Influence of Soil Matric Potential and Soil pH on Cephalosporium Stripe of Winter Wheat in the Greenhouse

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ABSTRACT

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The incidence of Cephalosporium stripe in winter wheat grown in the greenhouse increased twofold to fourfold as soil pH (1:2 in 0.01 M $CaCl_2$) decreased from 7.5 to 4.5; disease severity followed a similar pattern. Incidence of disease increased from twofold to 12-fold as soil matric potential increased from −1.0 to −0.1 bar. Cultivar Stephens exhibited two to three times more disease than either Nugaines or Daws, which were equally susceptible based on incidence and severity of disease. Ratings of these cultivars in the greenhouse correspond closely to ratings obtained under field conditions. In general, these cultivars were affected similarly by soil pH and soil matric potential. The development of severe disease in greenhouse-grown plants in the absence of frozen soil indicates that these factors are not requisite for infection of wheat by *Cephalosporium gramineum*, as previously proposed. It may be possible to screen cultivars for resistance to *C. gramineum* in the greenhouse faster and more reliably than current field screening methods by combining the soil factors most favorable for disease development.

Cephalosporium stripe, caused by the soilborne fungus *Cephalosporium gramineum* Nisikado & Ikata (*Hymenula cerealis* Ell. & Ev.), is a vascular wilt disease of winter wheat (*Triticum aestivum* L.) and other small grains and grasses (7). *C. gramineum* infects plants through root wounds (7,20,26), such as those caused by freeze stress (2), as well as by direct invasion (25). Infection is thought to occur during winter and early spring when frost heaving injures roots (8,22) and inoculum potential of the pathogen is greatest (8,31). Systemic spread of the fungus occurs when conidia are carried through the xylem vessels (7,24,30). Yield losses commonly exceed 50% in areas of the Palouse region of eastern Washington (8).

In Washington state, Cephalosporium stripe is most prevalent in areas with high soil water content in autumn (8). Excess soil and surface water during early winter favors development of the sporodochial stage of the pathogen, *H. cerealis*, which increases both sporulation by the pathogen and dispersal of inoculum (8). High soil moisture content during autumn and winter also increases soil heaving, caused by freezing and thawing, which injures roots. Pool and Sharp (27) suggested that high soil moisture predisposed wheat plants to infection by *C. gramineum*. More disease developed in the greenhouse when plants were grown in soil kept at 35% moisture than at 20% moisture before inoculation. Other vascular diseases, especially those caused by *Fusarium oxysporum* Schlecht emend. Snyd. & Hans., are widely known to be favored by wet soils (14).

Soil pH also influences the occurrence of Cephalosporium stripe. Bockus and Claassen (4) suggested that the wider geographic distribution and increased severity of the disease in Kansas was probably due to decreased soil pH associated with the heavy use of ammonia-based nitrogen fertilizers since World War II. Love and Bruehl (18) confirmed the effect of soil acidity on Cephalosporium stripe in winter and spring wheat by demonstrating increased incidence of disease with decreasing soil pH in the greenhouse.

Because the Palouse area of Washington and Idaho is experiencing rapidly decreasing soil pH due to the use of ammonia-based nitrogen fertilizers (19), it is important to study the relationship of soil pH to other factors related to the epidemiology of Cephalosporium stripe. This paper reports the effects of soil moisture, soil pH, and their interaction on incidence and severity of Cephalosporium stripe on different cultivars of

Table 1. Incidence and severity of Cephalosporium stripe in Nugaines and Stephens winter wheat grown in the greenhouse at four soil pH values

Cultivar	Initial soil pH 5.0	5.6	6.4	7.2
	Disease incidence[a]			
Nugaines	42.4[b]	17.8	14.7	6.6
Stephens	74.1	20.2	36.2	36.1
Mean	58.3	19.0	25.5	21.4
LSD (cultivar) = 20.6[d]				
LSD (mean) = 14.5[e]				
	Disease severity[f]			
Nugaines	0.8	0.1	0.1	0.0[c]
Stephens	2.1	0.3	0.6	0.8
Mean	1.5	0.2	0.4	0.4
LSD (cultivar) = 0.7[d]				
LSD (mean) = 0.5[e]				

