Identification of Resistance to Cephalosporium Stripe in Winter Wheat

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The authors express appreciation to D. H. Hall and R. K. Webster of the University of California, Davis, for assistance in planting field tests in California.

Contribution from the Montana Agricultural Experiment Station. Journal Series Paper 982.

Accepted for publication 1 March 1980.

ABSTRACT

MORTON, J. B., and D. E. MATHRE. 1980. Identification of resistance to Cephalosporium stripe in winter wheat. Phytopathology 70:812-817.

Seven winter wheat cultivars were examined for resistance to *Cephalosporium gramineum*. Two types of resistance were observed: exclusion of the pathogen and restriction of spread of the pathogen following successful colonization of the host. The former was expressed as a reduction in the percentage of diseased plants. The latter was expressed as a reduction in the percentage of diseased tillers per infected plant and also as a reduction in the rate and severity of disease development. Both types of resistance were expressed independently. PI 278212 exhibited a low infection percentage, but was rapidly and completely invaded after successful ingress. Crest LRC 40 demonstrated a high percentage of diseased plants, but restricted infection between tillers, and had a moderate rate of systemic invasion. Each type of resistance may be identified and evaluated separately if seeding rates permit recognition of individual plants. Maximum resistance would be attained if both types of resistance were incorporated into a single genotype. Infection occurred only in soils undergoing frost-heaving, confirming that broken roots are essential for ingress of the fungus into the host. Differential responses between cultivars to pathogen exclusion could not be attributed to gross changes in either propagule levels in the soil or root mass. Cumulative effects of microhabitat interactions between the soil-root interface or differential responses to wound-healing are suggested as possible explanations for dissimilarities between cultivars.

One of the most damaging pathogens of winter wheat (*Triticum aestivum* L.), especially in northern regions practicing monoculture, is *Cephalosporium gramineum* Nisikado & Ikata (= *Hymenula cerealis* Ell. & Ev.), the causal agent of Cephalosporium stripe. It stunts plants, blights leaves and heads, and can reduce yields 50% or more (10,20). *C. gramineum* is a facultative soilborne parasite, that overwinters as a saprophyte within infected plant residues carried over from the previous crop (3,4,24,25). Here it can remain viable in the soil for 2 yr by producing a broad-spectrum antifungal antibiotic (4). Crop rotation, refuse destruction, and deep-plowing reduce inoculum levels (3,11,19,26). Late planting, which minimizes root growth and future infection sites, also has been recommended for control (11,19). These cultural practices are not always dependable because they rely upon favorable climatic conditions for successful implementation and are influenced by economic factors. The most effective and desirable control method would be planting of resistant cultivars.

Resistance was noted first by workers in Japan (26). However, they observed winter wheats planted in naturally infested fields where inoculum and virulence levels were unknown. In the United States, Bruehl (3) identified four resistant cultivars by using hypodermic inoculations of a liquid conidial suspension into wheat culms above the crown, but they proved to be susceptible in the field under conditions of natural infection (21).

Until the development of oat kernel inoculum, genotypic differences, especially in large populations, were difficult to assess in the field. This technique called for addition of a measured quantity of oat kernels infested with *C. gramineum* isolates of known virulence with the seed at planting (12). Mathre and Johnston (14) used this inoculum to screen more than 1,000 hard red winter wheat cultivars from the major winter wheat growing areas of the world. Although most of these cultivars were susceptible, some promising sources of resistance were discovered. None of the cultivars tested was immune to the disease.

The major criterion for evaluating susceptibility to Cephalosporium stripe has been reduction in yield (3,10,14,26). Other tests have included general visual disease readings (3,26), disease readings early in host development based upon measuring the proportion of diseased tillers (12,14), and readings late in host development based upon measuring the number of white heads (12,14). These parameters provided information necessary to differentiate cultivars across a graded series which extended from extreme susceptibility to high resistance (3,12,14,26). However, these criteria did not reveal the specific phenotypic response(s) expressed by each genotype.

