Temperature Effects on Take-all of Cereals Caused by *Phialophora graminicola* and *Gaeumannomyces graminis*

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ABSTRACT

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Gaeumannomyces graminis var. *tritici* causes take-all of cereals at low to moderate temperatures. *Phialophora graminicola* is often also present in roots of cereals and was recently found to cause disease at high temperatures (above 24 C) in turfgrasses. Previous studies with *P. graminicola* on cereals, all conducted at 22 C or less, have shown this fungus to be avirulent. The relative virulence of *P. graminicola* and *G. g.* var. *tritici* was, therefore, assessed on wheat, oats, and barley grown at constant 14, 24, or 29 C. Severe take-all resulted from *G. graminis* at 14 and 24 C, and from *P. graminicola* at 29 C. A second study, in which wheat was grown initially at 14, 24, or 29 C, and then some plants transferred to 29 C, indicated that wheat was only susceptible to damage from *P. graminicola* when the plants were at high temperature during the seedling stage. A third study indicated that winter wheat, spring wheat, barley, and triticale were most susceptible to root rots by both pathogens, rye was intermediate, and oats and corn were least susceptible. Further evaluation of the potential for *P. graminicola* to complicate the etiology of take-all is needed where winter cereals are sown early into warm soils or where spring wheat or barley is sown later than normal.

Additional key words: biocontrol.

Take-all of wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) are generally caused by *Gaeumannomyces graminis* (Sacc.) Arx & Oliv. var. *tritici* Walker, and take-all of oats (*Avena sativa* L.) and take-all patch of turfgrasses (mainly *Agrostis* spp.) are caused primarily by *G. graminis* (Sacc.) Arx & Oliv. var. *avenae* (Turner) Dennis (7,13). Take-all diseases caused by these fungi are favored by cool, moist soils (2).

Other fungi with dematiaceous, ectotrophic mycelium similar to that of varieties of *G. graminis* also have been reported from roots of cereals (6,10,14,17). Many of these fungi are parasitic but are not considered pathogenic. *Phialophora graminicola* (Deacon) Walker (= *P. radicicola* Cain var. *graminicola* Deacon; = *P. radicicola* sensu Scott; 25) is one such parasite that has been studied as a potential biocontrol agent against take-all diseases (1,4,14,24). In contrast, we reported that *P. graminicola* incites a hot-weather patch disease of Kentucky bluegrass (*Poa pratensis* L.) turf (19,20) that is characterized by symptoms very similar to those of take-all patch caused by *G. g.* var. *avenae* during cool seasons. Strains of *P. graminicola* from New York have temperature optima of 28–31 C (22), and not all isolates are virulent.

Deacon (6) reviewed literature that indicated that *P. graminicola* may actually improve the growth of several grasses and cereals. We also have observed this trait at low temperatures with isolates that are strongly virulent at high temperatures (22). Turfgrass plants colonized by virulent isolates of *P. graminicola* typically remain asymptomatic at temperatures below 21 C and die within 7–14 days after the temperature is raised to 29 C (22). At 24 C the rate of disease progress (i.e., patch symptom development) on grasses is much slower than at 29 C.

Several studies have illustrated the inability of *P. graminicola* to infect cortical cells with viable nuclei (5,8,9). This is true for isolates of this fungus from New York, but it is also true that the rate of cortical anucleation in roots of *Poa pratensis* is slow at low temperatures and is greatly accelerated as the temperature of incubation is increased (21).

P. graminicola and *G. g.* var. *tritici* are both common in fields of cereal grains, although populations are strongly influenced by cropping and management histories (6,18). The identity of these fungi is based on their growth rates and cultural and conidial characteristics, as well as their ability to form perithecia on wheat (23,26). Vascular necrosis is another characteristic used to distinguish between the two fungi (3). The trap-crop procedure used to isolate the fungi, however, is typically conducted at 20 C or lower. All previous studies of *P. graminicola* in Europe and Australia have, in fact, been conducted at temperatures of 15–20 C, except one at 22 C. Isolates of *P. graminicola* from New York have been considered avirulent at 20 C (22), and pathogenic capabilities have been detectable only at higher temperatures.

This paper reports studies on the relative virulence of *P. graminicola* and *G. g.* var. *tritici*, alone and together, on spring wheat, oats, and barley grown at constant temperatures from 14 to 29 C in controlled-environment chambers. Two additional studies, one with spring wheat grown at constant or at stepwise increasing temperature, and one with seven cereals (spring wheat, winter wheat, barley, oats, rye (*Secale cereale* L.), triticale (*Triticosecale* Wittmack), and corn (*Zea mays* L.)] at constant temperatures are also reported.

MATERIALS AND METHODS

The fungi. One isolate of *P. graminicola* (#57-84) originally collected from *Poa pratensis* affected with patch disease (19) was used in this investigation. *G. g.* var. *tritici* was isolated from roots of winter wheat exhibiting symptoms of severe take-all. Both isolates were selected by a trap-crop technique (14) that favors isolation of pathogenic strains and was used in earlier studies with turfgrasses (20,22). Briefly, root and crown samples from disease-affected turfgrass or wheat were buried in pots of fine gravel in the greenhouse. Wheat seedlings were grown in the pots and isolations of fungi were made from surface-sterilized segments of seedling wheat roots on which ectotrophic, darkly pigmented hyphae were observed through a dissecting microscope. Because perithecia of *G. graminis* and vascular discoloration from either of the

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pathogens was not often evident at the time when isolations were made, all isolates were subsequently identified through distinctions of conidia and growth rate at 25 C, ability to produce perithecia, and characteristics of asci and ascospores of *G. g.* var. *tritici* (23,25,26). All isolates were also tested for levels of virulence in wheat seedling bioassays. Single hyphae tip subcultures were made for selected isolates of *P. graminicola*, and *G. g.* var. *tritici*, and they were then maintained at 5 C on half-strength potato-dextrose agar. Inocula for the studies reported below consisted of perennial ryegrass (*Lolium perenne* L.) grains, which had been autoclaved, infested with a single fungal isolate, and then air-dried. The inoculum was used within 1 yr, and was stored in polyethylene bags at room temperature (20–30 C). Noninfested ryegrass grains were used in control treatments.

