area received superphosphate (P_2O_5) at 210 kg/ha in August and then, just before seeding, each tilled and no-tilled split-block was divided into subplots that received either fumigation and the complete fertilizer treatment or the complete fertilizer treatment only. There were two applications at Puyallup to give a total of 170 kg of N/ha.

Plant samples for chemical analyses were collected from the winter wheat plot at Lind on 3 June 1977. About 300 g of flag leaf tissue was taken from plants in the noninoculated area of fumigated plots, washed in Basic H surfactant (Shaklee Corporation, Emeryville, CA), rinsed twice in deionized water, dried at ..., ground, passed through a 6.35-mm sieve, and analyzed for NH_4-N and PO_4-P in a Technicon Autoanalyser II (Technicon Industrial Systems, Tarrytown, NY 10591).

Disease assessment. The incidence of take-all generally was measured as the percentage of infected plants based on at least 25 plants selected at random per treatment and replicate. An exception was the spring wheat at Lind, where the incidence was measured as the percentage of infected plants in eight 25-cm lengths of row selected at random from the second and sixth rows in each treatment per replicate. Disease severity was assessed on plants sampled in March or April as the number of roots infected per plant. Disease severity was also assessed on samples collected in June or July on a scale of 0–5, with 0 = no roots infected; 1 = less ...% of roots infected, lesions mostly small; 2 = 25–50% of ... nfected, lesions coalesced, plants slightly stunted; 3 = 51–75% of roots infected, multiple lesions on many roots, moderate stunting, slight blackening of stem bases; 4 = 76–100% of roots infected, multiple lesions on most roots, severe stunting, conspicuous blackening of stem bases; and 5 = all roots infected, plants dead or nearly so.

For the bioassay of crown fragments screened from field soil, take-all was measured as the percentage of tubes that contained an infected wheat seedling and disease severity was assessed on the 0–5 scale described above.

For the soil core experiment, the incidence of take-all was measured as the percentage of soil cores with at least one infected plant. Severity was computed as the average number of lesions per

TABLE 1. Incidence and severity of take-all, caused by *Gaeumannomyces graminis* var. *tritici*, and yield or plant height of wheat in tilled and no-tilled natural soil in Washington

Location, crop, year	Incidence (%)[x]		Severity[y]		Yield (kg/ha)		Plant height (cm)	
	Tilled	No-tilled	Tilled	No-tilled	Tilled	No-tilled	Tilled	No-tilled
Pullman, spring wheat, 1976	15[z]	48	0.03[z]	0.15	1,733[z]	958	...	...
Pullman, winter wheat, 1976–1977	38	74	0.5	1.4	4,318	2,384	...	...
Lind, spring wheat, 1977	71	97	2.2	3.8	3,741	2,338	...	...
Puyallup, winter wheat, 1976–1977, March	33	79	1.0	2.6	...	...	33[z]	27
Puyallup, winter wheat, 1976–1977, June	78	90	1.5	2.2	...	...	101	88

[x] Percentage of plants infected in a random sample of at least 25 plants per treatment per replicate.
[y] Rated on a scale of 0–5, where 0 = no roots infected; 1 = less than 25% of roots infected, lesions mostly small; 2 = 25–50% of roots infected, lesions coalesced, plants slightly stunted; 3 = 51–75% of roots infected, multiple lesions on many roots, moderate stunting, slight blackening of stem bases; 4 = 76–100% of roots infected, multiple lesions on most roots, severe stunting, conspicuous blackening of stem bases; and 5 = all roots infected, plants dead or nearly so.
[z] Each value is the mean of three replicates at Pullman, four at Lind, and six at Puyallup. For each location, the differences between treatment means are significant ($P = 0.05$) according to Duncan's multiple range test.