The purpose of this work was to identify the types of Cephalosporium stripe resistance exhibited by selected winter wheat cultivars.

MATERIALS AND METHODS

The seven hard red winter wheat cultivars used in this study varied in susceptibility to Cephalosporium stripe and in agronomic characteristics. Based on yield reductions, Marias (PI 17595) and Lancer (PI 13547) were rated as highly susceptible, Winalta (CI 13670) and CI 07638 were rated as intermediate, Crest Line Row Component (LRC) 40 (MT 7579) and PI 094424 were rated as moderately resistant, and PI 278212 was rated as highly resistant (14).

Unless otherwise specified, all tests were conducted at the Montana Agricultural Experiment Station near Bozeman, MT. The cultivars were planted in early September of 1977 and 1978 at 200 seeds per 3.1 m row, with rows 36.0 cm apart. A split-plot experimental design with four replications was used, in which treatments comprised the main plots and the cultivars made up the subplots.

Inoculum consisted of either infested oat kernels or a liquid conidial suspension. The former was prepared by inoculating autoclaved oat kernels with a concentrated conidial suspension of *C. gramineum*, incubating them for 2–3 wk, and allowing them to air-dry (12). The oat kernels were added with the seed at the time of planting. In the second inoculation procedure, the liquid inoculum was prepared by growing the fungus in shake culture composed of modified Eckert's medium (22), and 1 L containing 10^6 conidia per milliliter was added to each side of a 3.1-m row by pouring the

0031-949X/80/08081206/$03.00/0

inoculum into a soil slice after cutting the roots with a knife.

Populations of *C. gramineum* in field soil were measured by dilution plating on selective green wheat agar (23). Soil samples were collected from rhizospheres of cultivars Marias, Crest LRC 40, and PI 278212 which had been planted in a randomized block design replicated six times. Twenty-gram subsamples were agitated in a Waring Blendor with 200 ml of distilled water for 20 sec and subsequently diluted to 10^{-3} and 10^{-4}. Colonies were counted after 5 days incubation at 22 C.

Expression of resistance to Cephalosporium stripe was scored 30 days after heading according to the number of symptomatic tillers per row and the number of symptomatic tillers per plant. In addition, the rate of appearance and severity of disease symptoms at periodic intervals before and after heading was determined. Symptom severity was rated on a scale of one to 11, with one denoting a single stripe on a leaf and 11 indicating complete chlorosis (15). To identify responses within individual plants, inoculated rows were thinned in the spring so that mitigating effects of different seeding rates were prevented.

Root growth of cultivars Marias, Crest LRC 40, and PI 278212 was measured by displacement in water and by dry weight. Single seeds of each cultivar were planted in a sandy-loam soil contained within polyvinyl chloride pipe sections 30.5 cm long and 3.8 cm in diameter. Four replications of five plants each were arranged in a randomized block design. The pipe sections were enclosed in a rectangular enclosure, the floors and sides of which were insulated with 2.5-cm-wide plastic foam.

The plants were grown for 60 days in a growth chamber at 5/20 C (dark/light) with a 12-hr photoperiod (3.8×10^4 ergs/cm^2/sec combined incandescent and cool-white fluorescent light). After 2 mo, roots were carefully removed from the pipe sections and washed, and soaked in 0.05% sodium hexametaphosphate for 5 days. Calcium chloride was added until the roots floated to the surface (H. Ferguson, *personal communication*). The roots were collected, washed again by agitation in water, and placed in a water-filled separatory funnel which was connected to a 10 ml pipette by rubber tubing. This allowed the determination of root displacement in water. Roots were weighed after drying at 70 C for 2 wk.

RESULTS

Phenotypic expression of resistance. The cultivars differed in the incidence of diseased tillers within inoculated rows (Table 1). Although an almost twofold difference in the number of infected tillers was observed for each cultivar between 1977 and 1978, the comparative differences between cultivars remained the same. Marias and Lancer were classified as susceptible; Crest LRC 40 and Winalta were intermediate; and CI 07638, PI 094424, and PI 278212 were resistant both years. Thus, environmental effects on infection between plants did not obscure inherent genetic differences between cultivars.

