Effect of Soil Shading by Surface Residues During Summer Fallow on Take-all of Winter Wheat

W. W. BOCKUS, Professor, M. A. DAVIS, Research Assistant, and B. L. NORMAN, Former Research Assistant, Department of Plant Pathology, Kansas State University, Manhattan 66506-5502

ABSTRACT

Bockus, W. W., Davis, M. A., and Norman, B. L. 1994. Effect of soil shading by surface residues during summer fallow on take-all of winter wheat. Plant Dis. 78:50-54.

Artificial inoculum of *Gaeumannomyces graminis* var. *tritici* was incorporated 10 cm deep in field plots about 1 mo after harvest of winter wheat and 2 mo before planting of wheat, and plots were either shaded with wheat straw or left bare. Plants grown in shaded plots had more severe take-all and lower grain yields than plants grown in plots left bare. During the oversummering period between wheat crops, soil temperatures at a depth of 5.1 cm were routinely 10 C cooler in shaded plots than in bare plots, and maximum soil temperatures reached 32.5–37.4 and 37.5–42.5 C on more days in bare plots than in shaded plots. Regression models of data from laboratory experiments indicated that the ability of inoculum (infested oat grains) to cause disease would be completely eliminated by 12 consecutive exposures for 6 hr/day to temperatures of 35 C (24 C at other times), four exposures for 6 hr/day to 40 C, or one exposure to 45 C. Thermal inactivation of oversummering inoculum is an important limiting factor to the development of take-all in Kansas. Management practices that increase soil shading (such as volunteer wheat, double-cropping, and no-till) tend to prevent high soil temperatures and may promote inoculum survival and disease.

Take-all is a severe root and crown disease of wheat (*Triticum aestivum* L.) caused by the soilborne fungus *Gaeumannomyces graminis* (Sacc.) Arx & D. Olivier var. *tritici* J. Walker. The fungus survives between susceptible crops as mycelium in infested host residue. Because the competitive saprophytic ability of *G. g. tritici* is low (3,16,17), roots and crowns colonized by the fungus during parasitism act as primary inoculum (14). The viability of inoculum declines as soil microorganisms subsequently colonize and decompose residue. Thus, the pathogen population is characterized by increasing inoculum potential during the parasitic phase, followed by decreasing inoculum potential during the saprophytic phase (13).

Crop rotation can effectively control take-all by exploiting the relatively short saprophytic survival of the fungus in soil (4,23). Similarly, delaying seeding can limit disease by extending the saprophytic period and thereby lengthening the time for inoculum potential to decrease (1,19). Tillage practices that fragment the inoculum and expose it to increased microbial degradation also can lower the inoculum potential of the pathogen and limit disease development (9,20,24). Therefore, the amount and vigor of the inoculum that survives between susceptible host crops are important determinants of disease severity.

Conservation tillage practices can influence the amount of take-all (26). Compared with conventional tillage, direct drilling (i.e., no tillage other than with the planter) has resulted in less take-all (21), more take-all (20), or no difference in the amount of take-all (27). Moore and Cook (20) showed that take-all is more severe with direct drilling in the Pacific Northwest. They attributed this to the large size of inoculum pieces associated with direct-drill conditions (20,24).

Environmental factors also can affect the saprophytic survival of *G. g. tritici* (23). These include exhaustion of nitrogen in the colonized crop residue (14) and high soil moisture. The latter favors microbial activity, accelerating the breakdown of pathogen-infested crop residue and hence the destruction of the food base and habitat of *G. g. tritici* (12).

In Kansas, the occurrence of take-all is erratic. During the past 14 yr, numerous field experiments have been established on sites where moderate to severe take-all would be expected on the basis of cropping history and experience; in about half of these cases, however, the

Present address of third author: The Land: EPCOT Center, P.O. Box 40, Lake Buena Vista, FL 32830.

Contribution 93-388-J from the Kansas Agricultural Experiment Station, Kansas State University, Manhattan.

Accepted for publication 6 July 1993.

disease did not occur in commercial or experimental fields, even though take-all had been severe the previous year (2; W. W. Bockus, *unpublished*). Few of these failures could be attributed to the development of a highly suppressive soil condition (4), because artificial inoculum introduced into the soil at planting caused severe take-all. Therefore, it was hypothesized that some environmental factor or factors greatly influence the survival of the fungus and/or its ability to cause disease in Kansas.

