Infection of Field-Grown Winter Wheat by *Cephalosporium gramineum* and the Effect of Soil pH

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ABSTRACT

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Field experiments were conducted at the Plant Disease Research Farm, Pullman, WA, from 1989 to 1993 to determine when *Cephalosporium gramineum* infects winter wheat, which plant parts are infected, and the effect of soil pH on infection (1991 to 1993). *C. gramineum* was isolated from winter wheat plants beginning in October each year before soil freezing occurred, confirming that soil freezing was not necessary for infection of winter wheat by the pathogen. *C. gramineum* was isolated frequently from seminal roots, crown roots, and stems, but infrequently from subcrown internodes. Since *C. gramineum* was rarely found in subcrown internodes, crown roots appeared to be the primary infection court. Likewise, *C. gramineum* was rarely isolated from roots with intact root tips or from root tissue near intact root tips, suggesting that the pathogen may have infected plants by colonizing senescent root cortical tissue, followed by penetration of the vascular system. In 2 years, *C. gramineum* was isolated from fewer crown roots of plants grown in soil with pH 6.7 to 7.2 than pH 4.7 to 5.9, but not until February or March. Increased infection of roots at low pH may have contributed to increased disease incidence; however, final disease incidence was greater for plants grown in the low pH soil in only 1 of the 2 years of this study.

Additional keywords: *Hymenula cerealis*, *Triticum aestivum*, vascular disease.

Cephalosporium stripe is a vascular disease of winter wheat incited by the soilborne fungus *Cephalosporium gramineum* Nisikado & Ikata (sporodochial stage: *Hymenula cerealis* Ellis & Everh.). The pathogen survives in colonized host tissue (10), sporulating profusely in the fall when temperature decreases and soil moisture increases (25). Previous workers concluded that *C. gramineum* infects plants in the winter and early spring through root wounds created by soil freezing and heaving (4,9,10,23,24,48), but direct evidence for this does not exist. Although infection of wheat plants by *C. gramineum* has been studied in the greenhouse and in vitro (4,8,37), the mechanism of infection under field conditions, the time of year when infection occurs, and the plant part(s) where infection occurs are not known. Nisikado et al. (36) observed hyphae and conidia of *C. gramineum* in roots only near the crown or stem bases, and not toward the root tips. Pool (38) was unable to find infected plants in December, March, or April in Montana and concluded that infection probably occurred in the spring. Bonde (8) attempted to isolate *C. gramineum* from stems and roots of field-grown plants beginning in November, but could not recover the fungus until April. Bruehl (9) believed that infection occurred through root wounds, but was unable to isolate *C. gramineum* from roots or crowns of field-grown, naturally infected plants.

Soil pH of agricultural soils in the Palouse area of Washington and Idaho is declining because of the long-term use of ammonium-based nitrogen fertilizers (21). Cephalosporium stripe is more severe in soils with pH 4.5 to 5.5 than soils with pH 6.0 or greater (3,7,20,34). The mechanism by which soil pH influences disease is unknown. Low pH favors growth, sporulation, and survival of *C. gramineum* both in culture and in soil (31,33,42). However, Specht and Murray (43) concluded that the increase in sporulation and survival is not large enough to completely account for the observed increase in disease in acid soils, since the relationship between inoculum density and disease incidence is logarithmic. In addition, when roots are mechanically wounded, thereby allowing conidia to directly enter the vascular system, soil pH has no effect on disease incidence (43). Low pH may cause direct injury to roots (18,28,44) or it may predispose roots to infection by *C. gramineum*, especially in years when root injury from soil freezing is not a significant factor (34,43).

The experiments described herein were designed to determine when infection of winter wheat occurs in the field and through which part of the wheat plant *C. gramineum* enters and becomes established. A third objective was to determine whether soil pH influences infection of roots by *C. gramineum*.

MATERIALS AND METHODS

Experimental sites and cultural practices. Experiments were conducted during the 1989 to 1990, 1990 to 1991, 1991 to 1992, and 1992 to 1993 crop years. Hereafter, these will be referred to as the 1990, 1991, 1992, and 1993 crop years, respectively. Two experimental sites, approximately 30 m apart, were located on the Washington State University Plant Disease Research Farm, Pullman. These two sites were used previously to investigate the effect of soil pH on disease incidence (34). Winter wheat was grown in the two experimental sites in alternate years with an intervening year of fallow; wheat was sown at site 1 (knoll) in 1990 and 1992 and at site 2 (flat) in 1991 and 1993. Both sites

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were on Thatuna silt loam (TSL) (fine silty, mixed, mesic Xeric Argialboll). In 1990, four cultivars (Stephens, Hyslop, McDermid, and Daws) were planted with a funnel seeder on 8 September 1989. Each cultivar was planted in four replicate rows 7.5-m long and 30.5-cm apart. In 1991, 1992, and 1993, winter wheat cultivars Stephens (highly susceptible) and Daws (tolerant) (11) were seeded in eight-row plots (2.4 × 4.9 m with 0.3 m between rows) with a one-pass drill (McGregor Co., Colfax, WA) having double-disc openers (Acra-Plant, Inc., Garden City, KS) between 9 and 16 September. Seeding rate was about 85 kg ha^{-1}; however, the same number of seeds was planted in each subplot to account for differences in weight of seed among cultivars. Soil fertility was determined by sampling each plot in August before planting. Liquid fertilizer containing enough N, P, and S to satisfy crop needs for estimated yield potential was added 7.5-cm below each seed row at planting. Chemical weed control was consistent with local commercial practices. Oat kernels (approximately 275 to 318 kg ha^{-1}) colonized by *C. gramineum* were scattered on the soil each October as a source of inoculum (11,12). Climatological data (35) from a weather station located 3.2 km northwest of Pullman, WA, were used to compare environmental conditions among years.