Thirty plants each of five cultivars were rated for the incidence of infection among tillers of individual plants. Crest LRC 40 was the only cultivar that significantly prevented systemic invasion of tillers within each plant (Table 1). In all of the cultivars, late tillers appeared because of spacing effects. Some of these tillers did not express disease symptoms, which could account for much of the variation among cultivars. However, the significant reduction in disease incidence among tillers within plants of Crest LRC 40 cannot be attributed to this environmental effect, since many of the earlier maturing tillers were disease-free.

Three cultivars were selected to examine the rate and extent of symptom expression. Marias and PI 278212 were chosen because they represented the extremes of resistance to pathogen penetration. Crest LRC 40 was selected, not only because of its intermediate resistance to infection, but also because it restricts stripe formation on flag leaves during the first month after heading (16).

The rate of stripe formation was monitored by scoring the

TABLE 1. Responses of selected winter wheat cultivars to the incidence of infection by *Cephalosporium gramineum*

	Pathogen exclusion (diseased tillers per infected row)[a]		Pathogen restriction (diseased tillers per infected plant)
Cultivar	1977	1978	1978
Marias	42 a[b]	77 a	99 a
Lancer	45 a	...	...
Crest LRC 40	26 b	53 b	66 b
Winalta	25 b	49 b	96 a
CI 07638	15 c	...	...
PI 094424	9 c	27 c	93 a
PI 278212	5 c	15 c	90 a

[a] Mean percentages of healthy controls across four replications.
[b] For each column, values with the same letter are not significantly different according to Duncan's multiple range test, $P = 0.05$.