The cereals and their culture. Seven untreated seeds of spring wheat cultivar Sinton, spring oats cultivar Ogle, or spring barley cultivar Rodeo were planted into 13-cm-diameter clay pots containing a 3-cm deep basal layer of autoclaved greenhouse soil mix under 9 cm of gravel (percentages in size ranges >2, 1–2, 0.5–1, 0.25–0.5, and <0.25 mm were 28, 38, 25, 7, and 2%, respectively). Inoculum of one fungus (1.25 cm^3 of colonized rye grain), both fungi (1.25 cm^3 each), or neither fungus was distributed over the gravel; seeds of the cereals were placed onto this surface; and 1 cm of gravel was placed over the seed and inoculum. Five replicates of four inoculum treatments for each of three cereals were placed into controlled-environment chambers at 14, 20, 24, or 29 C. All chambers had 12-hr photoperiods and photon flux densities of 275 $\mu E/m^2/sec$ (+/−10) at plant height. Watering was performed once daily. The plant density was reduced to four per pot 1 wk after emergence. Plants were fertilized weekly with a complete nutrient source, beginning at the time of emergence.

Sampling. Six weeks after emergence all plants were collected and evaluated for growth and disease after washing the potting medium from the root system and noting the growth stage (27). Other measurements included the length of the tallest leaf on each plant, number of leaves per plant, number of tillers per plant, and weight of oven-dried shoots and roots. Individual plants within each pot were rated for disease severity as well as presence or absence of perithecia. Seminal and coronal root rot ratings were as follows: 0 = no evidence of fungal colonization; 1 = colonization but no discoloration of cortex; 2 = light cortical browning; 3 = intense cortical browning; 4 = light vascular discoloration, usually also with cortical browning; 5 = intense cortical and vascular discoloration; and 6 = roots in an advanced stage of decay. Ratings of subcrown internode and culm disease were as follows: 0 = no discoloration; 1 = light discoloration; 2 = intense discoloration; 3 = advanced stage of decay.

Data analysis. Analysis of variance was performed on plant growth data for each cereal and temperature combination separately. The four inoculum treatments consisted of an untreated control, *P. graminicola* or *G. g.* var. *tritici* alone, and both fungi combined. Single-degree-of-freedom contrasts among the means were used to determine significant differences between treatments. Logarithmic transformations were performed as necessary to correct for nonnormality and heteroscedasticity. Disease severity data also were analyzed separately for each temperature and cereal combination. Chi-square analysis was used to determine the overall treatment effect as well as to evaluate specific comparisons among treatments. In order to minimize the number of cells with expected frequencies less than five, disease severity ratings were collapsed into two categories: 0 = healthy, >0 = diseased. When expected frequencies were small, i.e., less than 1, Fisher's exact test was employed as an alternative to the chi-square test for comparing treatments.

Constant or increasing temperature effects on infection of spring wheat. This study was performed in a manner similar to that reported above, with the following exceptions. Inoculated or uninoculated spring wheat cultivar Alondra was incubated at constant temperatures of 14, 24, or 29 C. Six replicate pots were prepared for each treatment at the two lower temperatures, and three replicates were prepared for treatments at 29 C. The plants were thinned to three per pot 4 days after emergence and, 14 days later, the experiment was divided so that three pots per treatment were removed from the 14 and 24 C chambers and placed into the 29 C chamber. One plant from each pot was sacrificed for evaluation of plant growth and disease at 24 days after seedling emergence, and the remaining plants were sampled at 38 days. Data for each treatment was converted to the proportion of its control, and analyzed by the Fisher's least significant difference test ($P = 0.05$).

Study with seven cereals. This study was similar to the principal experiment, with the following exceptions. Seven cereals were evaluated against inocula of the two pathogens alone, but not against dual inoculations. Incubation temperatures were a constant 14, 24, or 29 C. The cereals included spring wheat cultivar Alondra, oats cultivar Astro, and unidentified cultivars of winter wheat, rye, triticale, barley, and corn. Six replicate pots of each treatment were prepared; three were sacrificed for evaluations of plant growth and disease at 4 wk after seedling emergence and three at 8 wk.

RESULTS

Spring wheat. *P. graminicola* and *G. g.* var. *tritici* each caused take-all and influenced the growth of spring wheat. The influence of each fungus was temperature dependent, and the nearly opposite effects of temperature on diseases caused by the two pathogens were especially notable at 14 and 29 C (Figs. 1 and 2).

P. graminicola did not cause reduced growth at 14 or 20 C but did so at 24 and 29 C (Table 1). This effect was attributable mostly to a reduction in root weight at 24 C and in shoot weight at 29 C. Roots grew poorly in the controls at 29 C (Fig. 1). This pathogen did not influence the growth stage of inoculated plants at the three lower temperatures but reduced it from stage 19 to 17 in plants incubated at 29 C (data not presented). *P. graminicola* caused significant rotting of seminal roots at all temperatures (Table 1), of coronal roots at all except 14 C, and culm blackening only at 29 C. There was a striking influence of temperature on the ability of *P. graminicola* to cause symptoms of take-all (Fig. 2).

G. g. var. *tritici* was most effective in causing growth reductions at low to intermediate temperatures (Table 1). This pathogen reduced all three growth parameters at 14 and 24 C, and leaf elongation at 20 C. None of the growth parameters was significantly influenced at 29 C. Growth stages of plants inoculated with this pathogen did not differ from the controls (data not presented). *G. g.* var. *tritici* caused significant disease symptom development at all temperatures except 29 C (Table 1). The upper temperature limit for take-all by *G. g.* var. *tritici* was between 24 and 29 C (Fig. 2).

