Evidence that Microorganisms in Suppressive Soil Associated with Wheat Take-all Decline Do Not Limit the Number of Lesions Produced by *Gaeumannomyces graminis* var. *tritici*

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ABSTRACT

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A Shano silt loam from a field cropped consecutively for 22 yr to irrigated wheat and highly suppressive to wheat take-all caused by *Gaeumannomyces graminis* var. *tritici* allowed about the same number of root lesions per unit particle size and concentration of inoculum (fragmented plant debris colonized by the pathogen) as did a noncropped (virgin) Ritzville silt loam highly conducive to take-all. Infection efficiencies (the number of lesions produced per unit weight of colonized particles) and threshold particle sizes (minimum particle size required for maximum efficiency) were similar in the two soils for three inoculum sources (naturally colonized wheat crowns from the field, wheat roots infected in the greenhouse, and axenically colonized oat grains) compared at up to six particle sizes (1.0–2.0 mm, 0.5–1.0 mm, 0.25–0.50 mm, 0.15–0.25 mm, 0.10–0.15 mm, and <0.10 mm) and ten concentrations (10, 5, 2.5, 1.5, 1.0, 0.5, 0.25, 0.15, 0.1, and 0.01 mg/g of soil), in all combinations. The infection efficiency of the axenically colonized oat-grain inoculum was greater in pasteurized (60 C moist heat treatment for 30 min) than in untreated soil, but this greater efficiency occurred with both soils in response to pasteurization. Infection efficiencies for a given inoculum particle size in pasteurized soils were greatest for colonized oat grains, least for colonized roots, and intermediate for colonized crowns. Differences in nutrients available in the inoculum particle and in the rhizosphere for prepenetration growth by the pathogen may explain the differences in infection efficiencies of the different sources of inoculum in the treated and untreated soils. The known difference in take-all suppressiveness of the two soils could not be explained by effects on the incidence of root infections.

Additional key words: biological control, root disease, soilborne pathogens, *Triticum aestivum*.

Continuous cropping of wheat (*Triticum aestivum* L.) commonly results in a decline in severity of take-all caused by *Gaeumannomyces graminis* (Sacc.) Von Arx and Olivier var. *tritici* Walker, as the soil becomes suppressive to the pathogen (2,3). Even though the pathogen population remains virulent (1,5), and the pathogen may occur on most plants in the field (5), disease is either mild or undetectable after take-all decline. Pope and Jackson (11) noted that directional growth of the pathogen toward the root was less apparent in soil from a field where take-all decline had occurred compared with conducive soil. Wildermuth et al (17) reported further that fewer hyphae of *G. g.* var. *tritici* grow from infested debris in the rhizosphere of wheat roots in suppressive soil than in conducive soil. These studies indicate that suppression may act to limit the fungus during prepenetration growth. In contrast, Cook (4) observed that disease suppression occurred after the fungus was thoroughly established as a parasite in wheat roots and found no evidence that initial infection was less in suppressive soil in field plots than in conducive soil.

We reported (19) the development of an assay system with which the infection efficiency (number of infections per unit weight of inoculum) and the threshold particle size (minimum particle size required to achieve the maximum infection efficiency) can be determined for different kinds, particle sizes, and concentrations of plant residue containing *G. g.* var. *tritici*. The purpose of the research reported in this paper was to examine whether the infection efficiency and threshold particle size of inoculum from different sources is any different in soil after take-all has declined than in soil before take-all has declined.

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MATERIALS AND METHODS

Soils suppressive and conducive to take-all. The suppressive soil was a Shano silt loam from near Moses Lake, WA, that had been cropped to irrigated wheat for 22 consecutive years when sampled. Take-all had not been evident in the field for many years, although virulent cultures of the pathogen were obtained from 50–90% of plants randomly selected during any given growing season (5). The conducive soil was a noncropped (virgin) Ritzville silt loam from near Lind, WA. The two sites are about 80 km apart and both receive an average of 25 cm of precipitation annually. Soil samples were collected in October 1979, from the upper 20 cm of the profile. The soils were air-dried, sieved through a 2.0-mm-mesh screen, and stored at ambient temperature. Air-drying of the soil does not eliminate the suppressiveness associated with take-all decline and detectable by the pot assay (6,11). On the other hand, the suppressiveness associated with take-all decline is eliminated by moist heat at 60 C for 30 min (8,12); therefore, pasteurized soils were prepared by treating moist soil (15% water [w/w]) with aerated steam for 30 min at 60 C followed by air-drying in a laminar-airflow hood.