We undertook the experiments reported here to determine whether surfaceborne residue influences the amount of take-all in Kansas. The summer fallow period between wheat harvest and planting of a subsequent winter wheat crop is 3 mo in this state. We focused on the influence of a straw mulch layer during this period on the ability of the fungus to cause disease in a subsequent wheat crop in a field where wheat is planted every year. We also quantified the effect on inoculum of exposure to different soil temperatures that are likely to be encountered during an oversummering period in Kansas.

MATERIALS AND METHODS

Preparation and use of inoculum. Whole oat kernels (150 g) were placed in 1-qt canning jars with 140 ml of distilled water. Jars were capped with a perforated (1.5-cm-diam), cotton-plugged lid, shaken to moisten the oats, and incubated at room temperature for 2–16 hr to allow the oats to imbibe much of the water. Jars were then reshaken, autoclaved (125 C) for 1 hr, cooled in a laminar flow hood, and inoculated with four cubes (0.5–1.0 cm square) cut from a fresh culture of *G. g. tritici* growing on half-strength potato-dextrose agar. Jars were incubated at room temperature on a lab bench and shaken every 4–5 days for 2–3 wk. The kernels were then air-dried in the lab. Oat kernel inoculum was scattered over the surface of the soil (32.3 g/m^2) and rototilled to a depth of 10 cm to infest field plots.

Shading experiments. Field experiments were conducted in each of three consecutive crop years (1989–1990, 1990–1991, 1991–1992) on Chase silty clay loam (pH 6.5, 2.2% organic matter), which had been cropped to winter wheat in the previous season. At the sites, no naturally occurring take-all was observed in the previous wheat crop. The plot areas were moldboard-plowed within 2 wk after harvest and then disked and spike-tooth-harrowed about 2 wk later. After harrowing, five treatments were established for each of the first 2 yr: The first treatment was the noninoculated control. In the second treatment, inoculum was added to the soil at planting. In the third treatment, inoculum was added 2 mo before planting, and immediately thereafter a grain drill was used to seed plots with Arkan wheat (100 kg/ha) to simulate volunteer plants. In the fourth and fifth treatments, inoculum was added 2 mo before planting, and the soil was shaded with straw (5,600–6,000 kg/ha) (fourth treatment) or kept bare during the summer (fifth treatment).

In all treatments except the third, volunteer plants and weeds were controlled during the summer by two applications of glyphosate (1.5% a.i. at 187 L/ha). Plots given the third treatment were sprayed with glyphosate 2 wk before planting to kill the simulated volunteer wheat.

In the third year, there were eight treatments: four inoculum treatments (none, inoculum added at planting, 1 mo before planting, and 2 mo before planting) and two shading treatments (none and shaded with straw at 5,000 kg/ha) in all combinations. In all years, straw was removed from shaded plots 2–3 days before planting.

All experiments were arranged in a randomized block design with five replications. All plots measured 1.22 × 7.62 m and were seeded during the last week in September with Karl winter wheat at 57–67 kg/ha. All plots were sprinkler-irrigated (2.5 cm of water) shortly after planting. Soil tests indicated adequate phosphorus and potassium, but supplemental nitrogen (NH_4NO_3, 34% N) was applied for maximum yield potential.

Soil temperature. During the summers of 1989 and 1990, soil temperature was measured with an Omnidata Easy Logger (Logan, UT). Probes were placed 5.1 cm deep in soil in two plots each of the shaded and unshaded treatments, and temperature readings were recorded every hour for about 2 mo.

Disease evaluation in the field. The percentage of stunted and prematurely ripe tillers (whiteheads) was estimated visually in each plot on 1 and 8 June 1990, 29 May 1991, and 1 June 1992. These dates corresponded to soft- and medium-dough growth stages in 1990, soft-dough stage in 1991, and medium-dough stage in 1992. Grain yields were determined with a small-plot combine on 23 June 1990, 12 June 1991, and 1 July 1992. Yield losses from take-all were calculated by comparing yields with the yield from the noninoculated, unshaded treatment.

Thermal inactivation of inoculum. Air-dried, sieved (4.0 mm) Chase silty clay loam (30 g) was placed in glass petri dishes, and 2.0 g of whole oat kernel inoculum was sprinkled over the surface of the soil in each dish and covered with another 45 g of soil. Soil was moistened with 30 g of distilled water applied with a pipet to the surface, resulting in soil matric potentials of approximately −0.1 MPa. Petri dishes were sealed with Parafilm to reduce moisture loss, and four holes were poked in the film with a dissecting needle to aid in gas exchange.

