

Effects of Root-Wounding and Inoculum Density on Cephalosporium Stripe in Winter Wheat

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ABSTRACT

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Winter wheat cultivars Stephens and Nugaines were grown in soil adjusted to pH 4.6–7.7 and –0.01 MPa matric potential. Root-wounding, inoculum density of *Cephalosporium gramineum*, and soil pH each influenced the percentage of headed tillers with Cephalosporium stripe. In unwounded plants, average incidence of diseased tillers increased from 0.5 to 22.0% as inoculum density increased from 3.4 to 6.4 log₁₀ conidia/g of soil, and from 8.0 to 17.5% as soil pH decreased from 7.6 to 4.7. With plants whose root systems were cut immediately before infesting soil with conidia, average disease incidence increased from 16.1

to 76.7% as inoculum density increased from 1.4 to 4.4 log₁₀ conidia/g. Root wounds were important in infection; with wounding, disease incidence was high even at moderate inoculum densities, regardless of soil pH. Because disease incidence increased with decreasing soil pH in unwounded but not in root-wounded winter wheat plants (where rapid infection of exposed xylem vessels probably occurred), acid soil appears to favor Cephalosporium stripe, at least in part, by promoting increased host susceptibility to root infection, possibly as a result of greater root stress/damage in acid than in neutral or alkaline soil.

Additional keyword: host resistance.

Cephalosporium stripe, incited by the soilborne fungus *Cephalosporium gramineum* Nisikado & Ikata (sporodochial stage = *Hymenula cerealis* Ellis & Everh.), is an important vascular disease of winter wheat (*Triticum aestivum* L.), particularly in the northwestern United States. Mycelium present in parasitically infected

host debris (stubble and straw fragments) is the primary source of inoculum; the fungus does not form specialized resting structures and rarely is seedborne in winter wheat (3,11,13). During cool, wet weather in winter and spring, *C. gramineum* sporulates profusely on infested debris present at or near the soil surface (9,10,44). Conidia that have washed down into soil are the major infective propagules (28,43); inoculum densities as high as 2×10^6 conidia/g soil (Murray, unpublished data) can occur, and

1×10^5 conidia/g soil occur commonly in infested fields (44).

Root breakage caused by heaving of frozen soil increases the incidence of *Cephalosporium stripe* (10,31). In one study, *C. gramineum* rarely established systemic infection of winter wheat when roots were not wounded (39). Mathre and Johnston (28) suggested that conidia are "vacuumed" into exposed xylem vessels of broken roots, followed by systemic spread in the transpirational stream (34). *C. gramineum* produces a high-molecular-weight polysaccharide that restricts water flow through xylem vessels (35) and a phytotoxic compound that causes chlorosis and necrosis of wheat tissues (18).

The apparent requirement of *C. gramineum* for root wounding to infect wheat and its physical restriction within xylem vessels until plant senescence indicates a limited ability for penetrating living cells (32,39). Bailey et al (4), however, showed that hyphae of *C. gramineum* can penetrate the epidermis of wheat roots previously stressed or damaged by freezing; the significance of this type of infection in the epidemiology of *Cephalosporium stripe* is not known.

The incidence of *Cephalosporium stripe* is greater in acid than in neutral or alkaline soil (5), even with apparently unwounded winter wheat plants in the greenhouse (2,23). Love and Bruehl (23) hypothesized that high soil acidity may reduce the need for overt physical wounding of roots for infection to occur. Low soil pH may increase host susceptibility to infection because of greater leakage of pathogen-stimulatory root exudates under acid conditions (2). Low soil pH also favors greater growth, sporulation, and survival of *C. gramineum* (12,33,40).

The incidence of *Cephalosporium stripe* is a function of inoculum density of *C. gramineum*; and disease control resulting from long crop rotations (3 yr or greater), deep plowing, or removal/burning of infested straw has been attributed directly to reduced inoculum (6,19). Both arithmetic (25,27,31) and logarithmic (17,28) relationships between inoculum density and incidence of *Cephalosporium stripe* were found in previous studies. In many of these studies, colonized oat kernels were used as the source of inoculum, although naturally infested straw (14) or laboratory-grown conidia (17,28) were also used.

The primary objectives of our study were to evaluate the effects of root-wounding and inoculum density on the incidence and severity of *Cephalosporium stripe* in winter wheat. The influence of soil pH and stage of plant development at the time of infesting soil with conidia of *C. gramineum* also were evaluated in relation to these factors.

MATERIALS AND METHODS

Soil pH. A soil-mix containing 90% Thatuna silt loam, 5% vermiculite (Terralite 3, W. R. Grace & Co., Cambridge, MA), and 5% washed river sand (w/w) (2) was used. Natural pH of the soil was 5.5 (air-dried and measured in a 1:2 [w/v] suspension of soil and 0.01 M CaCl_2 [30]). Soil-mix was adjusted to pH values of 4.6–7.7 with either H_2SO_4 or $\text{Ca}(\text{OH})_2$ as described previously (2).