Dual inoculations of *P. graminicola* and *G. g.* var. *tritici* caused additive reductions in growth at 14 and 29 C (Fig. 1), temperatures at which the wheat plants grew less vigorously than at 20 or 24 C. This result was significant ($P = 0.01$) for root and shoot weights, but not for plant height. The presence of the two fungi caused plants at 14 C to be harvested at growth stage 16, as compared with stage 19 for the controls and for each pathogen alone (data not shown). A reduced growth stage in the presence of the two pathogens at 29 C was equivalent to that for *P. graminicola* alone. These influences of dual inoculations on plant growth were not reflected in the disease parameters (Fig. 2). In contrast, evidence is presented that dual inoculation of *P. graminicola* with *G. g.* var. *tritici* led to root disease levels comparable to the most virulent individual pathogen at that temperature (Table 1, Fig. 2). An exception is that *P. graminicola* suppressed the severity of culm blackening caused by *G. g.* var. *tritici* at temperatures below 24 C (Fig. 2). This biocontrol principal was significant at 20 C ($P = 0.05$) and 24 C ($P = 0.001$) but not at 14 C. Biocontrol, as reflected by culm blackening assessments, appeared also to be associated with the ability of plant shoots to grow at rates higher than those for plants treated only with *G. g.* var. *tritici* (Fig. 1). In contrast, *G. g.* var. *tritici* did not act as a biocontrol against take-all caused by *P. graminicola* (Fig. 2).

Production of perithecia on wheat infected with *G. g.* var. *tritici* was influenced by temperature (Table 1). The percentages of plants

with perithecia at 14, 20, 24, and 29 C were 32, 20, 0, and 0%, respectively. In contrast, at the same temperatures, the percentages in the dual inoculation treatment were 60, 30, 10, and 7, respectively. The production of perithecia by *G. g.* var. *tritici*, therefore, was markedly suppressed as temperature increased, and was stimulated when this fungus was placed in competition with *P. graminicola*. Perithecia other than those identified as *G. g.* var. *tritici* were not observed.

Inoculation of spring wheat with *G. g.* var. *tritici* in two similar studies conducted earlier yielded results very similar to those reported above, and are therefore not reported. The ability of *P. graminicola* to suppress growth of wheat, and to cause a high-temperature form of take-all, was also repeatable (Table 2). Additionally, when a lower incubation temperature was increased to 29 C when plants were 18 days old, the pathogen ultimately caused root rot equivalent in severity to that at a constant incubation of 29 C. In contrast, the increase in incubation temperature did not influence culm blackening or growth of plants inoculated with *P. graminicola*, as compared with plants incubated at constant temperatures. Take-all induced by *P. graminicola* was therefore important only when the plants were in the seedling stage and growing in a high-temperature environment when *P. graminicola* first colonized the roots.

Barley. Suppression of growth of barley by *G. g.* var. *tritici* was statistically significant mainly at 20 C (Table 3). This pathogen did not influence the stage of barley growth at any temperature; it was always at stage 19 at harvest for the controls and plants inoculated with *G. g.* var. *tritici*. In contrast, the suppressive influence of *P. graminicola* on plant growth and a reduction in growth stage (from 19 to 16) was again most notable at 29 C, although a reduction in