Fig. 1. Growth of irrigated winter wheat at Lind, 1976–1977, as affected by soil fumigation and method of tillage. Upper area, fumigated; lower area, nonfumigated. Left of center, no-tilled; right of center, tilled.

infected plant multiplied by a score based on average lesion size, with 1 = lesions less than 5 mm long, 2 = lesions 5–10 mm, 3 = lesions 11–20 mm, and 4 = lesions greater than 20 mm.

RESULTS

Occurrence of take-all in tilled compared with no-tilled soil with natural inoculum only. There was more take-all in no-tilled than in tilled plots at all three locations, in both seasons, and on both spring and winter wheat (Table 1). The greater amount of take-all with no tillage was apparent both as a greater incidence of infection and as more severe disease on infected plants. Even at low levels of disease, as occurred in the spring wheat plot at Pullman, both incidence and severity of take-all were greater with no tillage than with tillage.

In general, the increased take-all associated with no tillage was noticeable soon after seedling emergence, when stands were obviously poorer and plant vigor was less than in tilled plots (Fig. 1). At Puyallup, the plants were shorter in the no-tilled plots than in the tilled plots (Table 1).

Influence of tillage on wheat in the absence of take-all. In the absence of *G. graminis* var. *tritici*, other soilborne pathogens, and weeds (ie, in fumigated noninfested soil), wheat grew as well or better without tillage as with tillage (Fig. 1) and the yields were similar (Table 2).

Influence of tillage on take-all caused by introduced inoculum. When plots were fumigated with methyl bromide, then reinfested with *G. graminis* var. *tritici* (as oat-kernel inoculum), take-all was uniformly severe regardless of whether the plots were tilled (Table 2). This was true for irrigated spring and winter wheat at Lind and for rainfed winter wheat at Pullman.

The introduction of oat-kernel inoculum into nonfumigated soil increased take-all compared with that in plots containing natural inoculum only (Table 2). In tilled plots, the increase in take-all with introduced inoculum was apparent both as a greater incidence of infection and as more severe disease. In no-tilled plots, introduction of inoculum increased the incidence of infection in spring wheat at Lind but not in winter wheat at Pullman. For both spring wheat at Lind and winter wheat at Pullman, introduction of inoculum resulted in a relatively greater increase in take-all in tilled plots than it did in no-tilled plots. However, the total amount of disease (caused by natural and introduced inoculum combined), whether assessed as incidence or severity, was still greater in no-tilled soil. Only in the winter wheat plots at Pullman did the addition of oat-kernel inoculum result in an amount of take-all in tilled soil equal to that in naturally infested no-tilled soil (Table 2). At the other location (spring wheat at Lind), the incidence and severity of take-all in noninoculated (natural inoculum only) no-tilled plots were greater than in the inoculated (oat-kernel plus natural inoculum) tilled plots (Table 2).

Influence of tillage on inoculum of *G. graminis* var. *tritici*. Twenty-nine percent of the plants in the vigorously disturbed cores had take-all, compared with 57 and 58% for inverted and undisturbed infested cores, respectively. Disease severity (the average number of lesions per infected plant multiplied by a measure of the average lesion size) was 34.1 in undisturbed cores, compared with 2.2 and 11.8 for vigorously disturbed and inverted cores, respectively. Lesions on roots of infected seedlings in undisturbed cores occurred mostly on proximal portions of the root system and usually extended to the crown. In inverted cores, lesions occurred midway along the roots (corresponding to the layer of inoculum), and few were observed near the crown. In vigorously disturbed cores, lesions were scattered throughout the root system of the plants.

About five times (55.7 g vs. 11.3 g) the air-dry weight of crown material was recovered from no-tilled than from tilled (rotovated) areas (Fig. 2). Furthermore, 95% of this material (53.0 g) from the no-tilled plots was retained by a 1.25-cm square screen, compared with 81% (9.2 g) of the material from tilled areas (difference significant at $P = 0.05$). The disease rating for seedlings from bioassay tubes containing crown material retained by a 1.25-cm square screen was 1.9, compared with 0.5 for material sized between 0.63 and 1.25 cm. This indicates that not only was there more inoculum of *G. graminis* var. *tritici* in no-tilled soil, but also that a greater portion of this inoculum source was larger in size and thus more infectious than that recovered from tilled soil.