Experimental design. The three sources and particle sizes of inoculum were as described previously (19). Naturally colonized wheat crowns were collected fresh from a field where severe take-all had occurred that season. Colonized wheat roots were produced in the greenhouse by growing wheat in vermiculite infested with the pathogen. Axenically colonized oat grains were produced by growing a virulent culture of the pathogen on autoclaved oat grains in jars. Each inoculum source was fragmented and then separated

with screens into five particle sizes (0.5–1.0 mm, 0.25–0.5 mm, 0.15–0.25 mm, 0.1–0.15 mm, and <0.1 mm). A sixth size (1.0–2.0 mm) was obtained for oat-grain particles. Each kind and size of particle were then tested at ten concentrations (0.01, 0.1, 0.15, 0.25, 0.5, 1.0, 1.5, 2.5, 5.0, 10.0 mg/g of soil). The effect of the two soils, pasteurized and untreated, on infection efficiency was determined on roots of wheat seedlings after about 3 wk of growth in the variously infested soils contained in tapered plastic tubes (18; Ray Leach Conetainer Co., Canby, OR). By using data combined from the treatments with inoculum sources, particle sizes, and concentrations, it was possible to calculate and compare infection efficiencies and threshold particle sizes in the two soils, both treated and untreated. Inoculum particles smaller than the threshold particle size had significantly lower infection efficiencies compared to those of the threshold particle size and larger. All tests were replicated ten times and repeated at least twice.

Statistical analysis. A general linear model procedure (SAS Institute, Inc., Cary, NC) was used to compute linear models for each source of inoculum. Each model related the lesions per wheat seedling (Y) to seven terms: soil type (S), inoculum particle size (I), soil treatment (T), soil by inoculum particle size interaction ($S \times I$), soil by soil treatment interaction ($S \times T$), inoculum particle size by soil treatment interaction ($I \times T$), and a regression coefficient (β) times the logarithm of the inoculum particle concentration (C).

$$Y = \mu + S + I + T + S \times I + S \times T + I \times T + \beta C \qquad (1)$$

In this expression, μ represents the average number of lesions per wheat seedling of all data used to develop the linear model. The logarithm of the inoculum particle concentration was used to linearize the relationship between numbers of lesions and concentration of particles. An F-test for interaction between the logarithm of the inoculum particle concentration (C) and the soil type interaction with inoculum particle size ($S \times I$) was significant at $P = 0.05$. Therefore, it was meaningful to calculate and compare slope coefficients for the logarithm of C for each soil-inoculum/particle-size combination (13). Particle size was treated as a discrete independent variable for ease of interpretation because each interval represented an interval of sizes. Tests of hypotheses for common slopes among soil-inoculum/particle-size combinations were conducted and followed by pairwise comparisons to identify which slopes were different by using likelihood ratio F-tests (9).

RESULTS

Infection efficiency and threshold particle sizes of colonized wheat-crown fragments. In untreated soils, the maximum efficiency of *G. g.* var. *tritici* in the largest (0.5–1.0 mm) particles of wheat crowns was 8.15 and 9.33 lesions per milligram of particles in the suppressive and conducive soil, respectively (Table 1). Analysis of these data with the linear model ($R = 0.89$) indicated that the threshold particle size of wheat-crown particles was 0.25–0.5 mm in the suppressive soil and in this same range or larger (i.e., 0.5–1.0 mm) in the conducive soil. These same threshold particle sizes were indicated by the data for maximum infection efficiencies (Table 1). Root lesions were produced by inoculum in particles 0.15–0.25 mm and smaller, but the infection efficiency was markedly lower than that for larger particles. The measured efficiency was generally greater in untreated suppressive soil than in untreated conducive soil (Tables 1 and 2).

Pasteurization resulted in greater maximum infection efficiencies for the colonized crown fragments of all sizes in suppressive soil and for all sizes larger than 0.15 mm in conducive soil (Table 1), but the increase was not significant based on the statistical analysis of data for the linear model slope values (change in the number of lesions per plant per log milligram of inoculum particles [Table 2]).

Infection efficiency of colonized wheat-root fragments. In untreated soil, the maximum infection efficiency for inoculum in fragments of wheat roots was only 0.44 lesions per milligram for 0.5–1.0 mm particles in suppressive soil (Table 1). Particles ranging 0.25–0.5 mm produced only 0.14 lesions per milligram of particles in suppressive soil, and smaller particles produced no lesions (Table 1). Inoculum in 0.5–1.0 mm particles produced significantly more lesions per log particle concentration (slopes) than did inoculum in 0.25–0.5 mm particles (Table 2), indicating that in suppressive soil the threshold particle size for root-particle inoculum was 0.5–1.0 mm. In conducive soil, no lesions were produced by inoculum in any of the sizes of root particles that were tested. Apparently, the threshold particle size of infested root fragments in conducive soil was larger than 0.5–1.0 mm.