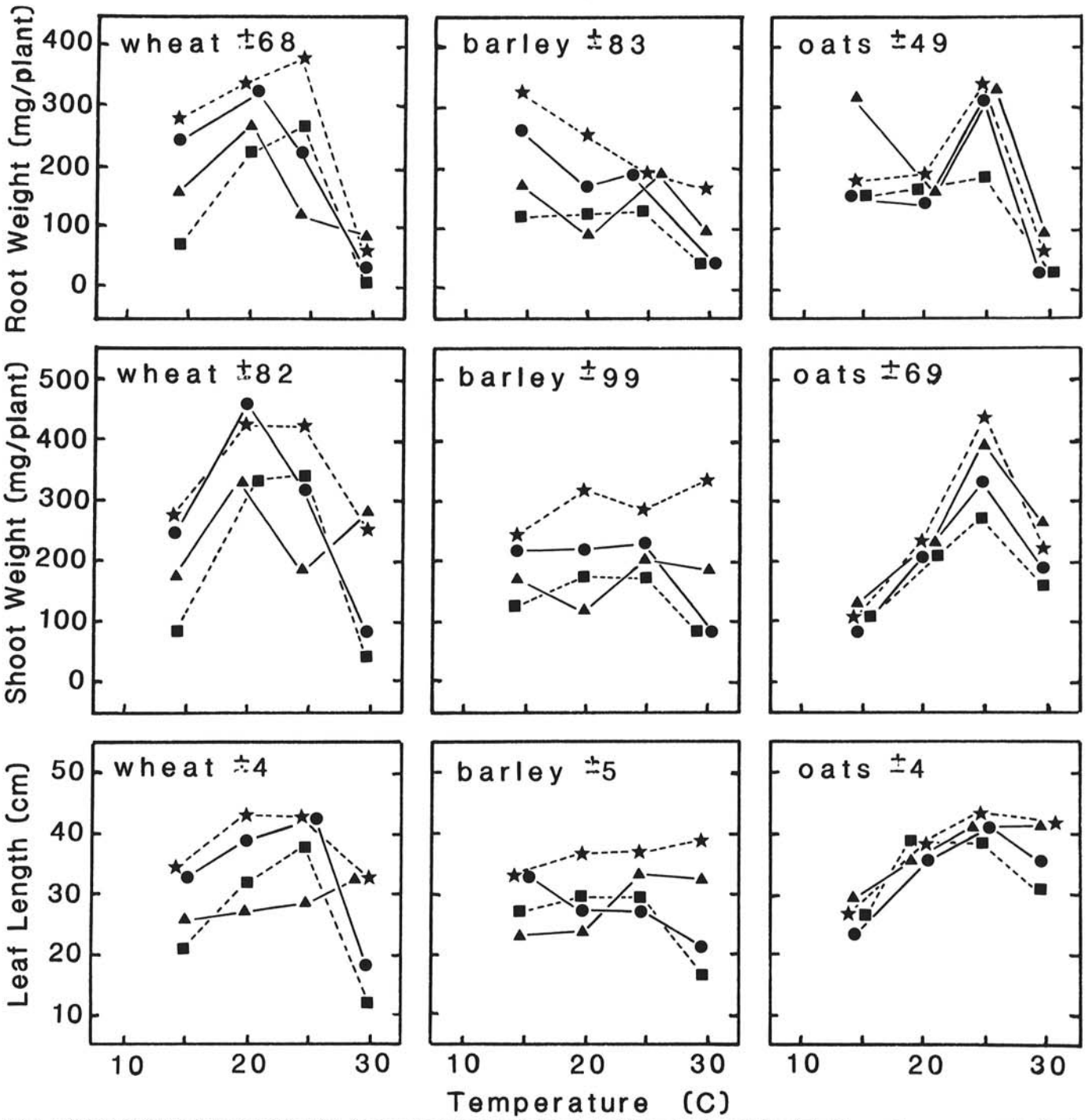

Fig. 1. Influence of *Phialophora graminicola* (•), *Gaeumannomyces graminis* var. *tritici* (△), or dual inoculations (■) of these pathogens on growth of spring wheat, barley, and oats at 14, 20, 24, or 29 C for 6 wk, as compared with noninoculated controls (★). Standard deviations of pooled means within each graph are appended to the cereal designations.

plant height was also caused by *P. graminicola* at 20 and 24 C. Both fungi caused significant rotting of seminal roots at all temperatures (Table 3), but the severity of disease caused by *P. graminicola* was much less than that by *G. g.* var. *tritici* at 14 C, and was equivalent at 29 C (Fig. 2). *G. g.* var. *tritici* caused significant blackening of barley culms at all except 29 C, and P. graminicola did so only at 29 C.

Dual inoculations of the fungi onto barley usually resulted in growth and disease symptoms comparable or greater than that of the more virulent pathogen for each temperature (Figs. 1 and 2). As with wheat, there was less culm blackening ($P = 0.01$) with *P. graminicola* compared with *G. g.* var. *tritici* alone at 20 and 24 C. The growth stage of barley plants at harvest was reduced by dual inoculations at 14 and 29 C. A comparable effect resulted from inoculations with *P. graminicola* at 29 C, but neither fungus, inoculated alone, caused the growth stage to be reduced at 14 C.

Production of perithecia by *G. g.* var. *tritici* on barley was statistically separable from that on uninoculated controls and plants inoculated with *P. graminicola* at all temperatures except 29 C (Table 3). The percentages of barley plants with perithecia at 14, 20, 24, and 29 C were 81, 100, 100, and 9%, respectively, for plants inoculated with *G. graminis*, and 90, 90, 85, and 0% for plants inoculated with both pathogens. Perithecia were produced on barley in much greater abundance than on wheat, and this process was less affected by incubation temperatures for barley than for wheat.