TABLE 2. Incidence and severity of take-all, caused by *Gaeumannomyces graminis* var. *tritici*, and yield of wheat in tilled and no-tilled soils with or without soil fumigation and with or without *G. graminis* var. *tritici* introduced into the soil as oat-kernel inoculum in three field trials in Washington

Location, crop, year Variable[x]	Inoculum added	Fumigated soil		Nonfumigated soil	
		Tilled	No-tilled	Tilled	No-tilled
Pullman, winter wheat, 1976–1977					
Incidence (%)	Yes	93 a[y]	88 a	76 a	83 a
	No	3 c	4 c	38 b	74 a
Severity	Yes	2.2 a	2.7 a	1.5 b	2.4 a
	No	0.1 c	0.1 c	0.5 c	1.4 b
Yield (kg/ha)	Yes	4,009 b	3,964 b	3,780 b	2,031 c
	No	4,723 a	4,750 a	4,318 ab	2,384 c
Lind, winter wheat, 1976–1977					
Incidence (%)	Yes	90 a	91 a	89 a	...[z]
	No	9 c	9 c	68 b	...
Severity	Yes	3.8 a	4.2 a	2.3 b	...
	No	0.4 d	0.2 d	1.5 c	...
Yield (kg/ha)	Yes	2,072 c	1,901 c	2,222 c	...
	No	5,460 a	5,786 a	3,634 b	...
Lind, spring wheat, 1977					
Incidence (%)	Yes	97 a	93 a	75 c	96 a
	No	5 e	0 e	67 d	85 b
Severity	Yes	3.6 a	3.5 ab	2.5 c	3.3 b
	No	0.2 e	0 e	1.6 d	3.2 b
Yield (kg/ha)	Yes	3,692 c	3,781 c	4,332 b	3,249 c
	No	7,325 a	7,508 a	4,505 b	4,069 bc

[x] Incidence assessed as percentage of plants infected in a random sample of at least 25 plants per treatment per replicate. Severity rated on a scale of 0–5, where 0 = no roots infected; 1 = less than 25% of roots infected, lesions mostly small; 2 = 25–50% of roots infected, lesions coalesced, plants slightly stunted; 3 = 51–75% of roots infected, multiple lesions on many roots, moderate stunting, slight blackening of stem bases; 4 = 76–100% of roots infected, multiple lesions on most roots, severe stunting, conspicuous blackening of stem bases; and 5 = all roots infected, plants dead or nearly so.

[y] Each value is the mean of three replicates for winter wheat at Pullman and Lind and of four replicates for spring wheat at Lind. For the eight values (six in the case of Lind, winter wheat) compared for each measurement (incidence, severity, yield) within each trial, those with a common letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

[z] Data not obtained because wheat was killed with herbicide.

Influence of host nutrition on take-all in tilled compared with no-tilled plots. For both tillage treatments, approximately 10% fewer plants were infected and the disease rating was approximately 1 unit less in plots fertilized with the complete treatment (P and K plus trace minerals in addition to N plus S) than in plots fertilized with N and S only (Table 3). Regardless of tillage or no tillage, and for each combination of fumigation and inoculation, take-all was most severe and yields were poorest in plots fertilized with N and S only (check treatment). The complete fertilizer also had a marked effect on early wheat growth in fumigated (pathogen-free) soil. As the season progressed, these differences became less apparent but were nevertheless reflected as greater yield (Table 3). Analysis of flag leaf tissue revealed little difference among fertilizers for NH_4-N and a difference for PO_4-P between the check (0.09 g/g dry tissue) and the complete fertilizer treatment (0.15 g/g dry tissue).