The infection efficiency of inoculum in colonized root fragments of wheat roots was greater in pasteurized suppressive and conducive soils than in the same soils not treated (Table 1). For example, particles 0.10–0.15 mm produced 2.09 lesions per milligram in pasteurized suppressive soil and no lesions in untreated suppressive soil. In pasteurized conducive soil, the maximum efficiency was 1.34 lesions per milligram of particles (0.5–1.0 mm) and the smallest infested root particle associated with a lesion was 0.15–0.25 mm, compared with no lesions produced by particles of these same sizes in untreated conducive soil. Analysis indicated that the threshold particle size of root particles was 0.5–1.0 mm in pasteurized suppressive soil and was larger than 0.5–1.0 mm in pasteurized conducive soil.

Infection efficiency of inoculum in oat grains. All sizes of oat-grain particles resulted in lesions on roots in conducive soil and all but the smallest particle (<0.1 mm) resulted in lesions in suppressive soil (Table 1). Analysis of the data with the linear model ($R = 0.92$) indicated that the threshold particle size for oat fragments was 0.25–0.50 mm in both untreated soils. This same

TABLE 1. Influence of a known take-all-suppressive (Shano silt loam) and known take-all-conducive (Ritzville silt loam) soil untreated and pasteurized on the infection efficiencies of different sources and sizes of inoculum of *Gaeumannomyces graminis* var. *tritici*[a] on wheat

Inoculum particle and size (mm)	Maximum infection efficiencies (lesions/mg of inoculum particle)			
	Suppressive		Conducive	
	Untreated	Pasteurized	Untreated	Pasteurized
Colonized wheat crowns				
<0.1	0.1 ± 0.1	0.32 ± 0.3	0	0
0.10–0.15	1.56 ± 0.5	2.8 ± 2.7	0.9 ± 0.6	0
0.15–0.25	2.09 ± 0.4	12.3 ± 4.7	1.15 ± 1.5	3.8 ± 0.7
0.25–0.50	7.26 ± 0.5	10.38 ± 5.1	4.00 ± 2.8	5.73 ± 1.1
0.50–1.0	8.15 ± 1.4	9.88 ± 3.7	9.33 ± 4.0	12.43 ± 1.6
Colonized wheat roots				
<0.1	0	0	0	0
0.10–0.15	0	2.09 ± 1.5	0	0
0.15–0.25	0	1.84 ± 1.0	0	0.29 ± 0.4
0.25–0.50	0.14 ± 0.1	4.56 ± 4.0	0	0.31 ± 0.6
0.50–1.0	0.44 ± 0.2	7.56 ± 7.1	0	1.34 ± 1.0
Colonized oat grains				
<0.1	0	3.41 ± 0.9	0.14 ± 0.1	5.73 ± 2.6
0.10–0.15	0.11 ± 0.1	3.88 ± 0.6	0.34 ± 0.3	11.10 ± 2.0
0.15–0.25	1.20 ± 1.0	7.73 ± 0.7	0.64 ± 0.9	22.76 ± 11.4
0.25–0.50	9.60 ± 2.5	31.20 ± 6.2	16.00 ± 4.0	42.22 ± 14.1
0.50–1.0	10.20 ± 5.1	55.33 ± 10.0	13.33 ± 6.1	46.67 ± 12.9
1.0–2.0	9.33 ± 2.4	21.33 ± 10.8	14.00 ± 7.0	52.67 ± 24.4

[a] Infection efficiencies (the number of lesions per unit mass of particles) were determined for each size of particle in two soils and for three sources of inoculum. Fragments of field-colonized wheat crowns, colonized wheat roots (greenhouse), and axenically colonized oat grains were used as the sources of inoculum. Each source was fragmented and separated into five size classes respectively (six classes for oat grains), and used as sources of inoculum at 10 concentrations (0.01–1.0 mg/g of soil). Maximum infection efficiency of *G. g.* var. *tritici* was the greatest number of lesions recorded per wheat seedling per milligram of inoculum particle. Shano silt loam from near Moses Lake, WA, and Ritzville silt loam from near Lind, WA, were used. Mean values for 20 replicates with standard deviations are presented.

threshold particle size was indicated by the data for maximum infection efficiencies (Table 1).