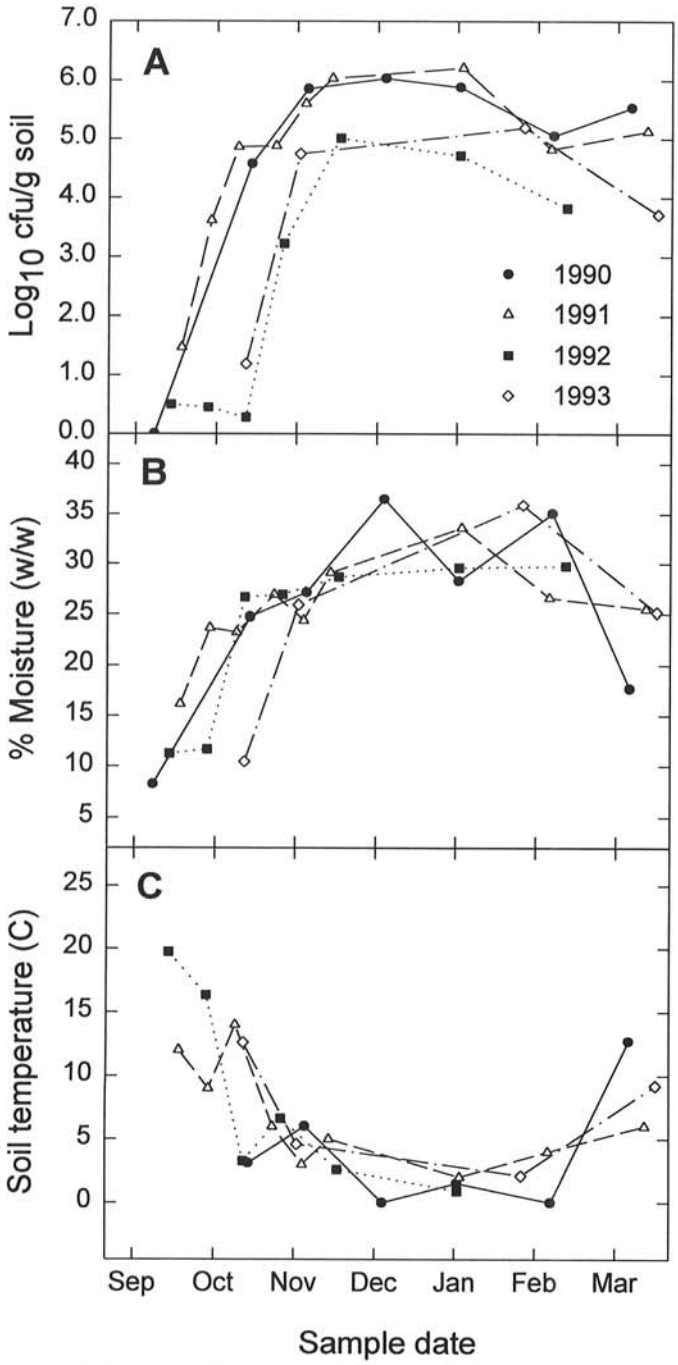

Fig. 1. A, Soil population density of *Cephalosporium gramineum*; **B,** gravimetric soil moisture; and **C,** soil temperature, in 0- to 7.6-cm soil depth from 1990 to 1993 at the Washington State University Plant Disease Research Farm, Pullman. Population density was determined by dilution-plating soil on a *C. gramineum* semiselective medium (CGSM); each point represents the mean of four replicates in 1990 and 1991 or nine replicates in 1992 and 1993.

Adjustment of soil pH. In 1992 and 1993, winter wheat plants were sampled from plots with different soil pH. Soil pH at the two experimental sites was originally adjusted in 1986 (34) by the addition of $Ca(OH)_2$ to increase pH or H_2SO_4 to decrease pH above or below the initial soil pH of 5.1 (site 1) or 5.3 (site 2). In July 1991, the top 15 cm of soil in main plots of site 1 was sampled with a 2.5-cm-diameter soil probe (10 to 15 cores per plot) and pH was determined by sieving (2-mm mesh) oven-dried soil, suspending the soil in 0.01 M $CaCl_2$ (1:2, wt/vol) (3), and measuring pH with a liquid-filled (1 M KCl saturated with AgCl) combination electrode. Additional H_2SO_4 was added to decrease pH in some plots so that three soil pH treatments (low, medium, and high) and three replicates per treatment were present; plots were then disked to incorporate the H_2SO_4 and irrigated to ensure reaction of the amendment with the soil. Soil pH in site 2 was checked in July 1992, but no additional adjustment was needed. Treatments within each experimental site were arranged in a randomized complete block, split-plot design with three replicates. The cultivars (subplot factor) Stephens and Daws were planted within each replicate of each soil pH treatment (main plot factor). At each sample date, soil cores from each main plot were bulked; thus, soil population densities (as below) were analyzed in a randomized complete block design with three soil pH treatments and three replicates.