[a] Disease incidence calculated as the percentage of stems with symptoms.
[b] Figures represent the mean of three replicates. Data were arc sin square root transformed before analysis. Transformed means are presented.
[c] Stripes were not present in the uppermost four leaves. Therefore, disease severity is rated 0 even though the stems were infected.
[d] Fisher's least significant difference ($P = 0.05$) for comparing means of cultivar within or between columns (simple effects).
[e] Fisher's least significant difference ($P = 0.05$) for comparing overall means of soil pH between columns.
[f] Disease severity based on a 0–4 scale where 0 = stems not exhibiting symptoms in the uppermost four leaves and 4 = stems with symptoms present in the flag leaf (5).

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winter wheat grown in the growth chamber and greenhouse. A preliminary report has been published (1).

MATERIALS AND METHODS

Soil. Thatuna silt loam (TSL) (fine-silty, mixed, mesic Xeric Argialboll) Ap horizon was collected from the Plant Pathology Farm at Pullman, WA in September 1985, air-dried, passed through a 2-mm-mesh sieve, and stored in galvanized cans until use. Soil tests indicated a saturation paste (water) soil pH of 5.84; 16.1 mg/kg NaOAc-extractable P; 273 mg/kg available K; 27.2 mg/kg available NO_3-N; 0.49 mg/kg available NH_4-N; 5 mg/kg available SO_4-S; and 3.0% soil organic matter.

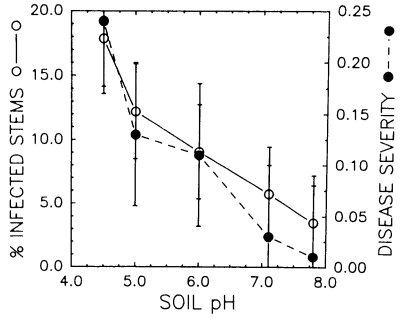

Fig. 1. Influence of soil pH on the incidence and severity of Cephalosporium stripe in the greenhouse. Each point is the mean of 12 cultivars and five replicates. Disease incidence is the percent infected stems, and disease severity is the extent of host colonization, where 0 = no symptoms in the uppermost four leaves and 4 = symptoms in the flag leaf (5). Bars represent the LSD (P = 0.05) for comparing values on the same line.

Table 2. Average incidence and severity of Cephalosporium stripe in 12 winter wheat cultivars grown in the greenhouse at five soil pH values

Cultivar	DS[a]	DI[b]
Cerco	0.1[c]	3.7
Selection-101	0.1	4.5
Luke	0[d]	4.9
Daws	0.1	5.1
Lewjain	0[d]	7.4
Nugaines	0.1	8.4
McDermid	0.2	8.7
Hill 81	0.1	10.8
Cappelle-Desprez	0.2	11.1
Stephens	0.2	14.3
Hatton	0.2	27.4
LSD[e]	0.1	5.5

[a] DS = disease severity based on a 0–4 scale where 0 = stems not exhibiting symptoms in the uppermost four leaves and 4 = symptoms in the flag leaf (5).
[b] DI = disease incidence calculated as the percentage of stems exhibiting symptoms.
[c] Figures represent the mean of five replicates averaged across five pH levels. Disease incidence data were arc sin square root transformed before analysis.
[d] Stripes were not present in the uppermost four leaves. Therefore, disease severity is rated 0 even though the stems were infected.
[e] Fisher's least significant difference (P = 0.05) for comparing means of cultivars within columns.