Plant-growth regimes. Growth regimes were similar to those in previous studies (2). Soil (1.1 kg oven-dry-wt equivalent) was added to 15-cm-diameter plastic pots, and each pot was sown 0.5-cm deep with four seeds (pregerminated 3 days at 15–18 C) of the winter wheat cultivar Stephens (highly susceptible to *C. gramineum*) or Nugaines (moderately susceptible). Pots were placed in controlled-temperature growth chambers with a 1:2 mixture of fluorescent Sylvania GRO-VHO-WS and Westinghouse CW-SHO-EW lights or a 1:2 mixture of sodium and metal-halide lights. Light intensity in all chambers was 100–170 $\mu\text{E m}^{-2} \text{sec}^{-1}$. Soil in pots was adjusted to a water content (w/w) of 45%, which corresponded to a matric potential of -0.01 MPa based on a moisture-release curve. Soil water content was maintained gravimetrically to within 1–4% of the desired amount by adding water 2–3 times per week. Plants initially were maintained at 15 C with a 12-hr photoperiod for 3 wk, or until they had reached the 4- to 6-leaf stage. Chamber temperature then was decreased to 5 C, with 8 hr light for 5–6 wk, followed by a 3-wk

postvernalization period of 15 C with 12 hr light. Plants then were moved to the greenhouse and watered three times per day with an irrigation system that maintained soil matric potential near -0.03 MPa . High-pressure sodium lights were used to supplement natural sunlight and to increase day length to 16 hr as needed. Temperature in the greenhouse generally was 19–24 C, but occasionally exceeded this range on hot summer days. Soluble plant fertilizer (NPK + NH_4NO_3) was added to all treatments as described previously (2).

Inoculum production. A virulent culture of *C. gramineum* (isolate Cg85-4) was used to produce inoculum. This isolate was selected because of its typical growth rate, cultural morphology, and response to pH in vitro (33), and also because it incites typical disease symptoms in winter wheat. Oat kernels artificially colonized by *C. gramineum* were prepared as described previously (15). Conidial inoculum was prepared by culturing the fungus 3–4 days at 20–23 C in 25–40 ml of freshly made potato-dextrose broth (200 g of potato and 20 g of dextrose per liter) in flasks on a shaker (85 rpm). Fungal mycelium was removed by filtering the liquid culture through cheesecloth. Conidia were washed twice by low-speed centrifugation (3,800 g) and resuspended in sterile deionized water. Concentrations of conidia in final suspensions were determined by hemacytometer counts and confirmed by dilution-plating on a medium selective for *C. gramineum* (CGSM) (40). Percent germination of conidia in final suspensions was 98–99%.

Soil inoculum densities. Inoculum was applied to soil either at the start of the 5-C vernalization period when plants were in the 4- to 6-leaf stage, (Feekes' scale 1–2) or 1 wk before the end of the 15-C post-vernalization period when plants had tillered (about Feekes' scale 3). The former will be referred to as "early inoculation" and the latter as "late inoculation." Early inoculated plants were used in all experiments unless indicated otherwise.

Conidial suspensions were applied as 100-ml drenches, which were diluted appropriately for desired amounts of inoculum. For example, to achieve inoculum densities of $0, 1 \times 10^2, 1 \times 10^4,$ and 1×10^6 conidia/g dry soil, respectively, pots were drenched with suspensions containing $0, 1.1 \times 10^3, 1.1 \times 10^5,$ and 1.1×10^7 conidia/ml. We have previously shown that the initial distribution of conidia in soil under these conditions is relatively uniform (40). An oat-kernel inoculum treatment (2) was included in some experiments by placing colonized oat kernels (4.5 g/pot) on the soil surface at the start of vernalization.

Root-wounding. Plant root systems were wounded immediately before (30–60 min) applying spore suspensions to soil. Roots were cut by inserting a sharp knife into the soil at a 45° angle about 2.5 cm from the base of each plant, which resulted in individual roots being cut at depths of 2–4 cm below the soil surface. A 4-cm-wide cut then was made through the soil directly underneath each plant.

Disease assessment. Disease incidence (% diseased tillers) was evaluated at the end of the 15-C postvernalization period ("immature" plants) and again after heading ("mature" plants). On immature plants, only tillers with four or more leaves were examined, because those younger often had no symptoms, even on otherwise severely infected plants. On mature plants, all headed tillers were evaluated for disease; symptomatic tillers also were rated for stripe severity by a modification of the rating system of Bockus et al (7), where 4 = striping on flag leaf, 3 = striping on penultimate leaf, 2 = striping on third leaf down, and 1 = striping on fourth leaf or below. Asymptomatic tillers were not included in the disease-severity ratings. Pieces of representative diseased tillers were placed on CGSM, and the presence of *C. gramineum* was confirmed by microscopic observation after incubation at 20 C for 2 wk. Plant height (mean of four plants per pot) and weight (air-dry weight of headed tillers) also were determined at the end of each experiment.