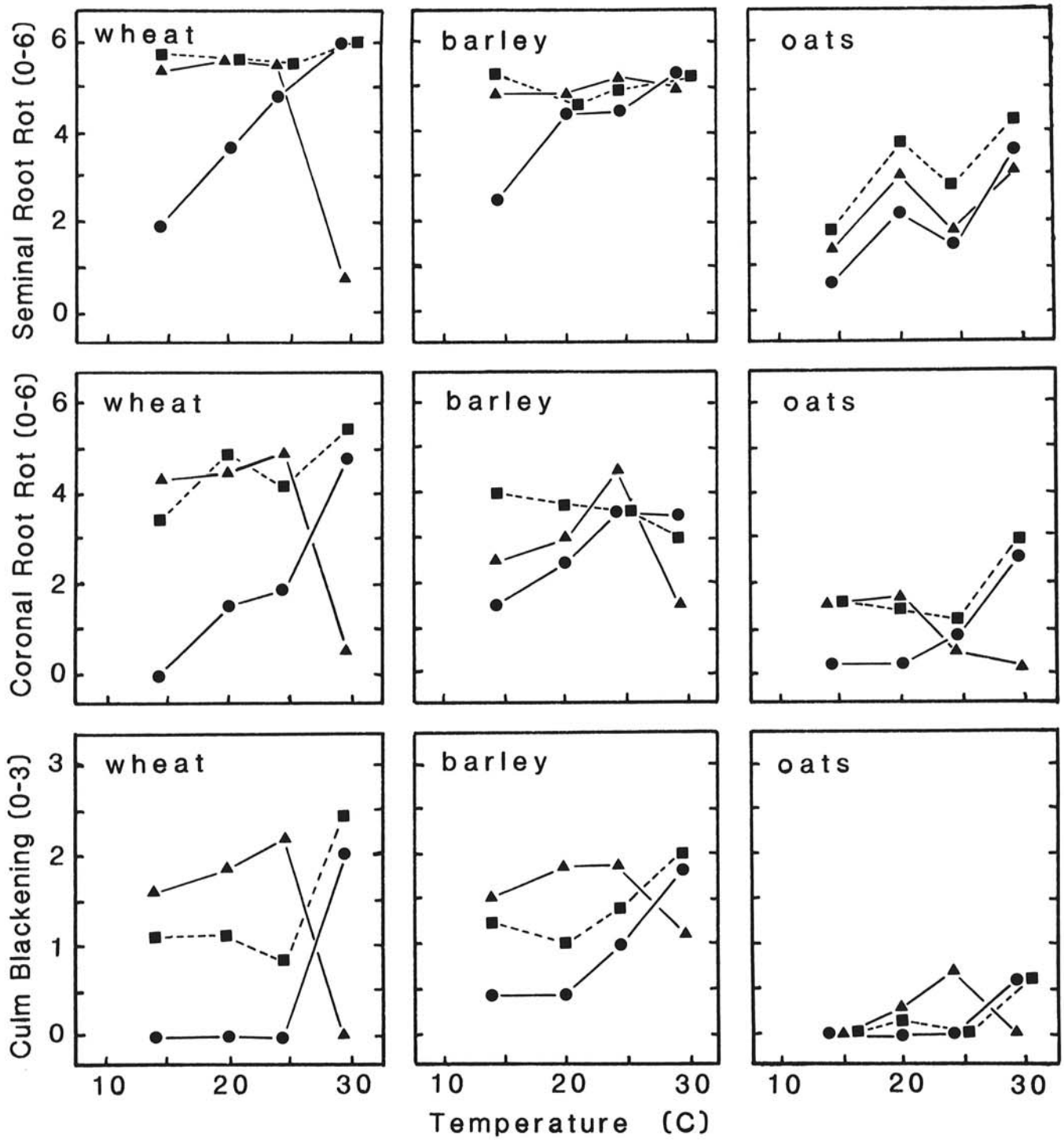

Fig. 2. Influence of *Phialophora graminicola* (•), *Gaeumannomyces graminis* var. *tritici* (△), or dual inoculations (■) of these pathogens on coronal and seminal root rot (0–6 scale, see text) and culm blackening (0–3 scale) of wheat, barley, and oats grown for 6 wk at 14, 20, 24, or 29 C. Plants grown in noninfested pots (controls) exhibited no root discoloration or culm blackening.

Oats. *G. g.* var. *tritici* caused statistically significant rotting of seminal roots at all temperatures, and of coronal roots at 14, 20, and 24 C (Table 4). Nevertheless, this pathogen never caused a reduction in any growth parameter at any temperature and caused root weights to increase ($P = 0.01$) at 14 C. In contrast, *P. graminicola* caused rotting of seminal roots at all temperatures and of coronal roots at 24 and 29 C, but in no case caused differences in plant growth (Table 4). In general, dual inoculations caused root rot indices comparable to those of the more virulent pathogen at any one temperature. *P. graminicola* and *G. g.* var. *tritici* only caused low to moderate levels of coronal root rot and culm blackening, even when temperatures were considered very favorable for pathogenesis. Neither pathogen, inoculated alone or together, caused a change in the growth stage of oats at any temperature.

The overall pattern of temperature effects on production of perithecia on oats (Table 4) was very similar to that on barley (Table 3). Percentages of oat plants with perithecia of *G. g.* var. *tritici* at 14, 20, 24, and 29 C were 65, 95, 70, and 5%, respectively, and 64, 100, 30, and 0% in the dual-inoculum treatment.

Comparisons among cereals. Data presented in Tables 1, 3, and 4 indicate that *P. graminicola* and *G. g.* var. *tritici* caused a higher level of disease on wheat than on barley and much higher than on oats. Comparisons between growth and disease parameters for the uninoculated controls vs. each of these pathogens were made 48 times (perithecia comparisons omitted) during statistical analyses. These comparisons for wheat, barley, and oats were significantly different in 60, 60, and 33% of all cases, respectively.

Findings similar to those reported above (6-wk-old plants) resulted from our investigation of relative tolerances of seven cereals (4 wk old) to these pathogens (Tables 5 and 6). The most informative measurements are reported, including leaf length, root weight, total biomass, culm blackening, perithecial development on culms, and root rot indices for seminal and coronal roots. Little information was achieved by measurements of shoot growth, tillering, and numbers of leaves on each plant.

The growth of wheat, barley, and triticale was affected more by *G. g.* var. *tritici* than was that of oats, rye, and corn (Table 5). The pathogen caused larger reductions in root growth and total biomass of wheat and triticale than of barley but had no effect on barley plant height. *G. g.* var. *tritici* caused more severe culm blackening and root rot on wheat, barley, and triticale than on rye,

TABLE 1. Summary of statistical analyses for measurements of the effects of *Phialophora graminicola* (Pg) and *Gaeumannomyces graminis* var. *tritici* (Ggt) on growth[a] and disease[b] of spring wheat incubated at four temperatures

Treatment comparisons	Leaf height	Shoot weight	Root weight	Seminal root rot	Coronal root rot	Culm blackening	Perithecia[c]
14 C							
Control vs. Pg	nd[d]	ns	ns	***	ns	ns	ns
Control vs. Ggt	**	*	*	***	***	***	**
Control vs. Pg + Ggt	**	**	**	***	***	***	***
Pg vs. Ggt	*	ns	ns	***	***	***	**
20 C							
Control vs. Pg	ns	ns	ns	***	***	ns	ns
Control vs. Ggt	**	ns	ns	***	***	***	*
Control vs. Pg + Ggt	**	ns	ns	***	***	***	**
Pg vs. Ggt	**	ns	ns	**	*	***	*
24 C							
Control vs. Pg	ns	*	**	***	***	ns	ns
Control vs. Ggt	**	**	**	***	***	***	ns
Control vs. Pg + Ggt	ns	ns	**	***	***	***	ns
Pg vs. Ggt	**	*	**	ns	*	***	ns
29 C							
Control vs. Pg	**	**	*	***	***	***	ns
Control vs. Ggt	ns	ns	ns	ns	ns	ns	ns
Control vs. Pg + Ggt	**	**	**	***	***	***	ns
Pg vs. Ggt	**	**	**	***	***	***	ns

[a] Growth parameters analyzed by single-degree-of-freedom linear contrasts.
[b] Disease parameters analyzed by chi-square analysis of Fisher's exact test, after data grouped as <1 = healthy or ≥ 1 = diseased.
[c] Perithecia data grouped by 0 = absent or >0 = present.
[d] Significance levels are $P<0.001$ (***), $P<0.01$, (**), $P<0.05$ (*), or $P>0.05$ (ns).