Plant and soil sampling. Soil (0- to 7.6-cm depth, eight cores per main plot) and plants were sampled from alternate rows in each replicate at 2- to 4-week intervals during the fall and winter each year. Subsequent plant samples were taken from areas away from previously sampled locations, so that plants wounded during previous sampling were avoided. In addition, the field plots were not sampled when soil was frozen or covered with snow, in order to avoid injury to plants remaining in the plots. Soil temperature at the 7.6-cm depth was measured at each sample date. Soil cores from each main plot were bulked and mixed by hand. Subsamples of 15 to 25 g of moist soil and 100 ml of water were placed in plastic bottles and mixed on a wrist-action shaker for 15 min, and then the liquid suspension was dilution-plated on a medium semiselective for *C. gramineum* (CGSM) (42) to determine soil population densities. Two subsamples of soil were dried at 70°C for 48 h to determine gravimetric soil moisture (wt/wt, oven-dry soil basis) and soil pH was measured as described above. Soil population densities of *C. gramineum* were calculated on a soil dry-weight basis.

Isolation of *C. gramineum* from plants. Plants were removed from soil, washed, and dissected into seminal roots, crown roots, subcrown internodes, and stems. Roots that form at the scutellar or coleoptilar node are nodal roots, but since they form at the lowermost end of the subcrown internode, they were included with the seminal roots. Plant tissue was surface-disinfested in 0.25% NaOCl or rinsed overnight with running tap water for the first three sample dates in 1990. Beginning with the fourth sample of 1990, plant tissue was surface-disinfested with a dip in 70% ethanol, blotted on paper towels to remove excess ethanol, and then placed in 1% NaOCl (+ 20 µl of Tween 20 per 100 ml of solution) for 1 (roots) or 2 min (subcrown internodes and stems). Roots and stems were then cut into 1- or 2-cm-long pieces, placed on CGSM, and incubated at 15°C for at least 2 weeks before

scoring for the presence of *C. gramineum*. Plant pieces were arranged on plates such that the approximate location of *C. gramineum* colonies could be determined. Intact root tips could be identified under a dissecting microscope; thus, young roots with intact root tips could be separated from older roots.

In 1990, isolation of *C. gramineum* from four plants per replicate was attempted; however, only a few roots and the main stem of each plant were sampled. In subsequent years, more frequent samples were taken in the fall, and all recovered primary roots and the lowermost 5 to 6 cm of all stems were used in isolation attempts. In 1991, four plants from each replicate of each cultivar within the lowest soil pH (pH 5.0) were tested for *C. gramineum*. In 1992 and 1993, three plants from each soil pH-cultivar combination were tested.

Disease incidence and severity. Disease incidence and severity were determined after anthesis in each year (11 June 1990, 5 July 1991, 7 June 1992, and 18 June 1993) by removing stems in 0.5-m sections of a row from each subplot. Individual stems were then rated for the presence of Cephalosporium stripe symptoms with a 0 to 4 scale; in which 4 = stems with stripes in the flag leaf or extending to the head, 3 = stems with stripes in the leaf subtending the flag leaf, 2 = stems with stripes in the second leaf down, 1 = stems with stripes in the third leaf down, and 0 = stems with no symptoms in the upper four leaves (43). Disease incidence was calculated as the percentage of stems with symptoms in the uppermost four leaves. Disease severity, that represents the extent of colonization of the plant, was the mean severity of the symptomatic stems (34,43).

Statistical analysis. Soil population densities were converted to $\log_{10}$ (colony-forming units/g of dry soil + 1) and expressed as $\log_{10}$ CFU/g. Final disease incidence, expressed as percent diseased stems, and percent recovery of *C. gramineum* from the various plant parts were transformed with the arc-sine square root function for statistical analysis. Data for soil population density, disease incidence, disease severity, and percent recovery were subjected to analysis of variance. Fisher's least significant difference was used to differentiate cultivars when appropriate. Significance of response curves to soil pH was determined by fitting linear and quadratic models (15). Differences were deemed significant only when $P \leq 0.05$.

RESULTS

Population density in soil. Each year, soil population density of *C. gramineum* increased in September or October (Fig. 1A) when soil moisture was increasing and soil temperature was decreasing (Fig. 1B and C). At the first sample date (24 September) in 1990, population density was below the level at which *C. gramineum* could be detected by dilution-plating (shown as 0 CFU/g of soil in Fig. 1A), but increased to greater than 1×10^4 CFU/g in October. Population densities were greatest in December or January each year, reaching 1×10^5 to 1×10^6 CFU/g of dry soil. Population densities did not differ significantly among soil pH treatments in 1992 and 1993.