A soil mix (TSL-mix) containing Thatuna silt loam, vermiculite (Terra-lite #3, W. R. Grace & Co., Cambridge, MA 02140), and washed river sand (90:5:5, w/w), adjusted initially to 17% moisture (w/w on a 105 C oven dry basis), was used for all work in the greenhouse. Preliminary experiments indicated that disease incidence and severity did not differ significantly for wheat grown in TSL alone or TSL-mix; the mix was therefore used in all subsequent studies. Soil moisture release curves for TSL and TSL-mix were similar in the range −0.10 to −15 bars. However, at saturation, TSL contained 50.1% moisture while TSL-mix contained 61.2% moisture. Soil moisture release curves for TSL-mix adjusted to pH 4.5, 5.5, 6.5, and 7.5 did not differ significantly from each other or from unadjusted TSL-mix.

Soil pH of the TSL-mix was adjusted by the addition of either H_2SO_4 or $Ca(OH)_2$ after generating adjustment curves using 0.167 N H_2SO_4 or anhydrous $Ca(OH)_2$ to determine the amounts needed for a given change in pH. $CaSO_4$ was added to soil receiving $Ca(OH)_2$ to compensate for sulfur added to soil adjusted with H_2SO_4. Equilibration occurred within 4–7 days and soil pH in storage was stable for at least 6 mo, the longest time tested. Soil pH was measured using air-dry soil (55 C) mixed 1:2 in 0.01 M $CaCl_2$ (21).

Inoculum. *C. gramineum* was isolated from plants with symptoms of Cephalosporium stripe in fields near Pullman, WA. These isolates were used to prepare the oat-kernel inoculum (13) that was used throughout the study. A mixture of isolates was used to avoid potential problems with differences in virulence among isolates.

Cultivars. The locally grown, soft white winter wheat cultivars Daws, Nugaines, and Stephens were used in most experiments because they differ in resistance to Cephalosporium stripe in the field (12). Nugaines and Daws are the least susceptible and Stephens is most susceptible. Other winter wheat cultivars used in some studies included Lewjain, Hatton, Hill 81, Luke, McDermid, Cappelle-Desprez, Cerco, Jacmar, and Selection 101.

Growth of plants. Four wheat seeds were planted per 15-cm-diameter plastic pot containing 1.15 kg oven-dry equivalent TSL-mix. Oat-kernel inoculum was sprinkled on the soil surface at the time of planting at the rate of 4.5 g/pot (15 ml volume). Pots remained in the greenhouse at 15 C until plants were in the 3–4 leaf stage (approximately 15 days), then moved to a growth chamber and vernalized at 5 C for 4 wk with 8 hr light (approximately 250 $\mu E \cdot s^{-1} \cdot m^{-2}$). After vernalization, the temperature was raised to 10 C with 12 hr light for 4 wk. The plants were then returned to the greenhouse where the temperature ranged from 20 to 28 C days and 15 C nights. Low-pressure sodium lights provided approximately 400–500 $\mu E \cdot s^{-1} \cdot m^{-2}$ of supplemental light for 18 hr/day.

Soil moisture was initially adjusted to the desired gravimetric value and then maintained at that value for 12 wk by watering pots gravimetrically every 3–4 days. In subsequent experiments, soil was initially watered to near-saturation, allowed to dry to the desired gravimetric moisture content, and then maintained at that moisture by regular gravimetric watering. The gravimetric soil moisture varied 1–3% around the target moisture content between waterings. After 3 mo, when plants were removed from the growth chamber, all pots were maintained at approximately −0.3 bar until disease ratings were made. Soil fertility was maintained using NPK + NH_4NO_3 to deliver 386 mg N/kg oven-dry weight of soil at 7 wk and every 3 wk thereafter for the duration of the experiment.