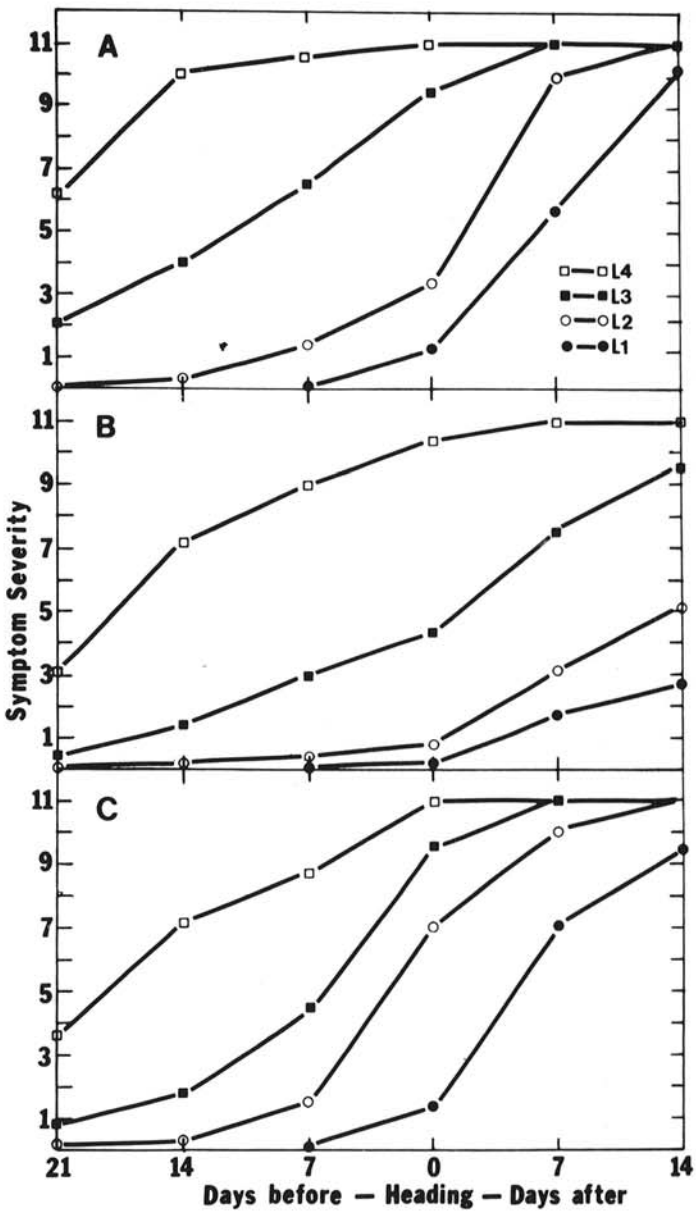

Fig. 1. The rate of foliar stripe formation on the upper four leaves of primary tillers from three winter wheat cultivars infected with *Cephalosporium gramineum*. Symptoms were quantified by using a severity index based upon the number of stripes per leaf. 1 = one stripe per leaf, 11 = complete chlorosis. Leaves numbered from flag leaf (L1) downward to fourth leaf (L4). Cultivars **A**, Marias; **B**, Crest LRC 40; and **C**, PI 278212.

uppermost four leaves of primary tillers for symptom severity from 3 wk prior to heading until 2 wk after heading (Fig. 1). The extent of symptom development was determined by scoring 30 infected plants of each cultivar 1 mo after heading. The severity readings for the uppermost four leaves of all tillers within each plant were averaged, so that a mean severity rating was obtained for each plant (Fig. 2). Measurement of height reduction and yield performance in relation to healthy controls provided indications of differential responses to disease severity between cultivars (Table 2).

After successful invasion of the host, both Marias and PI 278212 were equally susceptible to rapid systemic movement of *C. gramineum*. By 14 days after heading, the flag leaves of the primary tillers of infected plants of both cultivars were nearly blighted. A similar temporal pattern occurred in all other tillers of these plants as evidenced by the extent of symptom development 1 mo after heading. In Marias, 29 of 30 plants exhibited total blighting. The remaining plant was almost as heavily affected, with a mean severity rating of 10. PI 278212 differed only slightly from Marias, as 93% of the infected plants had average severity ratings between 9 and 11. Both of these cultivars suffered substantial height and yield reductions.

Crest LRC 40 limited the rate of symptom expression. Only the lowermost leaves of primary tillers were blighted 14 days after heading. Both the penultimate and flag leaves averaged severity scores of less than 5, indicating that less than half of each leaf expressed foliar chlorosis. Interestingly, the speed of stripe formation on the fourth leaf was similar to that observed on the fourth leaves of the two susceptible cultivars. Only as the pathogen moved up the plant did localizing responses become more effective. The extent of disease development in all tillers of Crest LRC 40 1 mo after heading also was greatly reduced compared to that of Marias and PI 278212. Most of the plants displayed mean severity ratings between 3 and 6. In part, these lower scores were due to the significant number of symptomless tillers within each plant. The moderate height and yield reductions of Crest LRC 40 further substantiated its tolerance to the physiological effects of pathogenesis.