After equilibration at 4 C for 24–48 hr, the dishes were placed in incubators and exposed to various temperature regimes. Incubators maintained temperatures within 2.0 C of the desired setting. In the first experiment, dishes were exposed to 24-hr cycles of 35 and 24 C for 6 and 18 hr, respectively, for 5, 10, or 15 days. In the second experiment, plates were exposed to 24-hr cycles of 40 and 24 C (6 and 18 hr) for 1, 3, or 5 days. And in the third experiment, plates were exposed to 45 C for 2.0, 3.5, or 5.5 hr. All three experiments included unexposed controls and were conducted at least twice. After exposure, inoculum was removed from the soil by wet-sieving and bioassayed to determine its ability to initiate root rot on wheat seedlings.

Bioassay. Oat kernel inoculum exposed to the various temperature regimes was introduced into vermiculite in 2.5 × 12.5 cm plastic cones (Stuewe & Sons, Corvallis, OR). Four kernels were placed in each cone at seed level with three seeds of TAM 105 winter wheat. Ten cones per replication and four replications per treatment were used in a randomized block design. Cones were maintained in the greenhouse (15–28 C) for 4–5 wk. Vermiculite was then washed from the roots, and the percentage of the root system with root rot or runner hyphae was estimated visually under a dissecting microscope (22).

Statistical analysis. Data from the field experiments were analyzed by the analysis of variance (ANOVA) procedure of SAS (SAS Institute, Cary, NC), followed by mean separation by least significant differences ($P = 0.05$). Values for the percentage of prematurely ripened tillers were transformed by the square-root arcsine transformation for analysis and transformed back for presentation. Data on the effect of exposure to high temperatures on inoculum potential were transformed by the square-root arcsine transformation and analyzed by linear regression with SAS. The data points for 15 daily exposures to 35 C and five daily exposures to 40 C were all zeros and were outside the linear part of the curves, so they were omitted from the analyses. Models generated by linear regression were used to predict the number of 6-hr exposures to 35, 40, and 45 C that would be needed to reduce root rot by 50, 90, and 100%.

RESULTS

The 1989–1990 field experiment. Inoculum that was added to the soil at planting resulted in a higher incidence of whiteheads and lower grain yields than inoculum that was added 2 mo before planting (Table 1). The incidence of whiteheads associated with the presence of volunteer wheat was relatively high compared to the noninoculated control treatment and the treatment in which soil

was infested but left bare. Plots with volunteer plants also yielded less (significant at $P < 0.06$) than the noninoculated control plots. The combination of soil infestation and shading 2 mo before planting also resulted in a high incidence of whiteheads and low grain yields relative to the noninoculated control plots and plots where the soil was left bare. In contrast, the percentage of whiteheads and grain yield in bare plots were similar to those in the noninoculated control plots.

Table 1. Effect of volunteer wheat and soil shading[v] during the summer of 1989 on take-all and yield of winter wheat in 1990

Treatment	Inoculum[w]	Whiteheads[x,y] (%) 1 June	Whiteheads[x,y] (%) 8 June	Grain yield[y] (kg/ha)	Yield loss (%)
Noninoculated check	None	14.4 c	31.8 c	3,040 a	...
Inoculated check	0 mo	80.6 a	90.0 a	1,279 c	57.9
Volunteer[z]	2 mo	33.0 b	66.0 b	2,637 ab	13.3
Shaded[v]	2 mo	39.0 b	67.8 b	2,356 b	22.5
Bare[v]	2 mo	16.0 c	25.2 c	2,876 a	5.4

[v] Immediately after inoculum was added to the soil, plots were covered with wheat straw at 5,600 kg/ha or were left bare during the summer of 1989. Straw was removed from shaded plots 2 days before planting.
[w] Oat kernels (32.3 g/m^2) colonized by *Gaeumannomyces graminis* var. *tritici* were rototilled into the soil at planting or 2 mo before planting as indicated.
[x] Percentage of mature heads determined on 1 June (soft-dough stage) and 8 June (medium-dough stage) 1990.
[y] Values within a column followed by a common letter do not differ significantly according to analysis of variance and least significant difference analysis ($P = 0.05$).
[z] Plots were seeded with winter wheat (100 kg/ha) 2 mo before planting to simulate volunteer plants. Volunteer plants were killed with glyphosate 10 days before planting. Grain yield with this treatment was significantly lower than that of the noninoculated control at $P < 0.06$.