Disease ratings. Disease incidence (DI) was calculated as the percentage of stems with striped leaves. Disease severity (DS) reflected the extent of colonization of the host and was determined by rating each stem on a 0–4 scale, where 4 = a stem with a stripe in the flag leaf; 3 = a stripe in the penultimate leaf; 2 = a stripe in the third leaf down; 1 = a stripe in the fourth leaf down; and 0 = no stripe on the top four leaves of the tiller (5), when plants were at Feeke's growth stage 10.5 (early anthesis) (17). A mean was then calculated and used as a disease severity index. Isolation of *C. gramineum* from randomly selected or suspect symptomatic leaf tissue on acidified Difco cornmeal agar (aCMA; 2 ml 25% lactic acid/L) (11) was used to confirm diagnosis and ratings.

Soil pH. The effect of soil pH on Cephalosporium stripe was studied first using the cultivars Nugaines and Stephens. Seeds were sown in TSL-mix adjusted to pH 5.0, 5.6, 6.4, or 7.2 and maintained with a soil matric potential of −0.2 to −0.1 bar during the first 3 mo of plant growth. In a second pH study, the response of 12 cultivars to Cephalosporium stripe was determined in TSL-mix adjusted to pH 4.5, 5.0, 6.0, 7.1, or 7.8, with the soil matric potential maintained at approximately −0.1 bar.

Soil moisture. The effect of soil moisture on Cephalosporium stripe was studied initially using Nugaines and Stephens sown in unadjusted TSL-mix (pH 5.4) maintained for the first 3 mo at soil matric potentials of −1.0, −0.6, or −0.3 bar. In a second experiment, the cultivars Daws, Lewjain, Nugaines, and Stephens were sown in unadjusted TSL-mix with soil matric potentials of −1.0, −0.3, or −0.1 bar, during the first 3 mo of growth.

Interaction of soil pH and moisture. The interaction of soil pH and soil moisture was first evaluated using Daws, Nugaines, and Stephens. Thatuna silt loam-mix was adjusted to pH 4.5, 5.5, 6.5, or 7.5 with soil matric potentials of −1.0, −0.3, −0.2, or −0.1 bar, during the first 3 mo of plant growth. Treatments were arranged in a 3 × 4 × 4 factorial design.

A second study on the interaction of soil pH and soil matric potential was conducted using the cultivar Stephens. Thatuna silt loam-mix was adjusted to pH 4.5, 5.5, 6.5, and 7.5, and maintained at soil matric potentials of −0.1, −0.3, and −0.6 bar during the first 3 mo of plant growth. Treatments were arranged in a 2×3×4 factorial design. Watering of plants in the greenhouse after vernalization was accomplished with a low-volume, automatic watering system that maintained soil matric potential in the range of −0.3 to −0.1 bar. All other cultural practices were as described previously.

Statistical design. All experiments were conducted using a randomized complete block design, with three to eight replicates, where individual pots represented the experimental units (plots). Analyses of variance of the resultant data were performed, and LSD values were used to differentiate treatment means when appropriate. Data for disease incidence were arc sin square root transformed before analysis; the data reported represent the transformed values (29).

RESULTS

Soil pH. Disease incidence and disease severity increased for all cultivars as soil pH decreased from 7.2 to 5.0. Soil pH and cultivar each had highly significant effects on DI and DS (Table 1). Cultivars differed at all pH levels, except 5.6, with greater DI and DS in Stephens than Nugaines (Table 1). The interaction of cultivar and soil pH was not significant for either DI or DS, indicating that the pH-disease relationship was the same for both cultivars. Small but significant differences occurred between initial soil pH and pH values after 7 wk (intermediate) and the final pH. The intermediate and final soil pH values were 5.1, 5.9, 6.8, and 7.2, and 5.1, 5.9, 6.6, and 7.3, respectively, for initial pH values of 5.0, 5.6, 6.4, and 7.2.

Results of the second soil pH experiment using 12 cultivars of wheat substantiated the influence of soil pH on Cephalosporium stripe (Fig. 1). Soil pH had a highly significant effect on both DI and DS. The effect of cultivar was significant at $P = 0.01$ for DI and at $P = 0.05$ for DS. There was no significant interaction between cultivar and pH, again indicating that the pH-disease relationship was the same for all cultivars. Cultivars varied in susceptibility to *C. gramineum*, with DI ranging from 4 to 27%; DS was low, ranging from 0 to 0.2 (Table 2).