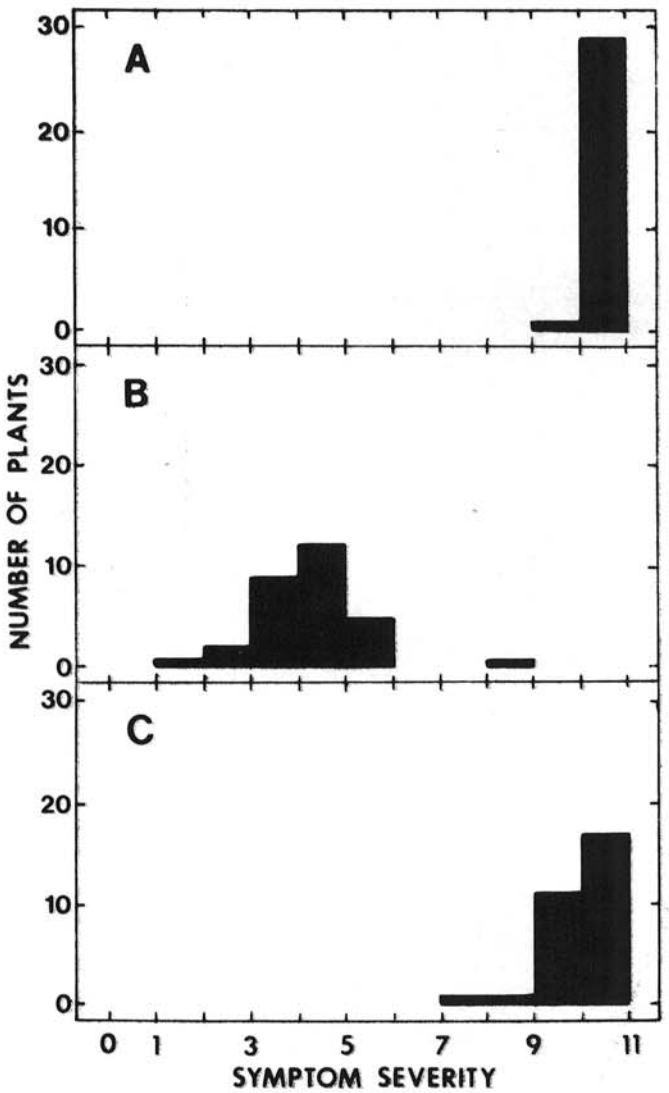

Fig. 2. The differential responses of three winter wheat cultivars to infection by *Cephalosporium gramineum* 1 mo after heading. The uppermost four leaves of all tillers within each of 30 plants per cultivar were scored for symptom severity. These readings were averaged into a mean severity score for each plant. 1 = one stripe per leaf, 11 = complete chlorosis. Cultivars **A**, Marias; **B**, Crest LRC 40; and **C**, PI 278212.

Mechanisms of resistance. Because *C. gramineum* is a soilborne pathogen, exclusion of the fungus by some cultivars may be due wholly or in part to soil-rhizosphere-pathogen interactions. Thus, the role of root wounding as a prerequisite for successful ingress of the fungus into the host was re-examined. Incidence of infection between plants of Marias, Crest LRC 40, and PI 278212 was evaluated in soils subjected to different environmental regimes both in the greenhouse and in the field. The influence of soil microflora on infection in a controlled environment in which mechanical root breakage did not occur was studied by transporting soil from the field into the greenhouse and heat-sterilizing half of it. The three winter wheat cultivars were replicated four times within each soil treatment. To approximate seeding and inoculum rates in the field, 70 seeds and 7 g of infested oat kernels were planted together in each 1-m row. In neither soil treatment was any substantial infection observed (Table 3). Hence, the soils tested in this study did not appear to contain microorganisms capable of promoting infection by *C. gramineum* in the absence of mechanical root wounding.

The possibility of root damage due to soil heaving in the field was eliminated by spring planting. Marias, Crest LRC 40, PI 278212, and a spring wheat, Lemhi (which is susceptible to Cephalosporium stripe when artificially inoculated) were planted with oat kernel inoculum in mid-April of 1977 at the Montana Agricultural Experiment Station near Bozeman. A randomized block design with four replications was used. Up to 5×10^5 *C. gramineum* conidia per gram of soil were present during the first month after planting. Even with these high inoculum levels, less than 2% infection was evident. The unvernalized winter wheat cultivars expressed symptoms only on the outer, older leaves of the few plants that became diseased.

To substantiate the above findings under conditions where vernalization would occur, the three winter wheat cultivars were planted with oat kernel inoculum in early September of 1977 at Bozeman, MT where severe winter conditions assured adequate root breakage in the spring from soil frost heaving; and at Davis, CA in November of 1977, where a mild winter did not create the soil-freezing conditions required for soil heaving but did allow vernalization. While extensive infection of plants was observed among cultivars at Bozeman, no infection was apparent at Davis (Table 3). Assuming that soil frost heaving causes root breakage, these data suggest that root wounding is necessary for successful pathogenesis by *C. gramineum*.