Pasteurization of the two soils resulted in even greater efficiency of inoculum for all sizes of oat-grain particles, with a maximum of 55.33 and 52.67 lesions per milligram of particles in the suppressive and conducive soils, respectively (Table 1). The smallest size oat particles (<0.1 mm) produced about 3.41 lesions per milligram in pasteurized soil (Table 1). The threshold particle sizes for oat particles were 0.10–0.15 mm in pasteurized suppressive soil and not definable in pasteurized conducive soil (Table 2). The linear model slope values were significantly increased for particles in pasteurized suppressive soil compared to untreated suppressive soil for particles 0.10–0.15 mm, 0.15–0.25 mm, and >1.0 mm (Table 2). In conducive soil, pasteurization increased the linear model slope values for particles up to 0.25 mm and decreased values for particles >0.50 mm.

DISCUSSION

The existence of a suppressive factor in the Shano silt loam from a field where take-all had declined but not in the virgin Ritzville silt loam has been previously established by using the pot-bioassay method (6,15). Suppression observed in the pot-bioassay method as well as that in the field (4) has been evident mainly as either retarded or less colonization of crowns and basal stems of the wheat plants. Unlike the pot bioassay and field tests, the tube test employed in the present study involved only one seedling per container, with the infested soil as a 1-cm-thick layer sandwiched between noninfested vermiculite, and with the inoculum as particles <2.0 mm and at concentrations >0.1% (w/w), which permits an accurate assessment of the relationship between inoculum concentration and disease incidence on the roots. Both the threshold particle size and the infection efficiency of different particle sizes would seem to be highly sensitive indicators of suppressiveness. However, neither the threshold particle size of particle (colonized wheat crowns from the field, colonized wheat roots from the greenhouse, or axenically colonized oat grains) nor the infection efficiencies of these inoculum sources were sufficiently different to account for the known suppressiveness of the Shano silt loam compared with the high take-all conduciveness of the virgin Ritzville silt loam. Indeed, the tendency was for more, rather than fewer, lesions per unit mass of inoculum in the suppressive than in the conducive soil. It would appear, therefore, that the limitation on *G. g.* var. *tritici* in the suppressive soil results from suppression after initial infection rather than suppression of the fungus during its prepenetration and penetration stages.

TABLE 2. The change in number of lesions per plant per unit increase in the logarithm of the inoculum particle concentration as estimated by linear models for a known take-all-suppressive (Shano silt loam) soil and known take-all-conducive (virgin Ritzville silt loam) soil, untreated and pasteurized, with three sources of inoculum of *Gaeumannomyces graminis* var. *tritici* on wheat

Inoculum particle and size (mm)[y]	Lesions/log particle concentration[z]			
	Suppressive		Conducive	
	Untreated	Pasteurized	Untreated	Pasteurized
Colonized wheat crowns				
<0.1	0.53 a	0.50 a	0.04 a	0.00 a
0.10–0.15	1.35 a	1.42 a	0.32 a	0.01 a
0.15–0.25	4.78 b	4.56 b	2.15 a	2.12 a
0.25–0.50	8.12 c	7.56 c	6.14 b	5.71 b
0.50–1.0	9.55 c	8.98 c	7.92 b	7.57 b
Colonized wheat roots				
<0.1	−0.06 a	0.20 a	0.17 a	−0.20 a
0.10–0.15	−0.03 a	0.28 a	0.03 a	0.05 a
0.15–0.25	−0.02 a	2.94 b	0.02 a	0.77 a
0.25–0.50	0.64 a*	5.10 b*	−0.09 a	1.75 a
0.50–1.0	5.28 b*	8.00 c*	0.13 a	2.41 a
Colonized oat grains				
<0.1	−0.26 a	0.98 a	0.88 a*	4.02 a*
0.10–0.15	0.93 ab*	5.00 b*	0.02 a*	4.04 a*
0.15–0.25	1.41 ab*	7.87 b*	0.82 a*	8.15 b*
0.25–0.50	6.80 c	8.06 b	8.67 b	11.65 c
0.50–1.0	7.24 c	8.30 b	10.97 b*	7.29 ab*
1.0–2.0	4.04 bc*	8.11 b*	9.74 b*	4.40 a*

[y] Each inoculum particle size was tested at ten concentrations (0.01–1.0 mg/g of soil) in an assay (19). Ritzville silt loam from near Lind, WA, and Shano silt loam from near Moses Lake, WA, were pasteurized (60 C moist heat for 30 min) or not treated. Inoculum particles were naturally colonized wheat crowns and harvested from a field near Pasco, WA; wheat roots infected in the greehouse; and oat grains axenically colonized.