Soil moisture. Disease incidence and disease severity increased in response to increasing soil matric potential in both experiments. In the first study using Nugaines and Stephens, the average DI increased about 12-fold as the matric potential increased from −4.8 bars to −0.3 bar (Table 3). Disease severity also exhibited a dramatic increase over the same range of soil matric potentials. Soil matric potential had a highly significant effect on both DI and DS. However, cultivar effects were significant only for DI. The interaction between soil matric potential and cultivar was not significant, indicating that the soil moisture-disease relationship was the same for all cultivars.

All four cultivars used in the second study on soil moisture responded similarly with increasing DI and DS accompanying increased soil matric potential. Again, the interaction between matric potential and cultivar was not significant. Therefore, only the data for soil matric potential are presented (Fig. 2). Soil matric potential had a highly significant effect on both DI and DS, but cultivars did not differ significantly for either DI or DS.

Interaction of soil pH and moisture. In general, the greatest DI and DS for each cultivar occurred near the lowest soil pH and in the wettest soil (Tables 4 and 5). Both DI and DS increased significantly as soil moisture increased (Table 4) and as soil pH decreased (Table 5).

Disease response of the cultivars to pH and matric potential was similar to previous experiments. Stephens had the largest values for DI and DS, followed by Daws and Nugaines, which were not significantly different.

Statistically, the interactions between soil pH and matric potential and pH and cultivar were significant ($P = 0.05$) for DS, but not for DI. Disease severity data were subsequently analyzed within cultivars and pH levels to determine the basis of these interactions. The pH × cultivar interaction resulted from a greater influence of pH on Stephens than on Daws or Nugaines. The significant interaction for soil pH × matric potential resulted from significant effects of matric potential on disease severity at pH 5.5 and 6.5, but not at pH 4.5 or 7.5.

Table 3. Incidence and severity of Cephalosporium stripe in Nugaines and Stephens winter wheat grown in the greenhouse in Thatuna silt loam and Thatuna silt loam soil mix (TSL and TSL-mix) (pH 5.4) at three soil matric potential values

Cultivar	Soil matric potential (bars)		
	−0.3	−0.6	−4.8
		Disease incidence[a]	
Nugaines	37.1[b]	15.3	0
Stephens	59.1	25.9	7.8
Mean	48.1	20.6	3.9
LSD (cultivar) = 17.2[c]			
LSD (mean) = 12.2[d]			
		Disease severity[e]	
Nugaines	0.7	0.2	0[f]
Stephens	1.6	0.3	0.1
Mean	1.1	0.3	0[f]
LSD (cultivar) = NS[c]			
LSD (mean) = 0.6[d]			

[a] Disease incidence calculated as the percentage of stems exhibiting symptoms.
[b] Figures represent the mean of TSL and TSL-mix with a total of six replicates. Data were arc sin square root transformed before analysis.
[c] Fisher's least significant difference ($P = 0.05$) for comparing means of cultivars within or between columns; NS = nonsignificant F test.
[d] Fisher's least significant difference ($P = 0.05$) for comparing overall means of soil matric potential.
[e] Disease severity is based on a 0–4 scale where 0 = stems not exhibiting symptoms in the uppermost four leaves and 4 = stems with symptoms present in the flag leaf (5).
[f] Stripes were not present in the uppermost four leaves. Therefore, disease severity is rated 0 even though the stems were infected.