Fig. 2. Influence of no tillage vs. tillage on the size and amount of wheat crown material recovered from soil. Top, tilled soil (rotovated three times to a depth of 10 cm); bottom, no-tilled soil. Left, material retained by a 1.25-cm square screen; right, material passed through a 1.25-cm square screen but retained by a 0.63-cm square screen.

DISCUSSION

Seeding wheat directly (no-till) into soil naturally infested with *G. graminis* var. *tritici* resulted in more take-all than where the soil was disturbed by moldboard or disk plowing or by simulated tillage. This was true for all field trials and for the experiment using soil cores naturally infested with the take-all fungus. The greater amount of take-all with no tillage cannot be explained by differences in soil physical environment because: (i) in soil fumigated, then reinfested so that available inoculum was the same, take-all was uniformly severe regardless of the tillage treatment (Table 2) and (ii) when temperature and moisture differences among naturally infested soil cores receiving different simulated tillage treatments were minimized by incubating the cores in cans in a lathhouse with standardized watering, take-all was still more prevalent and severe in the undisturbed soil (Table 3). This does not mean that temperature, moisture, and other physical factors are not important in the development of take-all; rather, they were not the critical factors in our study of take-all in tilled compared with no-tilled soil.

If the incidence of plants infected early in the season relates to the amount of natural inoculum in soil, then the data from Puyallup (Table 1) suggest that the amount of inoculum of *G. graminis* var. *tritici* was greater in no-tilled than in tilled plots; early in the season (March), 79% of plants sampled from no-tilled plots were infected with take-all compared with only 33% of those from tilled plots. Other findings implicating inoculum as the important variable in our experiments were: (i) the mass of crown tissue recovered by sieving at Lind was five times greater from no-tilled than from tilled soil and the fragments were larger and thus of greater inoculum potential and (ii) when inoculum was the same (fumigated reinfested soil), take-all was the same regardless of whether the plots were tilled.

Scott (19) reported that rotovation immediately after harvest significantly reduced the number of whiteheads caused by *G. graminis* var. *tritici* in the subsequent wheat crop, compared with later rotovation or digging. He concluded that this was probably

TABLE 3. Incidence and severity of take-all, caused by *Gaeumannomyces graminis* var. *tritici*, and yield of irrigated spring wheat at Lind, 1977, in tilled and no-tilled soils with two fertilizer treatments with or without soil fumigation and with or without *G. graminis* var. *tritici* introduced into the soil as oat-kernel inoculum

		Fumigated soil				Nonfumigated soil			
		Tilled		No-tilled		Tilled		No-tilled	
Variable[x]	Inoculum added	Check[y]	Complete fertilizer[y]	Check	Complete fertilizer	Check	Complete fertilizer	Check	Complete fertilizer
Incidence (%)	Yes	96 a[z]	94 a	98 a	87 bc	78 de	64 g	100 a	91 ab
	No	9 h	2 h	0 h	0 h	71 ef	60 fg	97 a	74 e
Severity	Yes	3.8 a	3.2 cd	3.8 a	3.1 cd	3.0 de	2.0 i	3.6 a	2.8 ef
	No	0.4 k	0.1 k	0 k	0 k	2.2 hi	1.4 j	3.8 a	2.6 fg
Yield (kg/ha)	Yes	3,192 ij	3,966 ghi	3,031 j	4,587 fg	3,297 hij	5,299 ef	2,120 k	4,386 gh
	No	6,078 de	8,271 ab	6,482 d	8,642 a	3,741 ghi	5,546 e	2,338 jk	5,482 ef

[x] Incidence assessed in June as percentage of plants infected in eight 25-cm lengths of row sampled at random from the second and sixth rows in each plot. Severity rated on a scale of 0–5, where 0 = no roots infected; 1 = less than 25% of roots infected, lesions mostly small; 2 = 25–50% of roots infected, lesions coalesced, plants slightly stunted; 3 = 51–75% of roots infected, multiple lesions on many roots, moderate stunting, slight blackening of stem bases; 4 = 76–100% of roots infected, multiple lesions on most roots, severe stunting, conspicuous blackening of stem bases; and 5 = all roots infected, plants dead or nearly so.