Disease incidence and severity. Disease incidence across all treatments was 74.7, 92.8, 29, and 69.5% in 1990, 1991, 1992, and 1993, respectively. In 1992, disease incidence for 'Daws' (28.7%) was lower ($P = 0.014$) than for 'Stephens' (35.7%), but differences among cultivars were not significant in the other 3 years.

In 1992, the effect of soil pH on disease incidence was not significant, but, in 1993, the relationship between soil pH and disease incidence was significantly linear ($P = 0.003$) (Fig. 2). The soil pH × cultivar interaction was not significant for disease incidence in 1992 or 1993.

Disease severity averaged 3.8, 3.9, 3.7, and 3.9 in 1990, 1991, 1992, and 1993, respectively. In 1990, cultivars differed significantly for disease severity ($P = 0.011$), with 'Daws' having lower disease severity (3.7) than 'Stephens' (3.9), 'McDermid' (3.9), or 'Hyslop' (4.0). Differences in disease severity between 'Daws' and 'Stephens' were not significant in 1991, 1992, or 1993. Disease severity was not influenced by soil pH in either 1992 or 1993.

Isolation of *C. gramineum* from plants. *C. gramineum* was recovered from 16, 78, 11, and 20% of plants in October and 47, 100, 35, and 50% of plants in November of 1990, 1991, 1992, and 1993, respectively. In 1991, 1992, and 1993, *C. gramineum* was isolated from seminal roots and crown roots beginning in October (Figs. 3, 4, and 5) and continuing through March, when sampling was ended. *C. gramineum* was recovered from only 10% (28/279), 0.5% (2/374), and 1% (2/195) of subcrown internodes of all plants in 1991, 1992, and 1993, respectively (Figs. 3, 4, and 5), and from stems or leaves but not roots of the same plant in 3.1% (9/288), 2.4% (9/378), and 1.4% (3/216) of plants in 1991, 1992, and 1993, respectively.

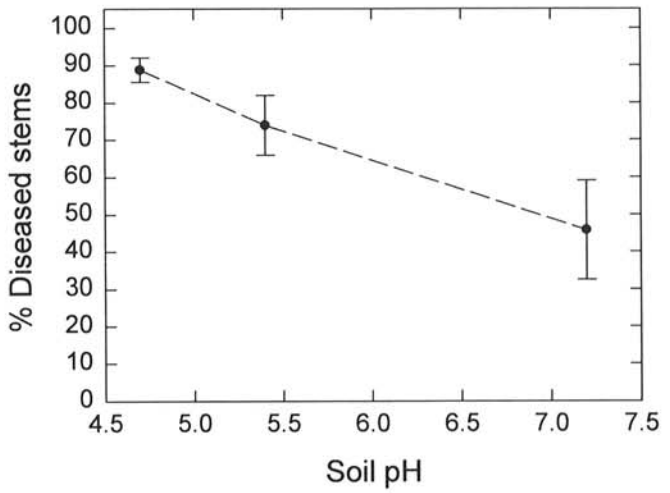

Fig. 2. Mean incidence of Cephalosporium stripe for winter wheat grown in soil with different pH at the Plant Disease Research Farm, Pullman, WA, in 1993. The relationship between soil pH and disease incidence was significantly ($P = 0.003$) linear and described by the equation $Y = 176.8 - 18.7X$ ($r^2 = 0.43$). Cultivar responses did not differ significantly and the cultivar × pH interaction was not significant. Each point is the mean of three replicates and two cultivars (Daws and Stephens). Bars represent ± the standard error of the mean.

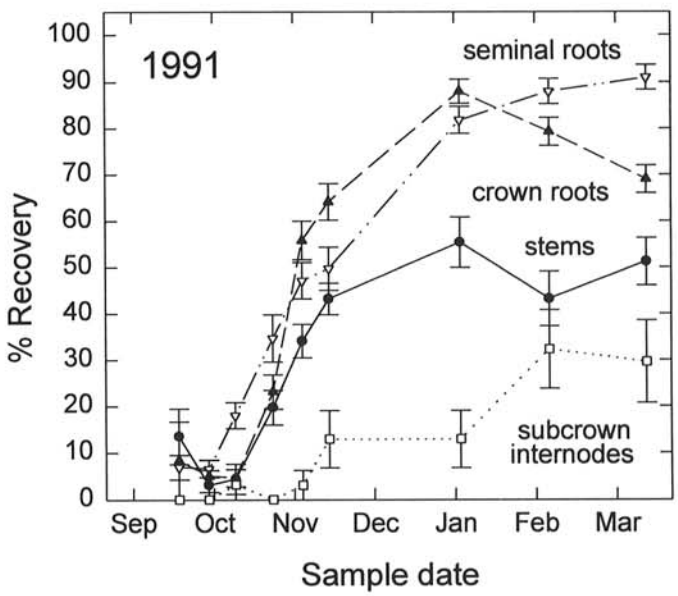

Fig. 3. The percentage of seminal roots, crown roots, stems, and subcrown internodes from which *Cephalosporium gramineum* was isolated during the 1990 to 1991 growing season (soil pH 5.0). Bars represent ± the standard error of the mean.