Table 2. Effect of volunteer wheat and soil shading[v] during the summer of 1990 on take-all and yield of winter wheat in 1991

Treatment	Inoculum[w]	Whiteheads[x,y] (%)	Grain yield[y] (kg/ha)	Yield loss (%)
Noninoculated check	None	4.2 d	2,138 a	0.0
Inoculated check	0 mo	86.8 a	1,035 d	51.6
Volunteer[z]	2 mo	64.4 b	1,581 c	26.1
Shaded[v]	2 mo	44.0 c	1,873 b	12.4
Bare[v]	2 mo	12.8 d	1,884 b	11.9

[v] Immediately after inoculum was added to the soil, plots were covered with wheat straw at 6,000 kg/ha or were left bare during the summer of 1990. Straw was removed from shaded plots 3 days before planting.
[w] Oat kernels (32.3 g/m^2) colonized by *Gaeumannomyces graminis* var. *tritici* were rototilled into the soil at planting or 2 mo before planting as indicated.
[x] Percentage of mature heads determined on 29 May 1991 (soft-dough stage).
[y] Values within a column followed by a common letter do not differ significantly according to analysis of variance and least significant difference analysis ($P = 0.05$).
[z] Plots were seeded with wheat (100 kg/ha) 2 mo before planting to simulate volunteer plants. Volunteer plants were killed with glyphosate 14 days before planting.

Table 3. Effect of soil shading[w] during the summer of 1991 on take-all and yield of winter wheat in 1992

Shade treatment[w]	Inoculum[x]	Whiteheads[y,z] (%)	Grain yield[z] (kg/ha)	Yield loss (%)
Shaded	None	1.4 d	3,766 a	0.8
Bare	None	0.6 d	3,800 a	0.0
Shaded	0 mo	93.4 a	1,056 e	72.2
Bare	0 mo	88.2 a	1,318 de	65.2
Shaded	1 mo	85.0 a	1,648 d	56.7
Bare	1 mo	66.0 b	2,240 c	40.9
Shaded	2 mo	61.2 b	2,488 c	34.5
Bare	2 mo	21.0 c	3,221 b	15.2

[w] Plots were either covered with wheat straw at 5,000 kg/ha or were left bare during the summer of 1991. All shaded treatments were shaded 2 mo before planting, except when inoculum was added 1 mo before planting, in which cases plots were shaded for 1 mo. Straw was removed 3 days before planting.
[x] Oat kernels (32.3 g/m^2) colonized by *Gaeumannomyces graminis* var. *tritici* were rototilled into the soil at planting or 1 or 2 mo before planting as indicated.
[y] Percentage of mature heads determined on 1 June 1992 (medium-dough stage).
[z] Values within a column followed by a common letter do not differ significantly according to analysis of variance and least significant difference analysis ($P = 0.05$).

The 1990–1991 field experiment. As in the previous year, take-all was less severe and grain yields were higher in plots where inoculum was added 2 mo before planting than in plots inoculated at planting (Table 2). In the three treatments in which inoculum was added before planting, take-all was most severe when volunteer wheat was present, least severe when soil was left bare, and intermediate when soil was shaded. Although shaded plots developed more whiteheads than bare plots, yields for these treatments were not significantly different.

The 1991–1992 field experiment. Grain yield potential was higher in 1991–1992 than in the previous 2 yr, as evidenced by the yields of the noninoculated controls (Table 3). Commercial wheat production in Kansas averages about 2,300 kg/ha. As in the previous years, plants grown in plots infested with inoculum 2 mo before planting produced fewer whiteheads and higher yields than wheat grown in plots where inoculum was added at planting. The presence or absence of surface residues had no effect on the percentage of whiteheads or grain yields for the noninoculated controls or when inoculum was added at planting. In contrast, when soil was infested 1 or 2 mo before planting, shading significantly increased the percentage of whiteheads and lowered grain yields compared to the bare (unshaded) treatment.