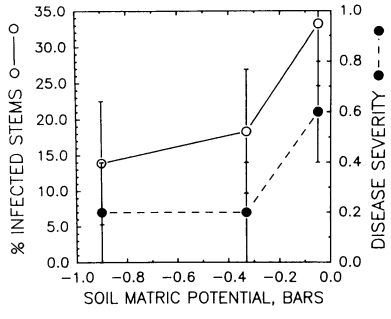

Fig. 2. Influence of soil matric potential on the incidence and severity of Cephalosporium stripe on winter wheat grown in the greenhouse. Each point represents the mean of eight replicates and four cultivars. Disease incidence is the percent infected stems, and disease severity is the extent of host colonization, where 0 = no symptoms in uppermost four leaves and 4 = symptoms in the flag leaf (5). Bars represent the LSD ($P = 0.05$) for comparing values on the same line.

Results of the second pH soil matric potential study were similar to the first: the greatest DI and DS occurred at the lowest pH and in the wettest soil (Table 6). In this experiment, however, the overall DI and DS were much greater than in the first experiment. Again, as in the first experiment, the interaction between soil pH and soil matric potential was not significant ($P = 0.05$) for DI, but was significant ($P = 0.03$) for DS. The interaction between pH and soil matric potential for DS was due to a significant increase in DS with increasing soil matric potential only at pH 4.5, but not from pH 5.5 to 7.5.

Final soil pH. The final soil pH in the first interaction study was affected by the initial soil pH and the matric potential during the first 3 mo of growth. Change in pH was least when initial pH was 4.5 or when matric potential was −0.1 to −0.4 bar, and greatest when initial soil pH was 6.8 or matric potential was −0.7 bar. Final soil pH averaged 4.6, 5.3, 5.9, and 6.7 for initial soil pH values of 4.5, 5.7, 6.8, and 7.5, respectively. There was a highly significant ($P = 0.01$) interaction between pH and matric potential.

In contrast, changes in soil pH in the second interaction study were larger in magnitude and greatest at pH 4.5 and 5.5 and least at pH 6.5 and 7.5. Soil matric potential during the first 3 mo of plant growth did not have a significant effect on final soil pH. Final soil pH averaged 5.9, 6.6, 6.8, and 7.3 for initial soil pH values of 4.5, 5.5, 6.5, and 7.5, respectively.

Table 4. Incidence and severity of Cephalosporium stripe in three winter wheat cultivars grown in the greenhouse at four soil matric potentials

Cultivar	Soil matric potential (bar)				Mean
	−0.1	−0.2	−0.4	−0.7	
			Disease incidence[a]		
Daws	20.7	21.3	17.8	8.8[b]	16.6
Nugaines	23.7	16.5	13.6	13.8	16.9
Stephens	54.8	47.0	37.6	27.2	41.7
Mean	33.1	28.3	22.7	16.6	
LSD (cultivar) = 11.3[c]					
LSD (mean) = 6.5[d]					
			Disease severity[e]		
Daws	0.8	0.6	0.5	0.2	0.6
Nugaines	0.9	0.6	0.4	0.4	0.6
Stephens	2.0	1.7	1.2	0.9	1.4
Mean	1.3	1.2	0.7	0.5	
LSD (cultivar) = 0.5[c]					
LSD (mean) = 0.3[d]					

[a] Disease incidence calculated as the percentage of stems exhibiting symptoms.
[b] Figures represent the mean of six replicates averaged across four pH values. Data were arc sin square root transformed before analysis.
[c] Fisher's least significant difference ($P = 0.05$) for comparing cultivar means within or between columns.
[d] Fisher's least significant difference ($P = 0.05$) for comparing means across soil matric potentials.
[e] Disease severity is based on a 0–4 scale where 0 = stems not exhibiting symptoms in the uppermost four leaves and 4 = stems with symptoms present in the flag leaf (5).