TABLE 2. Effect of infection by *Cephalosporium gramineum* on height and yield of three winter wheat cultivars in 1978

Cultivar	Reduction (%)[a]	
	Height	Yield
Marias	37 a[b]	73 a
Crest LRC 40	11 b	34 b
PI 278212	35 a	79 a

[a] Mean percentages with respect to healthy controls across four replications. Ten heads from infected main tillers were harvested within each replication.

[b] For each column, values followed by the same letter are not significantly different according to Duncan's multiple range test, $P = 0.05$.

Histological examination of root cross-sections by using standard embedding, sectioning, and staining procedures (9,15) and measurements of root mass by displacement in water and dry weight did not reveal any large differences in gross anatomy or in the extent of root growth between Marias, Crest LRC 40, and PI 278212 which might explain the differences in their susceptibility. The number of roots produced by plants of each cultivar were not counted directly, but the lack of any dissimilarities in total root mass would suggest that physical differences in root growth patterns do not significantly affect infection percentages between plants.

To determine if these cultivars differed in degree of root breakage, infection percentages were obtained from oat kernel-inoculated rows exposed only to natural root wounding in the field and from oat kernel-inoculated rows in which all of the roots were manually severed with a sharp knife in the spring after natural root wounding had occurred. Neither treatment resulted in disease development that differed substantially from the other (Table 4), suggesting that maximum root breakage probably occurred among all cultivars in the spring, regardless of physical factors such as root length or root tensile strength.

Inoculum levels in the rhizospheres of Marias, Crest LRC 40, and PI 278212 were monitored in the fall and spring, when propagule levels are high under natural field conditions (24). Wheat in each row was inoculated with 20 g of infested oat kernels. Although propagule levels varied from 4×10^4 to 1×10^5/g of soil, no appreciable differences between cultivars were observed which could account for the disparities in pathogen exclusion between plants.

The effect of various inoculum levels on differential cultivar responses to infection between plants was examined by adding known quantities of infested oat kernels as an inoculum source to soil with no previous history of Cephalosporium stripe. Under conditions of natural root wounding, inoculum density and the percentage of tillers infected per row were positively correlated (Table 5). The relative response of cultivars was unchanged. The same responses were noted when two isolates of the fungus were used, one of mild virulence (isolate 5) and one of high virulence (isolate17). Thus, an inoculum density of 20 g of oat kernels per 3.1-m row, which produced up to 1×10^5 propagules per gram of soil in the spring, cannot override the resistance mechanism affecting pathogen exclusion. Only the addition of 2 L of liquid inoculum containing 10^6 conidia per milliliter to both sides of a 3.1-m row immediately after manually severing the roots in the spring obliterated the differential response between cultivars (Table 4).

DISCUSSION

Three responses to Cephalosporium stripe by selected winter wheat cultivars were identified in this study. The first is expressed as a reduction in the number of diseased plants in a population. The second causes a reduction in the number of diseased tillers within plants, and the third reduces the rate and severity of disease development. These latter responses restrict the pathogen after successful ingress. Based on the responses among cultivars, the exclusion and restriction types of resistance are independent of each other. PI 278212 excludes the pathogen very effectively, yet it is highly susceptible to systemic movement of the pathogen; eg, all tillers of infected plants become diseased and infected plants are severely blighted. Crest LRC 40 is susceptible to pathogen entry but it is moderately resistant to systemic movement of the pathogen.

In heavily seeded rows, the percentage of tillers infected in a row reflected the percentage of plants infected per row for those cultivars in which most or all of the tillers in each plant were diseased. In the case of Crest LRC 40, though, the percentage of tillers infected per row reflected differences in infection not only between plants, but between tillers of each plant as well. Therefore, the intermediate reaction of Crest LRC 40 actually may be a susceptible response which was biased toward a more resistant phenotype because of errors in distinguishing reductions in diseased tillers per plant. In order to effectively differentiate the three types of resistance in cultivars such as Crest LRC 40, lower seeding rates are required so that individual plants can be identified. This would partition pathogen exclusion responses from pathogen restriction responses.