Recovery of *C. gramineum* from roots and stems of 'Daws' and 'Stephens' varied among sample dates in 1991 (Fig. 6). The cultivar × sample date interaction was significant for percent recovery from both stems ($P = 0.001$) and roots ($P = 0.004$). Variances were homogeneous when data for stem isolations from the first sample date were not included in the analysis. Crown root data for the first sample date were not included, because few crown roots had developed at that date. In 1992 and 1993, recovery of *C. gramineum* from crown roots was not significantly different between cultivars.

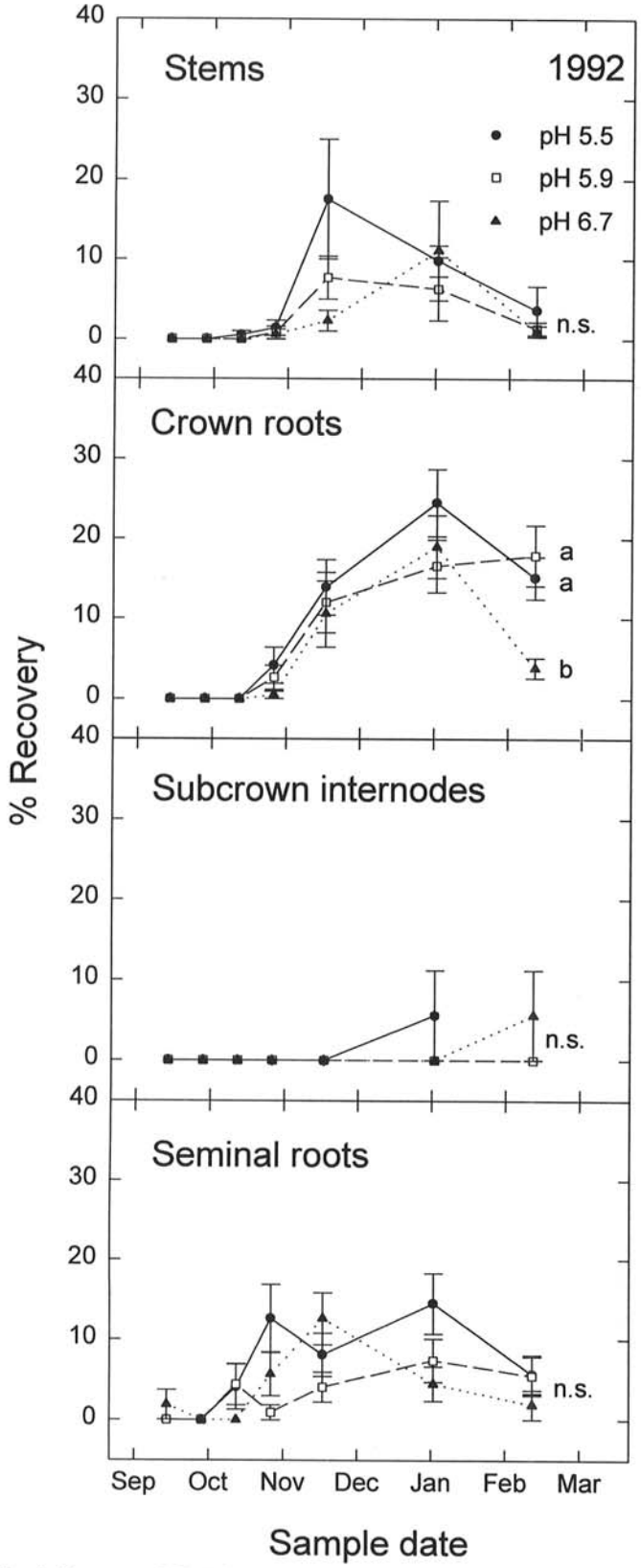

Fig. 4. Recovery of *Cephalosporium gramineum* from stems, crown roots, subcrown internodes, and seminal roots of wheat grown in soil at three pH levels in 1992. Within sample dates, means with the same letter are not significantly different. Bars represent ± the standard error of the mean.