TABLE 2. Influence of *Phialophora graminicola* on growth and disease of spring wheat at three constant and two increasing temperature regimes

Characteristic	Plant age (days)[a]	Temperature (C)[b] 14	24	29	14/29	24/29	lsd 0.05
Plant growth[c]							
Leaf length (cm)	24	1.0	1.0	0.5	1.1	0.9	...
	38	1.0	0.9	0.6	0.8	0.9	0.3
Root weight (mg/plant)	24	1.2	1.0	0.6	0.7	1.5	...
	38	1.2	1.0	0.6	0.8	1.2	0.3
Total biomass (mg/plant)	24	0.9	0.8	0.4	1.3	0.9	...
	38	1.0	1.0	0.3	1.6	1.2	0.4
Plant disease[d]							
Culm blackening (0–3)	24	0	0	0.7	0	0	...
	38	0	1.0	2.3	0	1.0	0.5
Roots potted (%)	24	14	34	80	59	63	...
	38	52	43	93	81	88	18.0

[a] Days after seedling emergence.
[b] Constant temperatures of 14, 24, or 29 C through the entire study, or transfer from 14 to 29 C or 24 to 29 C when seedlings were 18 days old.
[c] Growth parameters reported as proportions of the nontreated control values; i.e., controls = 1.0.
[d] See text for description of culm blackening scale; roots rotted include both seminal and coronal roots.

oats, and corn. This pathogen also caused some blackening of rye culms, and intermediate levels of root rot on rye, oats, and corn, but it did not reduce the growth of these species. Perithecial development was also high on wheat, barley, and triticale, less on rye, and absent on oats. A small percentage of corn culms supported perithecia at 24 C. These data report the results from a harvest of 4-wk-old plants. Trends were similar for plants grown at the constant temperatures for 8 wk, and only the trends for perithecial development warrant specific discussion. Perithecia were produced on every wheat, barley, rye, and triticale plant incubated for 8 wk at 24 C. At this temperature, perithecia were also formed on 75 and 8% of the oat and corn plants, respectively. Nearly all (86–100%) of the mature wheat, barley, and triticale plants also supported perithecial development at 14 C, whereas none was found at this temperature on oats, rye, and corn. At 29 C, perithecia only developed on triticale plants (20% of the plants).

Linear correlations of relative growth values (i.e., growth of infected plants/uninfected plants) for the seven cereals reported in Table 5 indicated that the effect of *G. g.* var. *tritici* on root growth at 14 C was the primary determinant of relative plant biomass ($R^2 = 0.995$; $P = 0.01$) production at this temperature. Correlations of growth vs. disease parameters at 14 C also indicated that *G. g.* var. *tritici* affected root growth in this experiment more by causing rotting of coronal roots ($R^2 = -0.880$; $P = 0.05$) than of seminal roots ($R^2 = -0.696$; not significant). The same pattern of correlations occurred for this comparison of plants incubated at 29 C ($R^2 = -0.991$, $P = 0.05$, and -0.769, respectively, for coronal and seminal roots).

TABLE 3. Summary of statistical analyses for measurements of the effects of *Phialophora graminicola* (Pg) and *Gaeumannomyces graminis* var. *tritici* (Ggt) on growth[a] and disease[b] of barley incubated at four temperatures

Treatment comparisons	Leaf height	Shoot weight	Root weight	Seminal root rot	Coronal root rot	Culm blackening	Perithecia[c]
14 C							
Control vs. Pg	ns[d]	ns	ns	***	***	ns	ns
Control vs. Ggt	**	ns	ns	***	***	***	***
Control vs. Pg + Ggt	**	ns	*	***	***	***	***
Pg vs. Ggt	**	ns	ns	*	*	**	***
20 C							
Control vs. Pg	**	ns	ns	***	***	ns	ns
Control vs. Ggt	**	**	*	***	***	***	***
Control vs. Pg + Ggt	*	**	*	***	***	***	***
Pg vs. Ggt	ns	ns	ns	ns	ns	***	***
24 C							
Control vs. Pg	**	ns	ns	***	***	ns	ns
Control vs. Ggt	ns	ns	ns	***	***	***	**
Control vs. Pg + Ggt	*	*	ns	***	***	***	**
Pg vs. Ggt	*	ns	ns	ns	ns	**	**
29 C							
Control vs. Pg	**	*	*	***	***	**	ns
Control vs. Ggt	ns	ns	ns	***	***	ns	ns
Control vs. Pg + Ggt	**	*	**	***	***	**	ns
Pg vs. Ggt	**	ns	ns	ns	*	*	ns

[a] Growth parameters analyzed by single-degree-of-freedom linear contrasts.
[b] Disease parameters analyzed by chi-square analysis of Fisher's exact test, after data grouped as <1 = healthy or ≥ 1 = diseased.
[c] Perithecia data grouped by 0 = absent or >0 = present.
[d] Significance levels are $P<0.001$ (***), $P<0.01$ (**), $P<0.05$ (*), or $P>0.05$ (ns).