Table 5. Incidence and severity of Cephalosporium stripe disease in three winter wheat cultivars grown in the greenhouse at four soil pH values

Cultivar	Initial soil pH				Mean
	4.5	5.5	6.5	7.5	
			Disease incidence[a]		
Daws	23.1[b]	23.2	18.1	3.3	16.9
Nugaines	29.3	25.3	9.7	3.4	16.9
Stephens	58.4	50.2	38.6	19.5	41.7
Mean	36.9	32.9	22.1	8.7	
LSD (cultivar) = 11.3[c]					
LSD (mean) = 6.5[d]					
			Disease severity[e]		
Daws	0.7	0.8	0.6	0.1	0.6
Nugaines	1.0	0.9	0.3	0.1	0.6
Stephens	2.2	1.9	1.2	0.4	1.4
Mean	1.3	1.2	0.7	0.2	
LSD (cultivar) = 0.5[c]					
LSD (mean) = 0.3[d]					

[a] Disease incidence calculated as the percentage of stems exhibiting symptoms.
[b] Figures represent the mean of six replicates averaged across four soil matric potential values. Data were arc sin square root transformed before analysis.
[c] Fisher's least significant difference ($P = 0.05$) for comparing cultivar means within or between columns.
[d] Fisher's least significant difference ($P = 0.05$) for comparing means across soil pH.
[e] Disease severity is based on a 0–4 scale where 0 = stems not exhibiting symptoms in the uppermost four leaves and 4 = stems with symptoms present in the flag leaf (5).

DISCUSSION

The incidence and severity of Cephalosporium stripe is strongly influenced by both soil pH and soil moisture. In all experiments, DI and DS increased as soil pH decreased from 7.5 to 4.5, or as soil matric potential (during the first 3 mo of growth) increased from −1.0 bar to −0.1 bar. The greatest DI and DS occurred near pH 4.5 and −0.1 bar matric potential in interaction studies. Soil pH appears to have a greater influence on disease development than soil matric potential because the effect of soil pH was always more significant than soil matric potential in statistical analyses. Our results with soil pH confirm those of Love and Bruehl (18) working with soil pH and Cephalosporium stripe of winter and spring wheat, and are similar to results of others working with soil pH and soil moisture effects on Fusarium wilt (3).

In general, final soil pH did not differ from initial pH by more than 0.5 pH unit. An exception was the last interaction study where final soil pH increased 1.4 and 1.1 units at pH 4.5 and 5.5, respectively. One explanation for this may be the low-volume irrigation system used in the greenhouse that applied small volumes of water one to three times per day. Soil moisture was, on the average, higher in this study, leaching of pots did not occur, and the change in soil matric potential between waterings was much less than in previous studies. Interestingly, the incidence and severity of Cephalosporium stripe were about twice that of the first interaction study conducted under very similar conditions without the low-volume irrigation system.

Root wounding as a result of frost heaving is generally thought to be necessary for disease development (8,22,26,28). However, severe disease occurred in this study without severing roots or freezing the soil. Obviously, *C. gramineum* does not require broken roots for penetration, and is capable of penetrating roots by another mechanism under conditions of low soil pH and high soil moisture. Whether the effects of soil pH and matric potential are on the host or the pathogen is not known.

Environmental stresses such as anaerobiosis, low pH, and low temperature probably affect both the host and the pathogen, as well as the other microorganisms in the soil. Increasing soil

moisture can cause incipient soil anaerobiosis, which affects permeability of root membranes, resulting in leakage of cell contents as membranes lose integrity (15). Bailey et al (2) found that exudates from cold-stressed but unruptured roots of wheat increased spore germination, conidiogenesis, and hyphal branching, thus increasing inoculum density in the soil and allowing active penetration of the host by *C. gramineum*.

Likewise, Al^{3+} and H^+ ions can cause injury to wheat roots. In the soils we studied, both H^+ and Al^{3+} ions are present at pH 4.5–5.5, although H^+ ions predominate in agricultural soils acidified by nitrification (6). Nutrient solution studies have shown that H^+ and Al^{3+} ions cause root membranes to become "leaky," and previously adsorbed cations, as well as organic substances, can be lost from roots (16). High soil moisture and low soil pH may thus be important factors that predispose wheat plants to infection by *C. gramineum*.