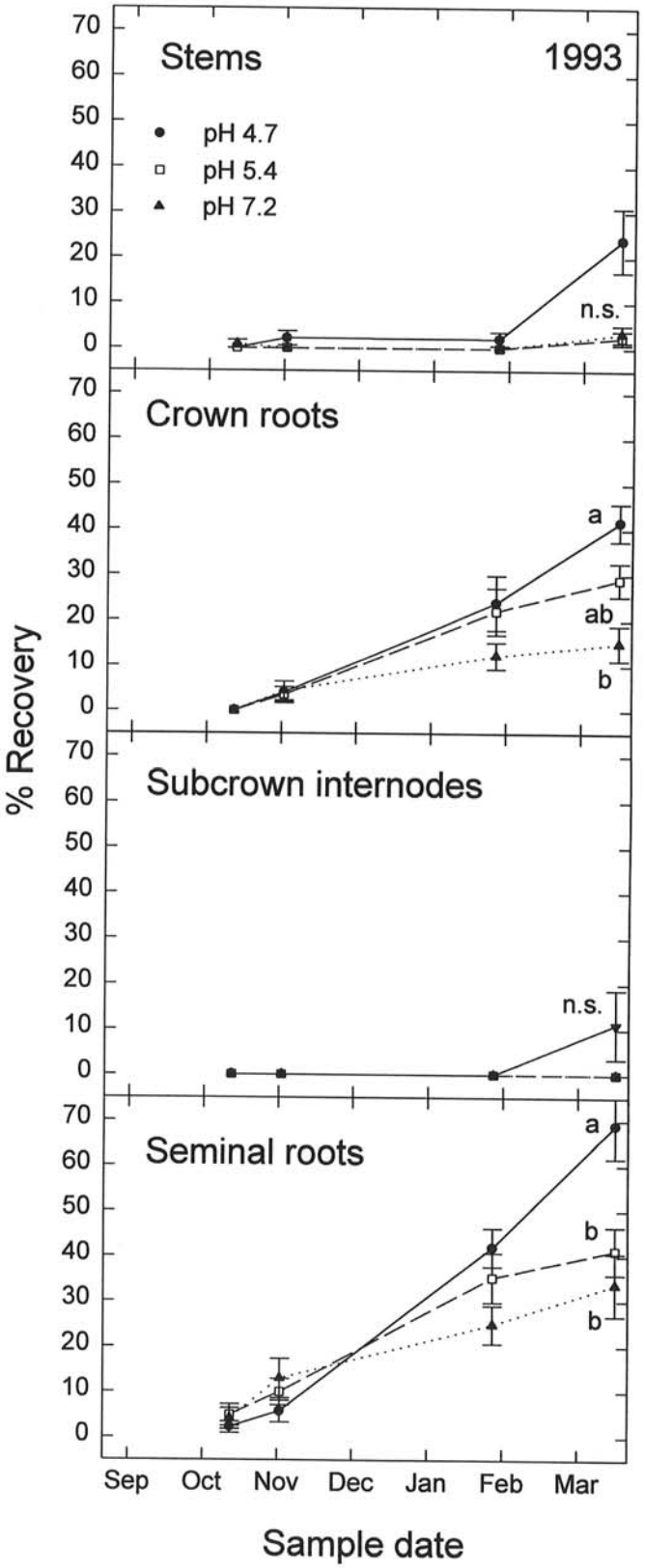

Fig. 5. Recovery of *Cephalosporium gramineum* from stems, crown roots, subcrown internodes, and seminal roots of wheat grown in soil at three pH levels in 1993. Within sample dates, means with the same letter are not significantly different. Bars represent ± the standard error of the mean.

Root age. From 29 November to 27 March 1991, *C. gramineum* was recovered from only 27% (56/209) of young roots with intact root tips, whereas the fungus was recovered from 81% (989/1,220) of roots without intact root tips that were darker in color and had many lateral roots. In January 1992, *C. gramineum* was isolated from 23% (98/424) of roots without intact root tips and 7.6% (5/66) of roots with intact root tips. In March 1993, the pathogen was isolated from 37% (218/592) of roots without intact root tips and 8.6% (23/269) of roots with intact root tips. In addition, *C. gramineum* was rarely observed growing from root tissue near intact root tips.

Effect of soil pH on infection. Soil pH in the three treatments averaged 5.5, 5.9, and 6.7 in 1992 and 4.7, 5.4, and 7.2 in 1993. In February 1992, recovery of *C. gramineum* from crown roots was greater at soil pH 5.5 and 5.9 than at pH 6.7 (Fig. 4; $P = 0.038$). At this date, the relationship between soil pH and percent recovery was significantly ($P = 0.0171$) quadratic and described by the equation $Y = -251.5 + 95.4X - 8.4X^2$ ($r^2 = 0.22$). Percent recovery at other sample dates was not significantly different among soil pH. In March 1993, recovery of *C. gramineum* from seminal roots was greater at soil pH 4.7 than pH 5.4 and 7.2 (Fig. 5; $P = 0.030$), and recovery from crown roots was greater at pH 4.7 than at pH 7.2 (Fig. 5; $P = 0.047$). At this date, the relationship between soil pH and percent recovery from crown roots was significantly ($P = 0.0001$) linear and described by the equation $Y = 74.3 - 8.6X$ ($r^2 = 0.30$). Percent recovery at other sample dates was not significantly different among soil pH. Differences in percent recovery from stems were not significantly different among soil pH in either year (Figs. 4 and 5).

DISCUSSION

In contrast to earlier work in which *C. gramineum* was isolated only in spring (8,9,37), the pathogen was recovered from roots of winter wheat plants in the fall and winter each year in this study. Infection of plants apparently began in the fall, when inoculum was abundant, and continued through the winter. Recovery of *C. gramineum* from wheat plants in October and November before soil freezing occurred indicated that soil freezing was not necessary for infection under natural field conditions, although freezing may have increased the amount of infection as a result of root injury.