Soil temperatures. During the summers of 1989 and 1990, maximum soil temperatures exceeded 32.5 C on more days in the bare plots than in the shaded plots (Table 4). Although soil temperatures never went above 42.5 C, such readings have been obtained in Kansas (B. L. Norman, *unpublished*). Soil temperature tracings throughout the day of 4 August 1989 are shown in Figure 1. During the hottest part of the day, there was about an 8–10 C difference between the shaded and bare plots. In addition, the tracing for the bare plot was above 35 C for about 7 hr, beginning at 1200 (noon), and reached a maximum of 38.9 C at 1500 (3 p.m.). Daily tracings throughout the summer showed similar trends.

Thermal inactivation of inoculum. Exposure of *G. g. tritici* contained in oat kernels to high temperatures in the laboratory had a significant effect on the ability of this inoculum source to induce disease symptoms on wheat roots. Root rot data from inoculum exposed to 35, 40, and 45 C for various periods, transformed by the square-root arcsine transformation, significantly fit linear models for all experiments (Figs. 2–4). According to these models, root rot would be reduced by 50% if inoculum was exposed to temperatures of 35 C 4.9 times for 6 hr each time (Fig. 2), 40 C 1.2 times

Table 4. Number of days during the summers of 1989 and 1990 when maximum soil temperatures 5.1 cm deep were below 32.5 C, between 32.5 and 37.4 C, between 37.5 and 42.5 C, and above 42.5 C

Year	Maximum soil temperature (C)[z]			
Treatment[y]	<32.5	32.5–37.4	37.5–42.5	>42.5
1989				
Bare	5	15	42	0
Shaded	62	0	0	0
1990				
Bare	5	31	6	0
Shaded	38	4	0	0

[y] Shaded soil was covered with wheat straw (5,600–6,000 kg/ha).
[z] Between 3 July and 2 September 1989 and 28 July and 7 September 1990.

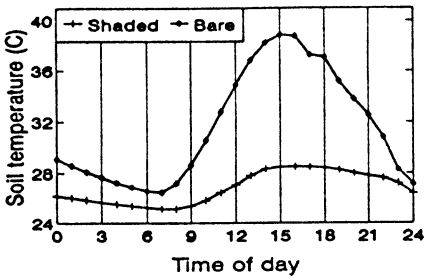

Fig. 1. Hourly soil temperatures at a depth of 5.1 cm in shaded plots (soil covered with wheat straw at 5,600 kg/ha) and bare plots on 4 August 1989.

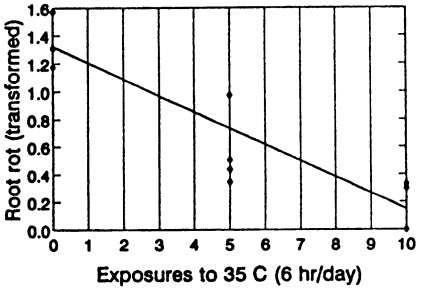

Fig. 2. Influence of daily exposures (6 hr/day) to 35 C (otherwise 24 C) on the ability of inoculum of *Gaeumannomyces graminis* var. *tritici* to cause root rot on wheat seedlings. Root rot data were transformed by the square-root arcsine transformation. The linear regression model for the response has an intercept of 1.3198, a slope of −0.1163, and an adjusted r^2 of 0.7973 ($P < 0.0001$ for all three parameters).

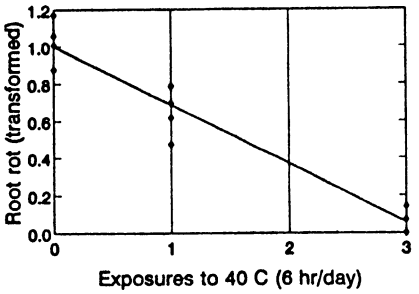

Fig. 3. Influence of daily exposures (6 hr/day) to 40 C (otherwise 24 C) on the ability of inoculum of *Gaeumannomyces graminis* var. *tritici* to cause root rot on wheat seedlings. Root rot data were transformed by the square-root arcsine transformation. The linear regression model for the response has an intercept of 1.0005, a slope of −0.3146, and an adjusted r^2 of 0.9338 ($P < 0.0001$ for all three parameters).