Statistical analyses. Experiments were designed as randomized complete blocks, with a factorial arrangement of treatments replicated three to six times. Inoculum densities of *C. gramineum* were converted to \log_{10} (conidia/g dry soil + 1), which are expressed as $\log_{10} c/g$. Disease-incidence data were subjected to

the arc sine square root transformation of percentages (0–100%) to degrees (0–90°) to improve homogeneity of error variances (21). Transformed means are presented and expressed as percent diseased tillers in figures. Data were subjected to analyses of variance, and the main effects of inoculum density and soil pH were partitioned into linear sums of squares (21). When significant ($P < 0.05$) interactions were present, separate regression sums of squares were partitioned out for each level of the interacting factor. The results of all studies were confirmed in one or more repeat experiments.

RESULTS

Unwounded plants. Effect of inoculum density. The incidence of disease on tillers of immature, unwounded plants was less than 1% regardless of inoculum treatment. On headed tillers, however, disease incidence increased in a linear ($P < 0.001$) manner with increasing inoculum density over the range of 3.4–6.4 \log_{10} c/g, whereas there was a negative linear ($P < 0.001$) relationship between disease incidence and soil pH (Fig. 1). Disease incidence averaged 15.5 and 9.8% ($P < 0.05$) in cultivars Stephens and Nugaines, respectively.

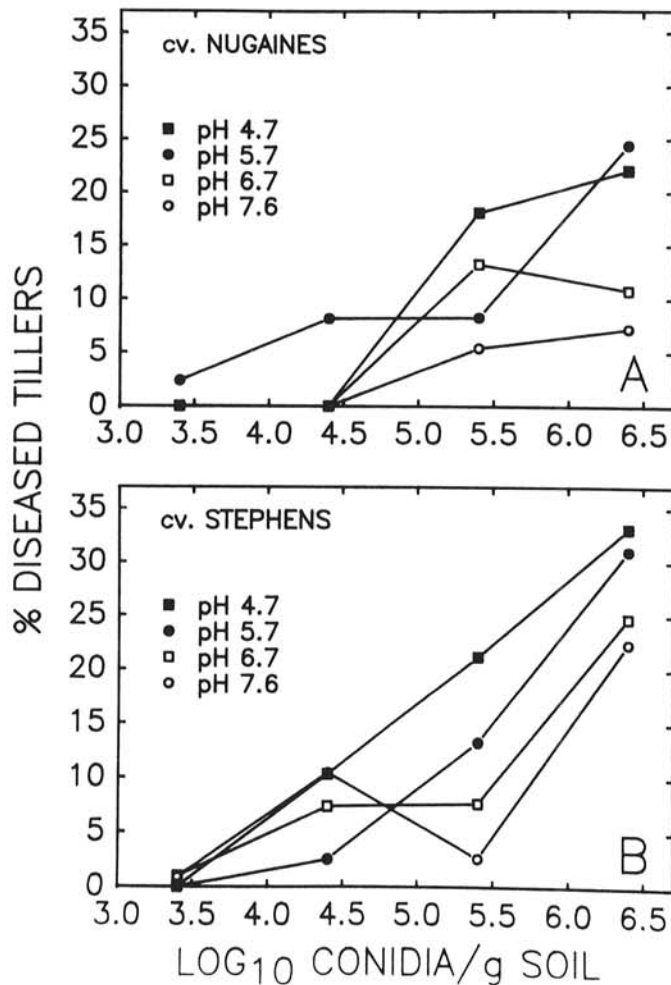


Fig. 1. Effect of inoculum density of *Cephalosporium gramineum* (\log_{10} conidia/g soil) and soil pH on incidence of *Cephalosporium* stripe in headed tillers of unwounded winter wheat (soil was infested with conidia before vernalization). **A**, Cultivar Nugaines. **B**, Cultivar Stephens. Each point represents the mean of six replicates. For both cultivars, there were significant ($P < 0.001$) linear regressions of disease incidence on both inoculum density and soil pH. Data for 3.4 \log_{10} c/g was not examined statistically; the 95% confidence interval for all other individual points is $\pm 9.5\%$.

Disease incidence on headed tillers of plants exposed to oat-kernel inoculum (which resulted in 6.0–6.6 \log_{10} c/g [40]) averaged 41.5, 45.2, 35.8, and 33.0% at soil pH 4.7, 5.7, 6.7, and 7.6, respectively, and 43.9 and 33.9% for cultivars Stephens and Nugaines, respectively.