The ability of *C. gramineum* to infect plants in the fall before soil freezing occurs may help to explain why early planting results in greater disease incidence. Pool and Sharp (39) showed that early planting results in greater root mass and longer roots, providing more infection sites when roots are broken during soil freezing and heaving in late winter and early spring. Early seeding allows more time for crown roots to form before soil freezing occurs, which increases the amount of senescent root cortical tissue and the number of potential infection sites. Greater crown root development may allow *C. gramineum* to become established in roots before soil population densities reach their peak in December or January (Fig. 1A; 48).

The specific mechanism of infection of unwounded roots under natural conditions is still not known. In other vascular diseases, species of *Fusarium* and *Verticillium* commonly colonize the host root surface and cortex (16), but penetration of the vascular system is apparently a rare event. The exact mechanism is unknown, but may involve colonization of injured, senescent, or necrotic cells or circumstances that provide entry to the vascular system through wounds (5). *F. oxysporum* Schlect. and *V. dahliae* are capable of colonizing root tips, reaching maximum colonization frequency at 5 and 15 mm, respectively, behind the root tips of cotton (16). In contrast, *C. gramineum* was rarely isolated from wheat roots with intact root tips or from the region of young root tissue near intact root tips. Bonde (8), using histological and microbiological culture methods, also did not find *C. gramineum* near the root apex of plants grown and inoculated aseptically in growth pouches. Cortical tissue in older portions of wheat roots begins to senesce soon after the roots develop (17,45,46). Thus, *C. gramineum* may infect plants by colonizing senescent root cortical tissue, followed by penetration of the vascular system. Bonde (8) and Bailey et al. (4) observed *C. gramineum* colonizing the root cortex of frozen and unfrozen roots inoculated in vitro, but did not observe *C. gramineum* penetrating the vascular system. *C. gramineum* is a xylem-inhabiting pathogen that apparently cannot penetrate living cells (30,47). Mathre and Johnston (26) suggested that the pathogen has a rudimentary ability to penetrate and grow through living cells that occur in the root-crown transition zone; thus, the pathogen also may be able to traverse the transition from the root cortex into the xylem. The current study showed that *C. gramineum* could become established in roots before soil freezing occurred. The pathogen was then in a position to enter the xylem, either by active penetration or passively through breaks in the vascular tissue. In years when soil freezing occurs resulting in root breakage, *C. gramineum* can more readily enter the xylem and disease incidence will be greater (23,43). During the current study, soil temperatures were below freezing 6, 38, 9, and 61 days in 1990, 1991, 1992, and 1993, respectively (35). In general, in years when soil freezing occurred frequently, disease incidence was moderate to high (92.8% in 1991 and 69.5% in 1993), although other factors may have been involved as disease incidence was also high (74.7%) in 1990.

Other points where *C. gramineum* may enter root xylem are where lateral roots emerge or through naturally occurring root wounds that are caused by root growth pressure, soil moisture changes, and the activity of insects, nematodes, pathogens, and other microorganisms (6,14). Slope and Bardner (41) indicated that infection of wheat by *C. gramineum* was increased in the presence of wireworms. Hutson and Smith (19) believed *F. oxysporum* and *V. dahliae* could enter tomato roots only at the origins of lateral roots, but Gerik and Huisman (16) were unable to find colonization of these sites by *F. oxysporum* in cotton roots. *C. gramineum* was frequently observed growing from points on the older portions of the root where lateral roots had been removed. It was not possible to conclude whether *C. gramineum* also entered roots at those points.

In this study, *C. gramineum* was recovered from all parts of the plant, but infrequently from subcrown internodes (Figs. 3, 4, and 5). This may have resulted from an anatomical barrier at the scutellar or coleoptilar node that prevented movement of *C.*

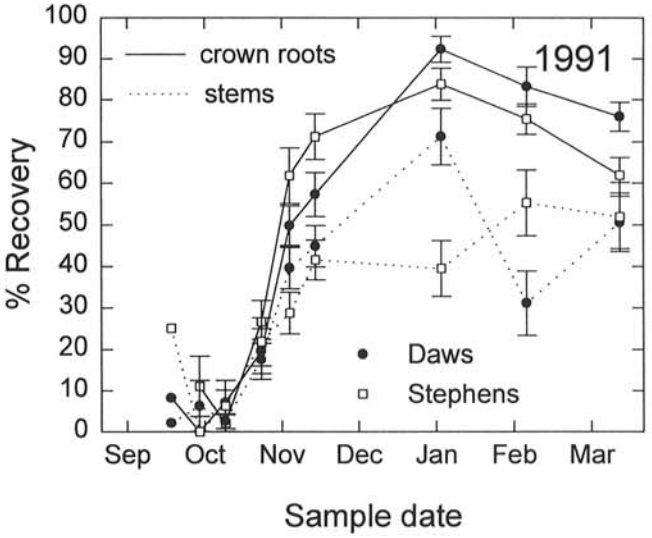

Fig. 6. Recovery of *Cephalosporium gramineum* from crown roots and stems of winter wheat cultivars Daws and Stephens in 1991. Bars represent ± the standard error of the mean.

gramineum from the seminal roots into the subcrown internode (2). Alternatively, other fungi that were observed commonly growing from the lower portion of the subcrown internode at the scutellar and coleoptilar nodes may have interfered with isolation of *C. gramineum* or with movement of the pathogen through the subcrown internode. Thus, it appeared that, under Pacific Northwest conditions, crown roots were the most important infection site and that seminal roots and subcrown internodes played a minor role in disease epidemiology.