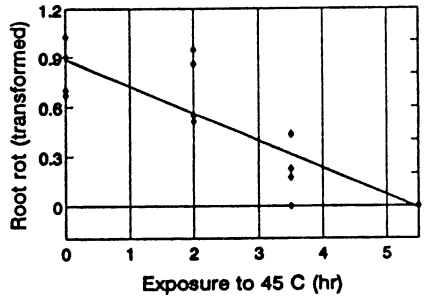

Fig. 4. Influence of time of exposure to 45 C on the ability of inoculum of *Gaeumannomyces graminis* var. *tritici* to cause root rot on wheat seedlings. Root rot data were transformed by the square-root arcsine transformation. The linear regression model for the response has an intercept of 0.8836, a slope of −0.1624, and an adjusted r^2 of 0.7801 ($P < 0.0001$ for all three parameters).

(Fig. 3), or 45 C for 1.9 hr (Fig. 4). The corresponding values for a 90% reduction in disease are 8.7 times, 2.3 times, and 3.9 hr and for no root rot are 11.4 times, 3.2 times, and 5.4 hr. Repeats of all inoculum inactivation experiments produced similar results.

DISCUSSION

Averaged over the 3-yr period, wheat yields in plots infested with inoculum of the take-all fungus 2 mo before planting and kept bare were 120% greater than those in plots to which an equivalent amount of inoculum was added at planting. Therefore, the ability of artificial inoculum of *G. g. tritici* to cause take-all is severely reduced during the oversummering fallow period in Kansas. Because the actual summer fallow period between wheat crops in this state is closer to 3 mo, survival of *G. g. tritici* during the summer is critical to the epidemiology of the disease. Any factor that favors or limits the survival of the fungus during this period can be expected to have a major effect on the severity of take-all in Kansas (23).

Grassy weeds can harbor the take-all fungus during the period when susceptible crop species are not being grown (7,26). Results presented here show that volunteer wheat plants have a similar effect during the summer in Kansas. When soil was infested with inoculum 2 mo before planting, the presence of summer volunteer plants before seeding was associated with higher percentages of whiteheads than were observed in bare-soil plots during both years (Tables 1 and 2). Grain yields in the volunteer plots were significantly lower than those in the bare plots in 1991 (Table 2). In 1990, the presence of volunteer plants, but not the bare treatment, resulted in significantly ($P < 0.06$) lower yields than the noninoculated control (Table 1). We conclude that summer volunteer wheat has the potential to increase take-all (or reduce inactivation of the pathogen) in Kansas and should be eliminated.

Similarly, when inoculum was incorporated into soil 2 mo before planting, shading the soil with wheat straw during the summer resulted in more severe take-all than leaving the soil bare. Surface residues resulted in more whiteheads in all 3 yr and in significantly lower grain yields in two of the 3 yr, relative to the bare-soil treatment (Tables 1–3). Because the straw used to cover the soil was removed just before planting, the effect on inoculum occurred during the summer.

Shading soil during the summer affects several soil environmental parameters, including moisture, fertility, texture, phytotoxins, temperature, and microbial activity. Any differences among treatments in soil moisture that occurred during the summer were probably reduced or eliminated by the irrigation immediately after planting. Similarly, because adequate fertilizer was applied for maximum yields, soil fertility was probably not a significant factor in the observed differences in take-all between shaded and bare treatments. Soil texture affects take-all (15) but was not measured in these experiments; however, differences among plots were probably of minor or no significance. Phytotoxins from straw have been reported to be a cause of poor performance of direct-drilled crops (10); however, our data tend to support the hypothesis (5) that root pathogens, not phytotoxins, are the primary cause of unthrifty direct-drilled wheat. Cook and Haglund (5) demonstrated increased parasitic activity of soilborne wheat pathogens under surface residues, and our data show increased survival of the take-all fungus between crops under surface residues.

Temperature influences survival of *G. g. tritici*. Fellows (11) found less disease in wheat grown in infested soil that had been stored for 230–777 days in warm (average temperature 21–29 C), moist conditions than in that grown in soil stored in cool (average temperature 3 C), moist conditions. He further observed that the thermal death point of the fungus