There was a positive linear ($P < 0.001$) relationship between inoculum density and disease severity on symptomatic tillers; disease severity averaged 1.7, 2.8, and 3.2 at 4.4, 5.4, and 6.4 \log_{10} c/g, respectively. Disease severity in plants exposed to oat-kernel inoculum was 3.5. There was no significant effect of soil pH or cultivar on disease severity.

Effect of inoculation time. Disease incidence on headed tillers averaged 31.2 and 14.0% ($P < 0.05$) in early and late-inoculated plants, respectively. Disease severity also was greater in early than in late-inoculated plants (2.3 and 1.5, respectively).

Root-wounded plants. Effect of inoculum density. The incidence of disease on both immature and headed tillers of root-wounded plants increased in a linear ($P < 0.001$) manner with increasing inoculum density over the range of 1.4–4.4 \log_{10} c/g; however, there was no significant effect of soil pH (Fig. 2A–D). Disease incidence in cultivars Stephens and Nugaines, respectively, averaged 39.8 and 29.1% ($P < 0.001$) on immature tillers (Fig. 2A & B), and 56.1 and 45.0% on headed tillers (Fig. 2C & D). Similar effects were found for root-wounded plants in another study (Fig. 3A–D), where linear relationships between inoculum density and disease incidence occurred over the range of 0–4.0 \log_{10} c/g. From 2.0–6.0 \log_{10} c/g, however, the relationships between inoculum density and disease incidence deviated significantly ($P < 0.001$) from linear, and maximum disease was reached at 4.0 \log_{10} c/g (Fig. 3C & D).

There was a positive linear ($P < 0.001$) relationship between inoculum density and disease severity; at 1.4, 2.4, 3.4, and 4.4 \log_{10} c/g disease severity averaged 1.9, 2.4, 2.3, and 2.7, respectively. Disease severity averaged 2.8 and 2.1 ($P < 0.001$) in cultivars Stephens and Nugaines, respectively. Soil pH had no effect on disease severity.

Effect of inoculation time. Overall incidence of disease on headed tillers of root-wounded plants was greater ($P < 0.001$) with late than with early inoculation (71.1 and 57.4%, respectively) (Fig. 3C & D), whereas disease severity was not affected by inoculation time.

Plant growth. Unwounded plants. Plant weight averaged 3.8–3.9 g at 3.4–6.4 \log_{10} c/g, which did not differ significantly from control plants (4.0 g); however, the weight (3.7 g) of plants exposed to oat-kernel inoculum was significantly less ($P < 0.05$). There was a positive linear ($P < 0.05$) relationship between soil pH and plant weight, which averaged 3.8, 3.6, 4.1, and 4.0 g at pH 4.7, 5.7, 6.7, and 7.6, respectively. Similar results occurred for plant height in other experiments, except in some studies the reduced growth at low pH was not statistically significant.

Root-wounded plants. Linear regressions of plant height and weight on inoculum density were highly significant ($P < 0.001$), whereas soil pH generally had little effect on growth of root-wounded plants (Fig. 4).

In all experiments (unwounded and root-wounded plants) there were moderate-to-high correlations of disease incidence with plant height ($r = -0.42$ to -0.87 , $P < 0.001$), plant weight ($r = -0.32$ to -0.78 , $P < 0.05$ – 0.001), and number of headed tillers per plant ($r = 0.36$ – 0.49 , $P < 0.05$ – 0.001).

Plant isolations. *C. gramineum* was isolated from all representative diseased plants. In one study, *C. gramineum* was isolated from 4.2, 12.2, 56.5, 74.4, and 64.7% of asymptomatic tillers from root-wounded, immature plants previously inoculated with 1.0, 2.25, 3.0, 4.75, and 6.0 \log_{10} c/g, respectively. In contrast, *C. gramineum* was detected in only 2–3% of asymptomatic tillers from unwounded immature plants, even with inoculum densities as high as 6.0 \log_{10} c/g.

Final soil pH. For all experiments, pH changed < 0.3 unit from initial values when soil was assayed at the end of the 15-C postvernalization period. Final soil pH at the end of one representative experiment was 5.3, 5.7, 6.3, and 6.9, respectively, for initial values of 4.7, 5.7, 6.7, and 7.6.

DISCUSSION

Broken roots appear to provide a major avenue for infection of winter wheat by *C. gramineum*. Regardless of soil pH, Cephalosporium stripe increased dramatically with root-wounding, resulting in 60–90% diseased tillers at 3.4–4.0 \log_{10} c/g. This contrasts with unwounded plants, where relatively little disease (7–33%) occurred even at 6.4 \log_{10} c/g, or with oat-kernel inoculum (6.0–6.6 \log_{10} c/g), where disease incidence was 27–49%. The greater incidence of disease in plants exposed to colonized oat kernels, which occurred without root-wounding, was probably an inoculum-density effect. Oat kernels provided a continuous source of conidia that resulted in very high inoculum densities (6.0–6.6 \log_{10} c/g) throughout the vernalization and postvernalization periods. In contrast, conidial drenches, which were applied only once, provide a gradually declining inoculum density because survival of conidia of *C. gramineum* in soil at 5 C and -0.01 MPa is only about 10–40% after 5–6 wk (40).