The conclusion that crown roots were the primary avenue of infection leading to colonization of the leaves and stems was in contrast to the results of Otieno (37), who found that the major point of infection was through the vascular traces of the senescent scutellum into the hypocotyl (subcrown internode). Movement of *C. gramineum* from crown roots, rather than seminal roots, to stems involves a shorter distance when a subcrown internode is present and, therefore, is likely to require less time for the pathogen to become established in stems. Infection of crown roots also explains why some stems of a plant are infected while others remain free of disease symptoms. Since crown roots are connected by vascular traces to the stem at the node from which they form (2), *C. gramineum* in a root would colonize the stem to which the root is connected as it moves from the crown root into the stem. In addition, the crown root system, especially the older portions of these roots, occupies the 0- to 7.6-cm-deep soil profile in which they are more prone to damage from frost heave and in which population densities of the fungus are greatest (24,48).

Cultivars without well-developed subcrown internodes may be more susceptible to *C. gramineum* as a result of increased movement of the pathogen from seminal roots into stems. Allan and Pritchett (1) and Poulos and Allan (40) studied heritability of subcrown internode length and concluded that one-gene semidwarf types could be selected with long or short subcrown internodes. Depth of seeding also influences the length of the subcrown internode (13); investigation of seeding depth in relation to disease development may be a worthwhile avenue for further research.

Occasionally, *C. gramineum* was isolated from stems or leaves, but not from roots, of the same plant. In these cases, the fungus may have been present in the roots, but not detected, or *C. gramineum* may have entered the stems directly in the crown area, which is in contact with soil. Bonde (8) also isolated *C. gramineum* from stems and leaves, but not roots, of some plants with symptoms in April. Otieno (37) was unable to find *C. gramineum* in adventitious roots emerging from already infected stems, but he also could not find evidence that the fungus entered stems through cortical ruptures caused by emerging adventitious roots.

The third objective of this study was to determine whether soil pH influences infection of wheat roots and stems in the field. Mahler and McDole (22) determined minimum acceptable soil pH values of 5.4 and 5.2 for the winter wheat cultivars Stephens and Daws, respectively, based on soil pH-yield relationships. Although yield was not determined in this study, because plants were destroyed during sampling, the lowest soil pH (5.5) in 1992 was above the level at which yield reduction occurs (22) and at which effects of soil pH on disease incidence are greatest (34). This was reflected by the fact that final disease incidence did not vary among soil pH in this year. In contrast, in 1993, disease incidence was significantly greater for wheat grown in soil with pH 4.7 compared with wheat grown in pH 7.2 (Fig. 2). Differences in percent recovery of *C. gramineum* from crown roots in response to soil pH were detected in both years, but not until February or March (Figs. 4 and 5). Soil pH may have direct effects on root surfaces, resulting in disintegration of the root cortex (44), which could allow active penetration of the root cortex similar to that observed by Bailey et al. (4) and Bonde (8). A greater number of infected crown roots in early spring may contribute to greater final disease incidence; however, in this study, final disease incidence was greater at lower soil pH in only 1 of the 2 years. In contrast to earlier work (32), soil population densities did not differ significantly among soil pH in this study. Therefore, differences in percent recovery of *C. gramineum* from crown roots among soil pH were not associated with higher population densities of *C. gramineum* at low soil pH.

Soil pH also may affect Cephalosporium stripe by stressing plants after infection and during disease development in the spring. However, because there were no differences in disease severity (which reflects the extent of disease development in the upper four leaves of the plant) among soil pH treatments in this and a previous study (34), any effects of soil pH on disease development in the spring likely occurred before upward movement of the pathogen in stems and symptom development in the upper plant canopy.

Possible mechanisms of resistance to *C. gramineum* include exclusion of the fungus from the plant, decreased movement through roots or from roots into stems (26,29). *C. gramineum* was commonly isolated from roots of both winter wheat cultivars, Stephens and Daws, and consistent differences in recovery from roots of these cultivars were not detected (Fig. 6). Although final disease incidence (determined at anthesis) generally was lower for Daws than for Stephens, differences in disease response between the two cultivars were not great enough to investigate potential differences in infection. Mathre and Johnston (26) found higher rates of movement of *C. gramineum* through roots and from roots to stems (through the crown) in the highly resistant wheat relatives *Thinopyron intermedium* (Host) Barkworth and D. R. Dewey and *Elytrigia elongata* (Host) Nevski (27) than in cultivars of wheat. Determining the amount of root infection under natural conditions in these resistant wheat relatives would be of interest in further elucidating the mechanism of resistance.

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