TABLE 4. Summary of statistical analyses for measurements of the effects of *Phialophora graminicola* (Pg) and *Gaeumannomyces graminis* var. *tritici* (Ggt) on growth[a] and disease[b] of oats incubated at four temperatures

Treatment comparisons	Leaf height	Shoot weight	Root weight	Seminal root rot	Coronal root rot	Culm blackening	Perithecia[c]
14 C							
Control vs. Pg	ns[d]	ns	ns	**	ns	ns	ns
Control vs. Ggt	ns	ns	**	***	***	ns	***
Control vs. Pg + Ggt	ns	ns	ns	***	***	ns	***
Pg vs. Ggt	*	ns	**	**	***	ns	***
20 C							
Control vs. Pg	ns	ns	ns	***	ns	ns	ns
Control vs. Ggt	ns	ns	ns	***	***	ns	***
Control vs. Pg + Ggt	ns	ns	ns	***	***	ns	***
Pg vs. Ggt	ns	ns	ns	*	***	ns	***
24 C							
Control vs. Pg	ns	ns	ns	***	**	ns	ns
Control vs. Ggt	ns	ns	ns	***	*	***	**
Control vs. Pg + Ggt	ns	ns	*	***	***	ns	**
Pg vs. Ggt	ns	ns	ns	ns	ns	***	**
29 C							
Control vs. Pg	ns	ns	ns	***	***	***	ns
Control vs. Ggt	ns	ns	ns	***	ns	ns	ns
Control vs. Pg + Ggt	*	ns	ns	***	***	***	ns
Pg vs. Ggt	ns	ns	*	ns	***	***	ns

[a] Growth parameters analyzed by single-degree-of-freedom linear contrasts.
[b] Disease parameters analyzed by chi-square analysis of Fisher's exact test, after data grouped as <1 = healthy or ≥ 1 = diseased.
[c] Perithecia data grouped by 0 = absent or >0 = present.
[d] Significance levels are $P<0.001$ (***), $P<0.01$ (**), $P<0.05$ (*), or $P>0.05$ (ns).

Spring and winter wheat, barley, and triticale were each very sensitive to *P. graminicola* (Table 6), and these cereals sustained considerable reductions in growth at high temperature. In this study, barley was the cereal most affected by the presence of *P. graminicola* in the root zone. Oats and corn were very tolerant of this pathogen, even though considerable rotting of seminal and coronal roots occurred on corn. Rye exhibited intermediate tolerance to *P. graminicola*.

Linear correlations for the seven cereals at 29 C were not significant for root rot severity and plant growth measurements (coefficients ranged from −0.143 to −0.484). In contrast, strong correlations existed for culm blackening and plant biomass ($R^2 = -0.936$; $P = 0.05$) or root weight ($R^2 = -0.903$; $P = 0.05$). As in the comparison of treatments inoculated with *G. g.* var. *tritici*, the correlation between root weight and plant biomass in the pots infested with *P. graminicola* was high ($R^2 = 0.929$; $P = 0.05$).

When results reported in Tables 5 and 6 are compared, it appears that the spectrum of cereals sensitive to *P. graminicola* is similar to that for *G. g.* var. *tritici*, but that these pathogens exert their influence at opposite temperatures. Root growth, plant biomass production, and culm blackening were affected similarly by the pathogens at their respective favorable temperatures, but there was some evidence from the plant height measurements that *P. graminicola* at 29 C affected growth of more species than *G. g.* var. *tritici* at 14 C. Similarities in effects of the pathogens on seminal root rot indices at 14 and 29 C was noted on each cereal except triticale and corn. On triticale, *G. g.* var. *tritici* caused seminal root rot but *P. graminicola* did not. *P. graminicola* rotted coronal roots on the corn, but *G. g.* var. *tritici* did not.

DISCUSSION

The capacity for *P. graminicola* to cause a high-temperature form of take-all on cereals was demonstrated. This observation

TABLE 5. Relative sensitivities to *Gaeumannomyces graminis* var. *tritici* among seven cereals incubated at 14, 24, or 29 C for 4 wk

Characteristic	Temperature (C)	Spring wheat	Winter wheat	Barley	Oats	Rye	Triticale	Corn
Plant growth[a]								
Leaf length (cm)	14	0.5	0.9	0.9	1.1	1.1	0.8	1.1
	24	0.7	0.6	0.9	1.2	0.9	0.6	1.0
	29	0.9	0.8	1.0	1.1	0.9	0.9	1.1
Root weight (mg/plant)	14	0.3	0.2	0.6	0.9	1.0	0.3	1.6
	24	0.2	0.1	0.2	1.5	0.8	0	0.8
	29	0.7	0.9	1.1	1.0	1.2	0.6	0.6
Total biomas	14	0.4	0.3	0.6	0.8	1.0	0.4	1.5
	24	0.1	0.1	0.3	1.9	0.9	0.1	0.8
	29	0.6	0.6	0.9	1.0	1.0	0.7	0.8
Plant disease[b]								
Culm blackening (0–3)	14	1.5	1.0	1.2	0.2	0.3	2.0	0
	24	2.6	2.4	2.2	0	1.6	2.8	0
	29	0.8	0.7	0.1	0	0	0.9	0
Seminal root rot index (0–3)	14	2.5	2.8	1.6	0.8	1.8	1.7	1.2
	24	2.8	3.0	3.0	1.3	2.6	3.0	1.0
	29	3.0	2.0	2.4	0.7	0.5	3.0	1.4
Coronal root rot index (0–3)	14	1.4	1.4	0.3	0.5	0.6	1.3	0
	24	2.3	2.3	0.4	1.0	1.0	2.6	1.2
	29	1.6	1.6	0.6	0.2	0.1	1.2	0.7
Plants with perithecia (%)	14	58	42	8	0	0	75	0
	24	100	91	72	0	58	92	8
	29	0	0	0	0	0	8	0

[a] Growth parameters reported as proportions of the nontreated control values; i.e., controls = 1.0.
[b] Disease parameters, except plants having perithecia, based on subjective rating scales: 0 = no discoloration; 1 = light discoloration; 2 = intense discoloration; 3 = advanced stage of decay.