Gradually declining inoculum densities (i.e., over time), which occur at both -0.01 and -0.03 MPa soil matric potential (40), complicate the observed relationships between inoculum density and disease incidence. This is especially true for disease incidence evaluations made on older plants whose roots have not been cut. With these plants, 'natural infections' (via naturally created root wounds or direct penetration) probably occurred over a relatively long period of time, during which conidial population densities would have been decreasing. This problem, however, should have

been less severe with plants whose roots had been cut, where the majority of infections probably occurred rapidly (within 1 wk) following inoculation but before appreciable root-healing or wound-plugging had occurred. For this reason, direct comparison of relationships between inoculum density and disease incidence between unwounded and root-wounded plants is difficult; however, conidial inoculum densities needed to cause disease in unwounded plants were several \log_{10} -fold orders of magnitude higher than those required to cause similar levels of disease in root-wounded plants (4.4 versus 1.4 \log_{10} c/g, respectively). Therefore, even with nonconstant levels of inoculum, differences in infection rates between unwounded and root-wounded plants still are clearly evident. There also appears to be a direct association between logarithm of conidial inoculum density and disease incidence; however, the exact mathematical relationships cannot be accurately determined from these studies because inoculum densities were not maintained at constant levels throughout the experiments.

The mechanism by which acid soil increases the incidence of Cephalosporium stripe in "unwounded" plants probably operates before or during infection of roots, and not postinfection. Additional evidence for the apparent lack of any aboveground, pH-mediated resistance mechanism is that soil pH did not affect disease severity. This result differs from previous work (2); however, evaluations for disease severity made here included only symptomatic tillers, whereas previous evaluations (2) were made from all tillers (i.e., symptomatic and asymptomatic). When all