[y] Check = 25% $(NH_4)_2SO_4$ plus 75% NH_4NO_3 (ANS); complete fertilizer = ANS plus $ZnSO_4$, KCl, Na_2MoO_4, boreated $CaSO_4$, and 11:55:0 (N:P:K) to supply 11.2 kg of Zn/ha, 78.5 kg of K_2O/ha, 0.5 kg of Mo/ha, 0.1 kg of B/ha, and 67.3 kg of P_2O_5/ha. All treatments applied at rates of 170 kg of N/ha and 120 kg of S/ha.

[z] Each value is the mean of four replicates. For the eight values compared for each measurement (incidence, severity, yield), those with a common letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

due to enhanced microbial activity and to greater competition for nitrogen in the well-aerated mixture of soil and stubble. Our observations similarly suggest that best take-all control in consecutive crops of wheat is achieved by thorough tillage, beginning as soon as possible after harvest. Ferraz (11), in attempting to explain less severe take-all with simulated plowing than with simulated direct drilling, suggested that the early looseness of the plowed soil promoted faster disappearance of the take-all fungus than did the more compact soil in containers where seed was direct-drilled; his suggestion is supported by our data (Table 3). In addition, more inoculum occurs near the crown zone in no-tilled soil, whereas the inoculum in tilled soil is more scattered (and diluted) throughout the tillage zone. Hornby (14) reported similar findings. Thus, the pathogen has a greater and earlier chance to move into the crown in no-tilled than in tilled soil. Garrett (12) showed that the age of the plant when the crown becomes infected is also important to subsequent survival and yield of the plant.

In contrast to our results, Brooks and Dawson (3) found in England that no tillage significantly reduced take-all. Because we obtained the same results at three different locations (Pullman, Lind, and Puyallup), any differences in edaphic and climatic factors between England and the Pacific Northwest would need to be greater than those among Pullman, Lind, and Puyallup, which themselves are very different in pH, rainfall, and temperature. Brooks and Dawson (3) performed their experiments in a sward that had not been plowed for over 100 years. Our experiments were performed in sites with histories of cultivated wheat. Also, their disease assessments were not made until the third wheat crop of their experiments, because they observed little difference in the first two crops in either yield or appearance of the wheat plants between direct-drilled and plowed plots. Our disease assessments were made in the first crop after establishment of the tillage treatments. Brooks and Dawson concluded that spread of the pathogen was restricted in the direct-drilled plots but did not determine how this occurred. They also noted differences in weeds; *Alopecurus pratensis* was the principal weed in their direct-drilled plots, whereas *Poa* and *Agrostis* spp. predominated in their plowed plots. Brooks (2) had found earlier that *G. graminis* survived better on *Poa* and *Agrostis* spp. than on *A. pratensis*. We made every effort to control weeds in our experiments, and in most locations weeds were virtually absent from the plots.

Application of a fertilizer mixture containing N, S, P, K, Mn, Mo, and B consistently resulted in less take-all in both fumigated and nonfumigated soil than application of N and S only. Phosphorus and potassium are known to suppress take-all through a nutritional effect on the host. Reis et al (18) showed for both the Lind and Puyallup locations that trace minerals also suppress take-all and that the effect is through host nutrition. The effects of the different fertilizer treatments in our study were evident regardless of whether the fertilizers were left on the soil surface (no-tilled plots) or mixed into the tillage layer (tilled plots). Even in the absence of diseases and weeds (fumigated noninoculated plots), plants with these treatments were more vigorous than plants fertilized with N and S only. The response occurred in both tilled and no-tilled plots, however, and is not likely to account for the greater disease with direct drilling.

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