in pure culture was 50 C for 10 min but that natural (air-dry) inoculum was not killed by exposure to 60–71 C for 1 hr on each of several days (11). In a related study (18), inoculum survived after 45 wk in dry soil at 15 C, but survival was reduced in dry, warm (35 C) soil, and the fungus was eliminated after 4 wk in warm (35 C), moist soil. Similarly, in warm (maximum about 35 C) greenhouse conditions, increasing soil moisture decreased the survival of soilborne inoculum after 3–5 mo of incubation (6). Using more controlled conditions, MacNish (18) demonstrated elimination of the fungus after 4 wk in warm, moist soil (35 C, −0.01 to −0.02 MPa), whereas cool (15 C), moist soil favored viability of the fungus. Wong (25) also showed that *G. g. tritici* was eliminated by exposure to −0.3 MPa and 30 C for 3 mo, whereas it survived at an "intermediate" level at −0.3 MPa and 15 C. Survival was not determined at intervals less than 3 mo; however, warm temperatures (30–35 C) combined with a moist environment resulted in the poorest survival rates. Our results expand on these findings by relating soil temperature effects to field conditions; in addition, our experiments were done under more controlled environments, and we derived regression models of the response of artificial inoculum to exposure to 35, 40, and 45 C.

Data presented here suggest that large differences in soil temperature between residue-covered and bare treatments could account for the observed effects on carryover of *G. g. tritici* between wheat crops in Kansas. Maximum soil temperatures 5.1 cm deep can routinely be 10 C higher in bare plots than in covered plots (Fig. 1). In moist (−0.1 MPa) soil in the laboratory, inoculum can be killed, or weakened so much that it is of no epidemiological significance, by 12 exposures of 6 hr/day to 35 C, four exposures to 40 C, or one exposure to 45 C (Figs. 2–4). However, thermal inactivation of inoculum is a very complex process, and the models generated here are valid only for certain specific conditions. For instance, it remains to be shown whether natural inoculum is similar to artificial inoculum in sensitivity to temperature. In addition, inoculum in equilibrium with dry soil is less sensitive to thermal inactivation than that in more moist soil (6; W. W. Bockus, M. A. Davis, and B. L. Norman, *unpublished*). Nevertheless, maximum soil temperatures reached the range where inoculum is adversely affected on more days during the summer in bare plots than in shaded plots (Table 4). Most infectious inoculum resides in the portion of the soil profile (2.5–7.5 cm deep [8]) that is exposed to these high temperatures.

The activity of soil microorganisms plays a major role in the saprophytic survival of *G. g. tritici*. Garrett (12) and Fellows (11) attributed poor survival of this fungus in warm, loose, and moist soils to increased antagonistic activity of soil microorganisms. Thus, the relatively small amount of take-all observed in bare plots may have been an indirect effect of high soil temperatures enhancing antagonism. However, in our laboratory experiments, we have obtained similar results whether inoculum is exposed to high temperatures in autoclaved or nonsterile soil (2; W. W. Bockus, M. A. Davis, and B. L. Norman, *unpublished*). Therefore, we believe that direct thermal inactivation of inoculum of *G. g. tritici* is of major importance in field soils in Kansas. The primary effect of surface residues during the summer, which apparently aid in the survival of the fungus, is the maintenance of cooler soil temperatures.

Wheat management practices that protect inoculum against exposure to high soil temperatures will probably result in more take-all. The shading effect reported here may be one of the factors involved in increased take-all associated with summer volunteer plants, double-cropping with soybeans (22), and no-till (20), all of which increase soil shading. However, the vulnerability of inoculum to inactivation by high soil temperatures would affect the epidemiology of take-all only in wheat-growing regions with significant summer rainfall (to produce moist soil) followed by days with relatively high temperatures. Such conditions are common in Kansas and are probably important determinants in the development of take-all in this state.