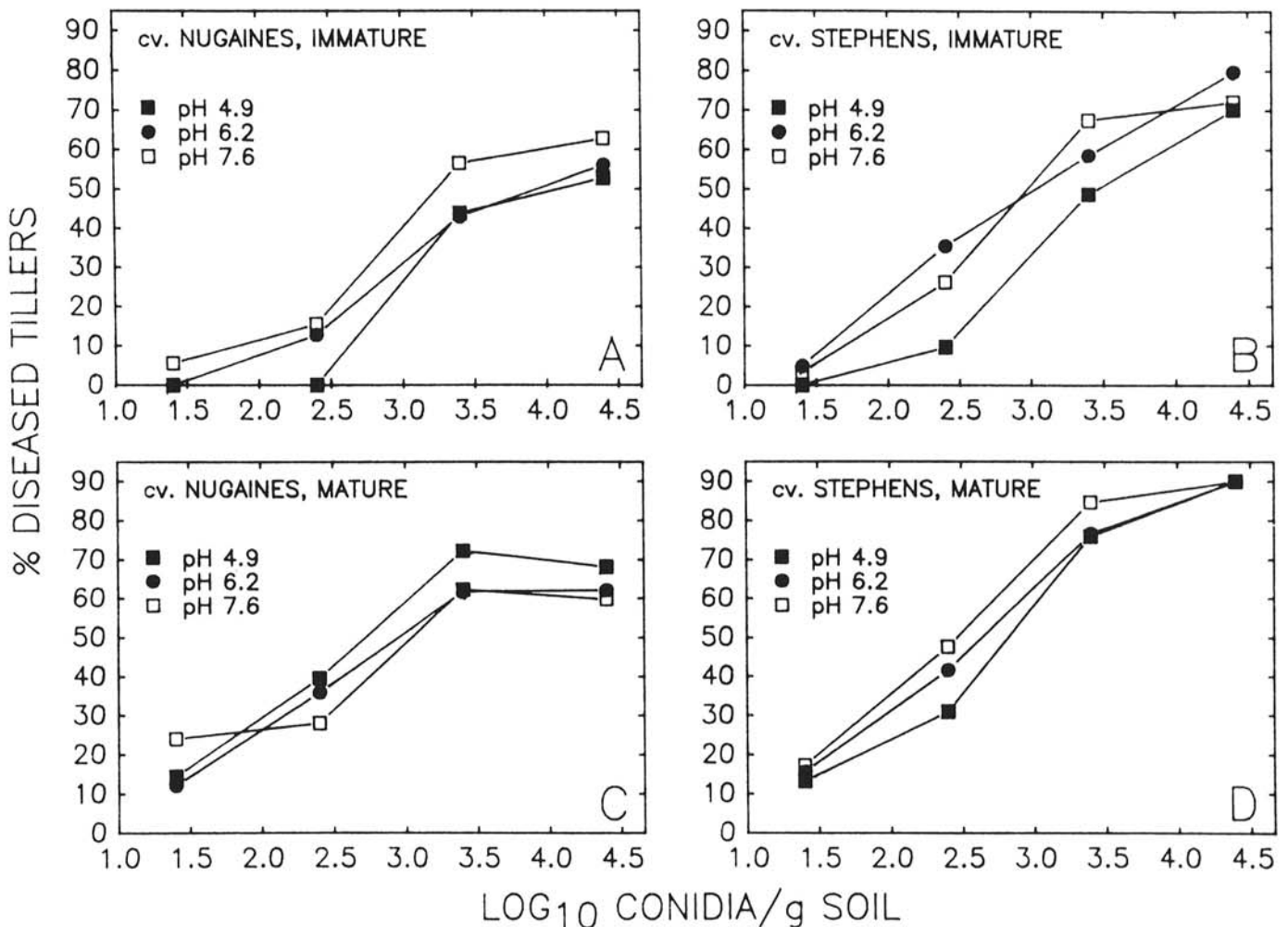


Fig. 2. Effect of inoculum density of *Cephalosporium gramineum* (\log_{10} conidia/g soil) and soil pH on incidence of Cephalosporium stripe in root-wounded winter wheat (soil was infested with conidia before vernalization). A, Cultivar Nugaines, immature plants. B, Cultivar Stephens, immature plants. C, Cultivar Nugaines, mature plants. D, Cultivar Stephens, mature plants. Each point represents the mean of five replicates. Linear inoculum density-disease incidence regressions all were significant at $P = 0.001$. The 95% confidence intervals of individual data points for immature and mature plants are ± 11.6 and $\pm 12.3\%$, respectively.

tillers are included in disease-severity evaluations, the overall rating is actually a composite value that reflects not only disease severity but also disease incidence.

Under natural field conditions, root breakage through processes such as soil heaving always would occur to some extent; wheat is only moderately tolerant of acid soil (24), and the amount of breakage may be increased at low pH due to decreased root elasticity or tensile strength resulting from damage to root surfaces. Wheat roots also could be more prone to natural breakage in acid than in neutral soil, especially at points of lateral-root emergence. Alternatively, low soil pH may slow down the rate of wound-healing in broken roots. Low soil pH also favors greater growth, sporulation, and survival of *C. gramineum* (12,33,40).

The logarithmic relation between inoculum density and incidence of Cephalosporium stripe has been found previously under natural field conditions (14) and could have important practical implications. Unless the amount of inoculum (i.e., naturally infested straw) in a field is reduced by rotation or other measures to a relatively low level, its influence on disease occurrence is likely to be small. Rather, the most important determinants will be environmental conditions (e.g., temperature, moisture, soil pH) and other epidemiological factors, such as root-wounding. Light intensity also may influence disease incidence. Relatively low intensities such as those used in these studies may stress wheat plants and cause increased exudation of pathogen-stimulatory root exudates, which may result in more disease as

compared with higher light intensities; however, this was not tested.

Logarithmic relationships between inoculum density and disease incidence occur with other vascular pathogens, such as the various forma specialis of *Fusarium oxysporum* Schlecht. (1,16,20,26,38). The theoretical basis for a logarithmic relation between inoculum density of *C. gramineum* and incidence of Cephalosporium stripe is not known. The number of root infections should be proportional to the arithmetic inoculum level, assuming the number of infection sites is not limiting (41). Perhaps, there are a limited number of infection sites, but the logarithmic relation also may be a function of the influence of internal pathogen-inoculum concentration (within xylem vessels of roots) on subsequent invasion of developing tillers. Alternatively, there may be a logarithmic relation between amount of inoculum in xylem vessels in stems/leaves and disease expression. For instance, when the pathogen is present in tillers at very low levels, only a small percentage may develop symptoms; based on plant-isolation data, we know that *C. gramineum* can occur within developing tillers without any visible striping. Supporting evidence for this hypothesis is that disease severity usually increased with increasing inoculum density of *C. gramineum* in soil. Also, with wounding, the severity of striping on tillers of immature plants was slight at 1.4–2.0 \log_{10} c/g, but increased steadily as inoculum was increased up to 6.0 \log_{10} c/g, which caused severe striping and sheath-necrosis.