[z] The number of lesions per plant for a unit increase in the logarithm of inoculum particle concentration (i.e., linear model slope values, see text) were calculated for each size of inoculum particle. Slope values followed by different letters within each column for each inoculum source were significantly different. Slope values followed by asterisks within each particle size in untreated soil versus pasteurized soil were significantly different according to the likelihood ratio *F*-tests ($P = 0.05$).

The greatest differences in infection efficiency for the various kinds and sizes of colonized residues occurred between pasteurized and untreated soils inoculated with axenically colonized oat grains (indicated by asterisks in Table 2). A significant increase in infection efficiency of the larger root particles in response to soil pasteurization also was measured in the Shano silt loam. In contrast, pasteurization of the soil had no significant effect on infection efficiency of infested crown particles of any size tested. This markedly greater infection efficiency of colonized oat particles but not of the crown particles in pasteurized compared with untreated soil suggests that colonization of the particles by soil microorganisms (10) is a major factor in suppression of *G. g.* var. *tritici* in the system we used. The infected crown particles, having come from the field, contained numerous microorganisms as cohabitants with *G. g.* var. *tritici* (7,18). These prior colonists of the infected crown tissue would limit the opportunity for other microorganisms in the soils to colonize the particles once buried in soil (7). This can explain why the elimination of soil microorganisms by pasteurization had no effect on the infection efficiency of this inoculum source; the main competitors were already in the particles. Infested oat grains, on the other hand, contained only *G. g.* var. *tritici* when added to soil, and the infected roots, having been produced in vermiculite in the greenhouse, may have been occupied mainly by *G. g.* var. *tritici*. These inoculum sources, when mixed with soil, were still available for colonization by soil microorganisms (10), which would have reduced the energy available in the residue for *G. g.* var. *tritici*. Pasteurization at 60 C for 30 min would have eliminated the common fast-growing fungi as potential colonists of the inoculum sources (10), which can explain why such treatments resulted in more infections per unit mass of particles. Pasteurization would also produce a flush of nutrients, especially in the suppressive soil, which might also account, in part, for the greater increase in infection efficiency of the pathogen in treated suppressive soil than in treated conducive soil.

Wildermuth et al (16,17) found that the number of hyphae of *G. g.* var. *tritici* in the wheat rhizosphere that grew from axenically colonized oat grains was less in a suppressive soil than in a conducive soil. They suggested on this basis that suppression of the pathogen occurs during growth of the pathogen in the rhizosphere. They introduced untreated soil into fumigated soil, which could have reintroduced fast-growing microorganisms capable of colonizing the oat particles. Our findings, based on number of lesions produced by the pathogen, confirm that prepenetration activity of *G. g.* var. *tritici* is probably greater in fumigated or pasteurized soils than in untreated soils if axenically colonized oat grains are used as the source of inoculum. However, our findings suggest further that the number of infections differ insignificantly between untreated soils whether known to be suppressive (take-all decline) or conducive, except possibly as the soils differ in microorganisms available to compete with the pathogen for the food base. It appears that the agents responsible for take-all decline

are relatively ineffective as saprophytic colonists of the infested particles.

Suppressiveness of soil to take-all is of at least two kinds: specific and general (8). Specific suppression is associated with take-all decline, whereas general suppression is a characteristic of all soils. We propose that the differences in numbers of lesions as noted between the treated and untreated soils for oat-grain and infected-root inoculum is an expression of the general suppression characteristic of all soils. The nutrient supply available in the food base could be reduced (general suppression increased) by any treatment or condition that intensifies competition from organisms capable of colonizing the food base and/or available to compete with the pathogen for root exudates. Specific suppression on the other hand, as detected by the pot bioassy (6,15) and by field observation (4), retards disease after infection but may have little or no detectable effect on the initial frequency of infection. The evidence of Vojinović (14), Cook and Rovira (6), and Weller and Cook (15) indicates that Gram-negative bacteria, especially fluorescent pseudomonads, suppress *G. g.* var. *tritici* both on the root and in the lesions after infection. The present study is in agreement with the hypothesis that postinfection inhibition is responsible for take-all decline. However, once established in lesions, these bacteria could then carry over as cohabitants in the host residue with *G. g.* var. *tritici* and thereby continue to exert a suppressive effect on numbers of emerging hyphae and on prepenetration growth of *G. g.* var. *tritici* in response to new roots (11,19). Specific and general suppression both may be caused by the inhibitory effects of secondary colonists, but with specific suppression resulting mainly from secondary colonists of the developing lesions and general suppression mainly from secondary colonists of the organic food base.

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