TABLE 6. Relative sensitivities to *Phialophora graminicola* among seven cereals incubated at 14, 24, or 29 C for 4 wk

Characteristic	Temperature (C)	Spring wheat	Winter wheat	Barley	Oats	Rye	Triticale	Corn
Plant growth[a]								
Leaf length (cm)	14	1.0	1.1	1.1	1.0	1.2	1.0	1.0
	24	1.0	0.7	0.7	1.0	1.0	0.9	1.1
	29	0.7	0.9	0.6	1.0	0.5	0.7	1.0
Root weight (mg/plant)	14	1.3	0.8	1.3	0.8	1.4	0.8	1.1
	24	1.8	0.4	0.2	1.1	0.9	0.9	1.0
	29	0.3	0.4	0.1	1.1	0.8	0.3	0.8
Total biomass	14	1.2	0.9	1.1	1.0	1.2	0.9	1.1
	24	1.8	0.5	0.5	1.1	0.4	0.9	0.9
	29	0.3	0.3	0.1	0.8	0.6	0.3	0.9
Plant disease[b]								
Culm blackening (0–3)	14	0.2	0	0	0	0	0	0.3
	24	0	0	0.8	0	0	0.4	0
	29	1.3	1.3	2.3	0.4	0.2	1.4	0.1
Seminal root rot index (0–3)	14	1.4	0.2	0	0.1	0.4	0.7	0.8
	24	1.9	2.3	2.1	0.2	1.8	1.9	2.2
	29	3.0	3.0	3.0	1.8	2.7	1.7	3.0
Coronal root rot index (0–3)	14	0	0	0	0	0	0.4	0.7
	24	0.1	1.1	1.2	0.2	0.7	0.9	1.1
	29	1.9	2.1	1.3	0.4	0.4	1.6	2.3

[a] Growth parameters reported as proportions of the nontreated control values; i.e., controls = 1.0.
[b] Disease parameters based on subjective rating scales: 0 = no discoloration; 1 = light discoloration; 2 = intense discoloration; 3 = advanced stage of decay.

supports results of studies with this fungus on Kentucky bluegrass turfs (20,22), and does not conflict with the prevailing viewpoint that this fungus is avirulent on cereals at low temperatures (1,4,9,14,24). Our results also indicate that wheat roots are only susceptible to pathogenesis by *P. graminicola* when the plant is in the seedling stage. When the temperature of incubation was increased to a point more favorable to the fungus than to the plant, after the plant had passed the seedling stage, *P. graminicola* failed to reduce growth even though it did increase disease.

Further studies in growth chambers and in the field are needed to determine whether these findings are of importance only under conditions highly favorable to pathogenesis or are of broader importance. This is important because *P. graminicola* or similar fungi have been found with increasing frequency, either alone or in combination with *G. g.* var. *tritici* varieties, on take-all affected cereals in England and Brazil, according to Hornby (12). It is of particular interest to determine if *P. graminicola* can serve as a take-all pathogen when cereals are seeded during periods when soil temperatures are high. In New York, for instance, winter cereals are typically sown in late September and spring cereals are sown in late April. At planting depth, the mean daily soil temperatures in this region exceed 24 C from mid-May until early September. The mean daily maximum temperatures exceed 30 C from early April to early October (at 5-cm depth), mid-May to early September (10-cm depth), and early June to late August (20-cm depth). Mean daily maximums are also above 24 C from late March to late October (5-cm depth), late April to early October (10-cm depth), and early May to late September (20-cm depth). In New York, the maximum soil temperatures at planting are, therefore, high enough that pathogenesis by *P. graminicola* is possible. Unfortunately, facilities were not available for studies on the effects of fluctuating temperatures at several temperature levels, thus precluding an assessment of the true impact of pathogenesis by *P. graminicola*.

G. g. var. *tritici* was used as a control for comparative purposes in all experimental work reported here. Results of the studies with *G. g.* var. *tritici* alone yielded little new information. We, too, found that this pathogen is most damaging to cereals in cool soils (2), and that wheat, barley, and triticale are more susceptible than rye to take-all, and that oats and corn are the least susceptible of the commercial cereals (15,16). It is important, however, to also note that the overall tolerances of these cereals to infection by *P. graminicola* followed nearly the same pattern as for *G. g.* var. *tritici*, and that the damaging effects from each fungus were most important at temperatures optimal to suboptimal (*G. g.* var. *tritici*) or supraoptimal (*P. graminicola*) for the host, as indicated by growth rates for the uninoculated control plants. It is recognized that cereal species differ in susceptibility to infection by *G. g.* var. *tritici*, and that little or no differences in susceptibility are present among cultivars or lines within species (15). In the work reported here we presented an assessment of relative susceptibilities to *P. graminicola* that are found among single cultivars of seven cereals, but we provided no information about relative differences in susceptibility among cultivars and lines within species. Although the relative susceptibilities to *G. g.* var. *tritici* that we found among species agrees with that reported previously (15), the full expression of triticale's tolerance to *G. g.* var. *tritici* is known to depend on the presence of a field environment (16). This would suggest that the response of triticale to take-all by *P. graminicola* in our study should be interpreted with caution until field studies have been conducted.

Perithecia of *G. g.* var. *tritici* were enumerated on the different cereals to determine the influence of temperature on their occurrence. This was considered important because the presence or absence of perithecia is sometimes used as a diagnostic aid for take-all. Perithecia of *G. g.* var. *tritici* were seldom formed at 29 C in this study. Additionally, the presence of vascular discoloration and/or cortical blackening on roots and culms at high temperature could not be used as presumptive evidence for the presence of *G. g.* var. *tritici*. Therefore, at high temperatures, take-all caused by *P. graminicola* is unlikely to be distinguishable from that caused by *G. g.* var. *tritici* unless more elaborate diagnostic procedures are followed in the laboratory and growth chamber.

The relative abundance of perithecia on each of the cereals at various temperatures is unlikely to have epidemiological significance (11). The role of ascospores in dispersal of *G. g.* var. *tritici* is unclear, but the preponderance of evidence suggests that they are of little or no importance. The fact that the presence of *P. graminicola* on wheat stimulated the production of perithecia when *G. g.* var. *tritici* was also present is interesting, but is unlikely to have an impact on take-all or on survival and spread of the pathogen.

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