In unwounded plants, more disease resulted with early than

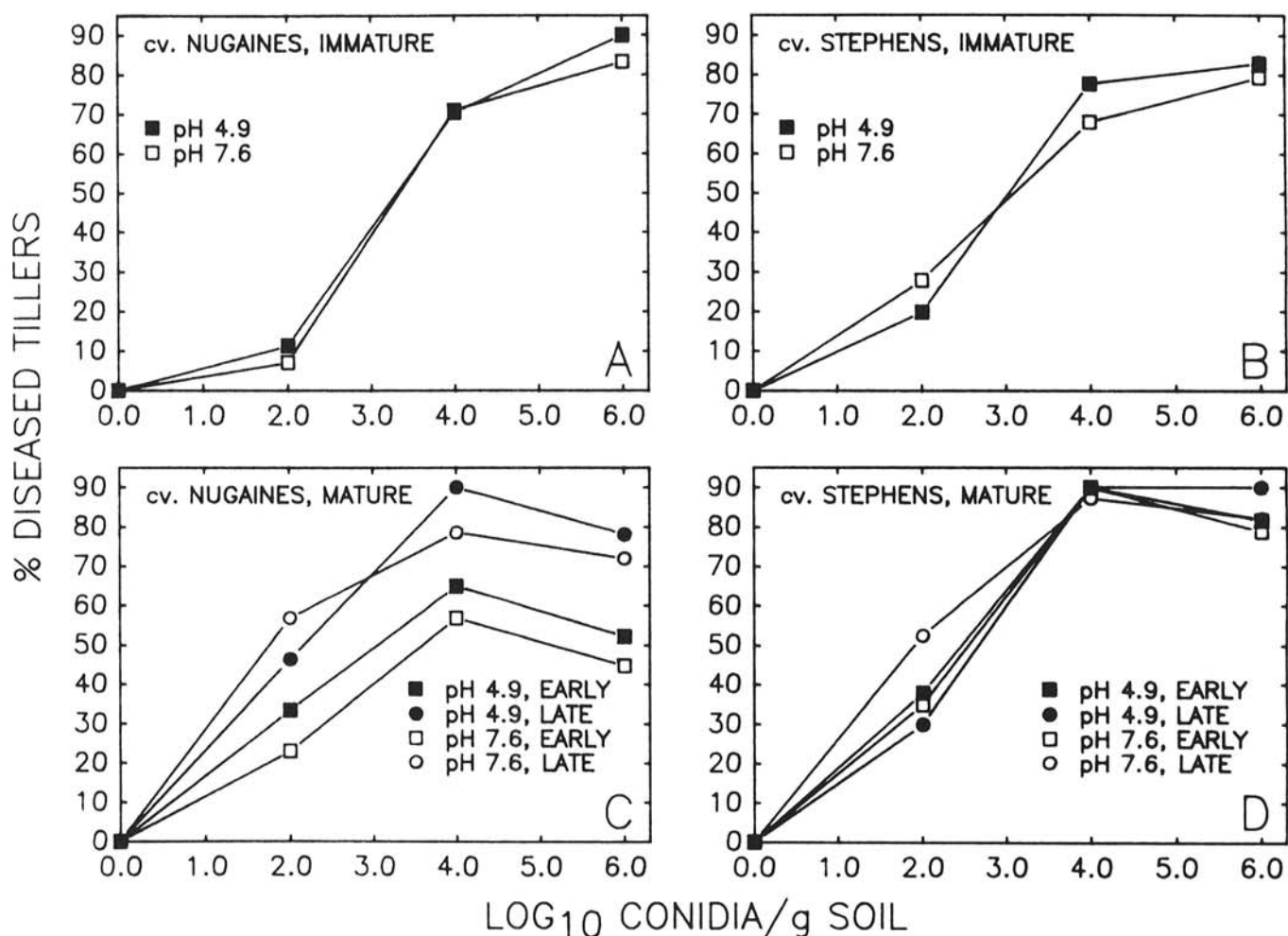


Fig. 3. Effect of inoculum density of *Cephalosporium gramineum* (\log_{10} conidia/g soil), time of inoculation, and soil pH on incidence of Cephalosporium stripe in root-wounded winter wheat. Each point represents the mean of five replicates. A, Cultivar Nugaines, immature plants (early inoculated only). B, Cultivar Stephens, immature plants (early inoculated only). C, Cultivar Nugaines, mature plants. D, Cultivar Stephens, mature plants. For mature plants, early = soil infested with conidia before vernalization, and late = soil infested with conidia after vernalization. The 0 inoculum level was not examined statistically, but over 2.0–6.0 \log_{10} c/g there were significant ($P < 0.001$) quadratic regressions of inoculum density on disease incidence. The 95% confidence intervals of individual data points for immature and mature plants are ± 12.1 and $\pm 12.0\%$, respectively.

with late inoculation. When plants are not subject to overt root-wounding, survival of conidia in soil would be a major factor affecting the number of root infections. Conidia in soil survive longer at 5–10 than at 15–25 C (22,44). In early-inoculated plants, root infections probably occurred throughout the entire vernalization period due to relatively good survival at 5 C. However, in late-inoculated plants, the number of infections probably was reduced because of poor survival at 15–25 C, even though late-inoculated plants had substantially larger root systems (dry weights four to five times greater, unpublished data) than early inoculated plants.