Resistance, as manifested by low infection percentages, was first thought to reside in roots or crowns of the winter wheat plant (13). Several cultivars, which were resistant when inoculated through the roots, were susceptible after stem inoculations. Reductions in infection percentages, concomitant with reduced inoculum densities, further indicated that the factor(s) governing resistance was inherent to the roots or crown. Resistance to root injury or a lower root mass do not appear to significantly influence the number of potential infection sites available to the fungus. Mathre and Johnston (13) determined that the optimum period following root injury in which conidia can successfully enter roots is 1 day. Possibly, cultivars vary in the rate of wound-healing, thus affecting the incidence of root infection by closing off infection sites. Otieno (17) observed many conidia near roots and root hairs prior to infection of seedlings germinated on petri plate cultures of *C. gramineum*. Similar localized pockets of conidia were observed

TABLE 3. Effect of different soil environments relative to root injury or breakage on the percentage of plants infected with *Cephalosporium gramineum*

	Diseased tillers per row (%)[a]			
	Winter wheat			Spring wheat
Test	Marias	Crest LRC 40	PI 278212	Lehmi
Greenhouse				
Sterile Soil	2	1	0	0
Non-sterile Soil	1	0	1	1
Field				
Spring planted, Bozeman, MT	1	0	0	2
Fall planted, Bozeman, MT	77	53	15	...
Fall planted, Davis, CA	0	0	0	...

[a] Mean percentages of four replications.

TABLE 4. Effect of different inoculation procedures in the field on the percentage of tillers infected with *Cephalosporium gramineum* among three winter wheat cultivars in 1978

	Percent infection[a]		
Cultivar	Natural wounding + oat kernels[b]	Root slice + oat kernels[c]	Root slice + liquid inoculum[d]
Marias	75	79	76
Crest LRC 40	48	52	77
PI 278212	21	17	76

[a] Mean percentages of tillers infected per row across four replications.
[b] Rows inoculated with 20 g of infested oat kernels. Wounding due solely to soil frost heaving in the spring.
[c] Rows inoculated with 20 g of infested oat kernels. In addition to root breakage from soil heaving, roots were severed on both sides of each row with a sharp knife in late March. No additional inoculum was added.
[d] Uninoculated 3.1-m rows sliced on both sides in late March with a sharp knife. Immediately after severing roots, 2 L of 10^6 conidia per milliliter were poured into the soil slice.

TABLE 5. Effect of *Cephalosporium gramineum* inoculum density on infection of three winter wheat cultivars of differing susceptibility

	Diseased tillers per row (%)[a]		
	Inoculum density[b]		
Cultivar	5 g	10 g	20 g
Marias	39	57	73
Crest LRC 40	30	38	50
PI 278212	14	18	24

[a] Mean percentages of four replications.
[b] The quantity of oat kernels infested with *C. gramineum* applied with the seed to a 3.1-m row.

next to roots collected in the field early in the spring (Morton, *unpublished*). This distribution of conidia could be altered significantly if cultivars differed in capacity to synthesize the mucilaginous coating around the roots, which might serve to concentrate propagules around potential infection sites. The ability of liquid conidial suspensions to override the resistance to entry could be attributed to high concentrations of propagules in the immediate vicinity of roots at the time of wounding. While this study failed to delineate major changes in the soil-root-pathogen interaction, the results do not rule out smaller, more significant localized effects within microhabitats in and around the soil-root interface.