LITERATURE CITED

1. Bockus, W. W. 1983. Effects of fall infection by *Gaeumannomyces graminis* var. *tritici* and triadimenol seed treatment on severity of take-all in winter wheat. Phytopathology 73:540-543.
2. Bockus, W. W., and Norman, B. L. 1990. Heat inactivation of *Gaeumannomyces graminis* var. *tritici* (GGT). (Abstr.) Phytopathology 80:1024.
3. Butler, F. C. 1953. Saprophytic behaviour of some cereal root-rot fungi. I. Saprophytic colonization of wheat straw. Ann. Appl. Biol. 40:284-297.
4. Cook, R. J. 1981. The influence of rotation crops on take-all decline phenomenon. Phytopathology 71:189-192.
5. Cook, R. J., and Haglund, W. A. 1991. Wheat yield depression associated with conservation tillage caused by root pathogens in the soil not phytotoxins from the straw. Soil Biol. Biochem. 23:1125-1132.
6. Cotterill, P. J., and Sivasithamparam, K. 1987. Intermittent wetting of soils at high temperatures reduces survival of the take-all fungus. Plant Soil 103:289-291.
7. Cotterill, P. J., and Sivasithamparam, K. 1988. Survival of the take-all fungus in the presence and absence of susceptible grasses. Aust. J. Soil Res. 26:313-322.
8. Cotterill, P. J., and Sivasithamparam, K. 1989. Inoculum of the take-all fungus (*Gaeumannomyces graminis* var. *tritici*) in a Mediterranean-type climate: Spatial distribution at a field site in western Australia. Phytophylactica 21:45-48.
9. Cunningham, P. C. 1967. A study of ploughing depth and foot and root rots of spring wheat. Ir. J. Agric. Res. 6:33-39.
10. Elliott, L. F., McCalla, T. M., and Waiss, A., Jr. 1978. Phytotoxicity associated with residue management. Pages 131-146 in: Crop Residue Management Systems. W. R. Oschwald, ed. Special Publication 31. American Society of Agronomy, Madison, WI.
11. Fellows, H. 1941. Effects of certain environmental conditions on the prevalence of *Ophiobolus graminis*. J. Agric. Res. 63:715-726.
12. Garrett, S. D. 1938. Soil conditions and the take-all disease of wheat. III. Decomposition of the resting mycelium of *Ophiobolus graminis* in infected wheat stubble buried in the soil. Ann. Appl. Biol. 25:742-766.
13. Garrett, S. D. 1963. A comparison of cellulose decomposing ability in five fungi causing cereal foot-rots. Trans. Br. Mycol. Soc. 46:572-576.
14. Garrett, S. D. 1970. Pathogenic Root-Infecting Fungi. Cambridge University Press, Cambridge.
15. Garrett, S. D. 1985. Effect of soil texture on microbial abbreviation of saprophytic survival by the take-all fungus of wheat. Proc. Indian Acad. Sci. (Plant Sci.) 94:85-90.
16. Hornby, D. 1969. Methods of investigating populations of the take-all fungus (*Ophiobolus graminis*) in soil. Ann. Appl. Biol. 64:503-513.
17. Macer, R. C. 1961. The survival of *Cercosporella herpotrichoides* Fron in wheat straw. Ann. Appl. Biol. 49:165-172.
18. MacNish, G. C. 1973. Survival of *Gaeumannomyces graminis* var. *tritici* in field soil stored in controlled environments. Aust. J. Biol. Sci. 26:1319-1325.
19. Maloy, O. C., and Cook, R. J. 1981. Take-all in wheat: New developments for control. Ext. Bull. Wash. State Univ. Coop. Ext. Serv. EBO 988.
20. Moore, K. J., and Cook, R. J. 1984. Increased take-all of wheat with direct drilling in the Pacific Northwest. Phytopathology 74:1044-1049.
21. Rothrock, C. S. 1987. Take-all of wheat as affected by tillage and wheat-soybean double-cropping. Soil Biol. Biochem. 19:307-311.
22. Rothrock, C. S., and Langdale, G. W. 1989. Influence of nonhost summer crops on take-all in double-cropped winter wheat. Plant Dis. 73:130-132.
23. Shipton, P. J. 1981. Saprophytic survival between susceptible crops. Pages 295-316 in: Biology and Control of Take-all. M. J. C. Asher and P. J. Shipton, eds. Academic Press, London.
24. Wilkinson, H. T., Cook, R. J., and Alldredge, J. R. 1985. Relation of inoculum size and concentration to infection of wheat roots by *Gaeumannomyces graminis* var. *tritici*. Phytopathology 75:98-103.
25. Wong, P. T. W. 1984. Saprophytic survival of *Gaeumannomyces graminis* and *Phialophora* spp. at various temperature-moisture regimes. Ann. Appl. Biol. 105:455-461.
26. Yarham, D. J. 1981. Practical aspects of epidemiology and control. Pages 353-384 in: Biology and Control of Take-all. M. J. C. Asher and P. J. Shipton, eds. Academic Press, London.
27. Yarham, D. J., and Hirst, J. M. 1975. Diseases in reduced cultivation and direct-drilling systems. Bull. OEPP 5:287-296.