Several workers have discussed the effects of soil pH and matric potential on *C. gramineum*. Love and Bruehl (18) concluded that soil pH was affecting the parasitic phase of *C. gramineum* rather than saprophytic survival in the soil, because they used a conidial drench when plants were in the 3–4 leaf stage and, therefore, survival was not important. However, the importance of both soil pH and soil moisture on saprophytic survival of *C. gramineum* in colonized straw has been reported (7,9,10) and is probably important under field conditions. Pool and Sharp (27) suggested that inoculum density was reduced under low soil moisture conditions (20%, w/w) because conidia could be adsorbed onto soil colloids and would be unavailable to infect plants. Murray and Campbell (23) found increased sporulation by *C. gramineum* in vitro and on colonized oat kernels on soil as substrate or soil pH decreased from 7.5 to 4.5. Sporulation did not increase as soil matric potential increased from −0.7 to −0.05 bar. They concluded that increased inoculum potential as a result of increased sporulation may be involved in the response of Cephalosporium stripe to soil pH, but it was not involved in the response to soil matric potential.

Low temperature (i.e., < 10 C) during the first 3 mo of growth in this system is important to the development of Cephalosporium stripe. Neither soil pH nor soil moisture affected DI (which was very low; DI = approximately 5%) when wheat plants were grown at 20 C in the greenhouse from seed prevernalized in the refrigerator (Anderegg & Murray, *unpublished data*). It appears that the time interval when wheat is exposed to temperatures less than about 10 C is critical to subsequent disease development. The reason for this apparent low-temperature requirement is unknown. It is known that sporulation by *C. gramineum* in vitro is greatest at 20 C, but on colonized oat kernels on soil it is greater at 5 and 10 C than at 15 C (23). These data suggest that low temperatures are important for inoculum production because some biological factor is reducing sporulation at higher temperatures in soil.

The DS rating, which reflects the extent of host colonization, is more sensitive to soil pH differences than DI, although they respond similarly to the various soil conditions. The severity index is more useful for screening varieties because yield is inversely correlated with disease severity (5). Our system has potential value for screening cultivars for resistance to *C. gramineum* because the ratings for cultivars in greenhouse experiments agree with ratings for the same cultivars in the field (12). It may be possible to screen potential cultivars in the greenhouse using the soil pH and matric potentials most favorable for disease development. Such a system offers the advantages of reducing the time required to screen cultivars in the field and reducing the variation observed in such trials (12).

Table 6. Incidence and severity of Cephalosporium stripe in Stephens winter wheat grown in the greenhouse at four soil pH values and three soil matric potentials

Initial soil pH	Soil matric potential (bar) −0.1	−0.3	−0.6	Mean
		Disease incidence[a]		
4.5	84.2[b]	67.9	50.4	67.5
5.5	56.3	53.3	46.3	52.0
6.5	37.6	23.3	23.8	28.3
7.5	21.4	12.2	27.3	20.3
Mean	49.9	39.2	36.9	
LSD[c] (matric potential) = 10.3				
LSD[d] (pH mean) = 11.9				
		Disease severity[e]		
4.5	4.3	3.2	2.1	3.2
5.5	2.7	2.7	2.3	2.6
6.5	1.7	0.9	0.7	1.1
7.5	0.7	0.4	1.0	0.7
Mean	2.4	1.8	1.5	
LSD[f] (simple effect means) = 1.0				

[a] Disease incidence calculated as the percentage of stems exhibiting symptoms.
[b] Figures represent the mean of four replicates. Data were arc sin square root transformed before analysis.
[c] Fisher's least significant difference ($P = 0.05$) for comparing matric potential means.
[d] Fisher's least significant difference ($P = 0.05$) for comparing pH means.
[e] Disease severity is based on a 0–5 scale where 0 = stems not exhibiting symptoms in the uppermost four leaves and 5 = stems killed prematurely (5).
[f] Fisher's least significant difference ($P = 0.05$) for comparing simple effect means within rows or columns. A significant interaction between soil pH and matric potential prevents comparison of main effect means.

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