Reduction in the percentage of tillers infected within plants was observed only in Crest LRC 40, which was also unique in its ability to restrict vertical and lateral movement of *C. gramineum* throughout its vascular network (15). If the close association between these types of resistance is more than circumstantial, then the same responses which slow movement of the fungus in the culms and leaves of infected tillers also might be responsible for retarding systemic invasion of the fungus between tillers. Limiting invasion between tillers of a plant may be loosely analogous to dwarf bunt resistance in winter wheat which interferes with the ability of the fungus to successfully colonize the growing point before the onset of stem elongation (6). In the case of Cephalosporium stripe, the fungus may need to enter the vascular system of each tiller prior to a restrictive host response. The crown region of a winter wheat plant is a complex aggregation of compressed nodes (18), which the fungus must traverse in order to invade developing tillers. The complex linkages and short vessel elements would influence pathogen movement and distribution. An active host response would impose additional barriers to the pathogen.

Differential responses between cultivars to percentage of diseased plants and to localization of pathogen movement have been identified in other vascular wilt diseases (1,8). It is doubtful, however, that the mechanisms are the same. Whereas other vascular pathogens of herbaceous annuals, such as *Fusarium oxysporum* and *Verticillium dahliae* actively penetrate the host root systems at different ontogenetic stages of development (7), *C. gramineum* apparently enters winter wheat roots after they have been injured by soil heaving in the spring. None of the responses related to hyperauxiny, such as tylosis formation, vessel collapse, or cell proliferation (2,5) have been observed in the vascular network of winter wheat plants infected with *C. gramineum*. Such significant differences in disease etiology suggest that Cephalosporium stripe cannot be compared with other vascular diseases. It follows, therefore, that the mechanisms and the inheritance of resistance may not be comparable.

Many aspects of Cephalosporium stripe etiology have relevance to germplasm evaluation. Yield reductions often have been measured by harvesting all plants within individual rows (10,12,14). Early visual disease readings have been recorded at a given time in the field without regard to heading dates of cultivars (12,14). This scoring procedure fails to account for differences in maturation rates, which are closely associated with symptom development, regardless of susceptibility to disease (15). Disregarding heading date when making disease readings in a germplasm development program would obscure genotypic differences in active host response similar to that exhibited by Crest LRC 40 and would favor the selection of late-maturing cultivars at the expense of the more agronomically preferable early maturing cultivars. The white head readings made several weeks after heading (12,14) more accurately reflect genotypic differences that condition different host responses and different disease incidence between plants.

The identification of distinct responses to infection by *C. gramineum* establishes a basis for selecting parental materials and subsequent segregating populations may be more carefully screened for different manifestations of resistance. Both pathogen exclusion and pathogen restriction, being independently expressed, might be effectively combined to produce a superior genotype with the maximum potential to prevent, as well as check, infection by *C. gramineum*.

To examine disease incidence between plants, white heads or diseased plants per row must be counted. Disease incidence between tillers within infected plants, however, must be enumerated in space-planted materials. Both of these phenotypes should be appraised at approximately 1 mo after heading, when disease symptoms are fully expressed. Yield may be used to measure cultivar responses to symptom severity, but only if infected plants within a row are examined. More definitive gauging of this phenotype would include a disease index rating system by evaluation of seed size (which reflects the extent of grain-filing) height reduction, or the rate of symptom development of flag leaves.

Mathre (*unpublished*) observed up to 90% infection in an inoculated susceptible cultivar at a seeding rate of approximately 50 seeds per 3.1-m row, suggesting that reduced seeding rates are not mitigating with respect to infection between plants. Identification of each phenotype and evaluation of cultivar responses are facilitated by space-planting. In addition, pedigree analysis and early generation testing currently employed at Montana State University (12,14), necessitates space-planted progeny rows. There is some question whether early generation testing is the most effective method for increasing resistance because the inheritance of Cephalosporium stripe resistance is unknown. If resistance is quantitatively inherited, then testing progeny populations in later generations may be more reliable. Some selection pressure may be applied on earlier bulk progeny populations by screening for seed size, which selects for disease-free plants as well as plants more tolerant to disease development. This approach would keep populations manageable over a number of selfing generations. Screening for seed size may also be effective in a recurrent selection program, should stable, genetic male-sterile sources in winter wheat be developed which could facilitate out-crossing.

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