Time of inoculation had the opposite effect in root-wounded plants, where more disease occurred with late- than with early inoculation. This indicates that *C. gramineum* does not have an absolute requirement for cold temperature to infect wheat roots. With root-wounded plants, the majority of infections probably occurred within 1 wk of inoculation; therefore, conidial survival would not have been important. Rather, the most important factor affecting disease would have been the number of available infection sites at the time of inoculation. Cut-roots of late-inoculated plants undoubtedly had more infection sites (due to greater number and size of roots) than those of early inoculated plants. Early-fall planting of winter wheat typically increases the incidence of Cephalosporium stripe as a result of greater root mass during the winter and early spring months, when infection by *C. gramineum* normally occurs (27,36,37).

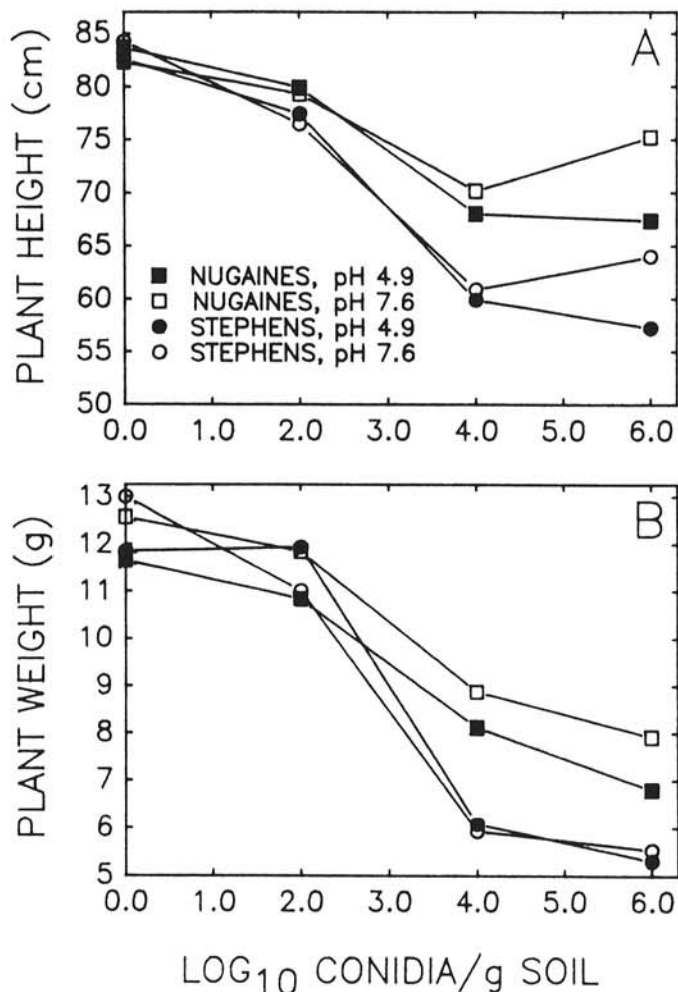


Fig. 4. Effect of inoculum density of *Cephalosporium gramineum* (\log_{10} conidia/g soil) and soil pH on growth of winter wheat (roots were wounded before infesting soil). **A**, Plant height. **B**, Plant weight (air-dry wt of tillers with heads). Each point represents the mean of 10 replicates. Linear regressions of plant growth on conidial inoculum density were significant at $P = 0.001$. The 95% confidence interval of individual data points for plant height and plant weight are ± 2.8 cm and ± 3.6 g, respectively.

Host resistance was not overcome completely by root-wounding; similar results have been reported by others (25,42). Mathre and Johnston (28) and Martin et al (25) speculated that host resistance may operate by restricting pathogen movement through the crown, because above-ground hypodermic inoculation of tillers overcame resistance. The crown region of a winter wheat plant is a complex aggregation of compressed nodes through which the fungus must pass in order to infect developing tillers (31). Based on our studies with root-wounded plants, a crown-associated resistance mechanism is possible, but host resistance may operate at the level of root-infection as well, because in other studies (23,29) differences among cultivars were minimized with root wounding. Morton and Mathre (31) found no differences among cultivars in resistance to root injury, but still thought that there may be differences in rate of wound healing.

Cultivar Stephens always had greater reductions in plant growth than Nugaines under severe disease conditions; however, growth of both cultivars was substantially reduced. Cephalosporium stripe has been reported to cause reduced growth and yield in numerous studies. Increased tillering of diseased plants also was observed along with reduced growth, which concurs with observations made by Bruehl (8). However, increased tillering in diseased plants does not always occur (17).

The effect of soil pH on plant growth appeared primarily to be a function of the influence of soil pH on incidence of Cephalosporium stripe. In unwounded plants, low soil pH always increased disease incidence and, thus, was associated with reduced plant growth. However, disease incidence in root-wounded plants was high regardless of soil pH, and all plants showed greatly reduced growth.

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