Effect of Illuminance on the Resistance of Inbred Lines of Corn to Isolates of *Colletotrichum graminicola*

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ABSTRACT

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Three-week-old plants of six inbred lines of corn were inoculated in all combinations with four isolates of *Colletotrichum graminicola*. From 1 wk before to 1 wk after inoculation the plants were grown at day/night temperatures of 30/26 C and daytime illuminances of 455, 228, or 114 hlx. Lesion length, lesions per square centimeter, and sporulation per square centimeter decreased with increasing illuminance. Sporulation per lesion was highest at 228 hlx, slightly lower at 114 hlx, and lowest at 455 hlx. Isolate × line interaction effects were significant at $P = 0.11$, $P = 0.10$, and $P = 0.07$ for lesions per square centimeter, sporulation per lesion, and sporulation per square centimeter, respectively, when analyzed over all three illuminance treatments. When data for each illuminance level in each of the two trials were analyzed separately, the isolate × line interaction was significant at $P < 0.05$ for one of six analyses for lesion length and sporulation per square centimeter. The levels of specific resistance present in the lines were estimated by three methods and the consistency of the estimates were compared. Estimates of specificity differed for different components of resistance.

Additional key words: maize, quantitative disease resistance, *Zea mays*.

The effectiveness of disease resistance in plants can vary under different environmental conditions and in combination with different pathogen genotypes. Although polygenically inherited disease resistance is often sensitive to environmental variation, it is commonly regarded as durable with respect to genetic variation in the pathogen. Significant pathogen isolate × host cultivar interactions have been found, however, in several diseases for which resistance is quantitatively inherited (1,2,10,12). Our previous studies of interactions between isolates of *Colletotrichum graminicola* (Ces.) G. W. Wils. and *Bipolaris maydis* (Nisik.) Shoemaker and inbred lines of corn (*Zea mays* L.) suggested that isolate × line interactions themselves may be sensitive to environmental variation (6). In those studies, statistically significant isolate × line interactions were detected in analyses of individual runs of experiments but not in the combined analyses over all six runs of each experiment with the two pathogens.

Our previous studies with isolate × line interactions involving *C. graminicola* and *B. maydis* were conducted in a greenhouse in which both temperature and light intensity fluctuated (6). The experiments with *C. graminicola* were performed from September 1980 to January 1981; during that time the minimum daily temperatures varied from 19 to 23 C and the maximum daily temperatures from 26 to 30 C. Although Leonard and Thompson (9) found that lesion length increased with increasing temperature between 20 and 30 C, there was no obvious relationship between temperature and significant isolate × line interactions. Illuminance, although not measured, probably varied more than temperature during the course of the six greenhouse trials and seemed more likely to have affected isolate × line interactions.

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Hammerschmidt and Nicholson (3) found that anthracnose lesions on leaves of four corn lines resistant or hypersensitive-resistant to *C. graminicola* were smaller under high than under low light intensity, although the sizes of lesions on three of the four susceptible corn lines tested were unaffected by light intensity. Schall et al (13) found that necrotic leaf area was greater if corn seedlings were exposed to reduced light during the day after inoculation with *C. graminicola*.

The objectives of the present investigation were to examine more thoroughly the effects of illuminance on various components of resistance of corn to *C. graminicola* in addition to lesion size and to determine whether isolate × line specificity would be detected consistently in repeated trials under controlled conditions of temperature and illuminance.

MATERIALS AND METHODS

Isolates of *Colletotrichum graminicola*. Twenty-five isolates of *C. graminicola* from North Carolina, two from Indiana, and one from Kentucky were screened in the greenhouse. Seedlings of inbred line 349 from the open-pollinated corn cultivar Jarvis were grown as described (5) in a greenhouse at 20–43 C. Plants were fertilized as described (5) once per week from 14 days after planting. Thirty days after planting, the plants were inoculated by placing ten 5-μl droplets of inoculum on the fifth leaf.

Inoculum consisted of an aqueous suspension of 100,000 conidia per milliter prepared from cultures of *C. graminicola* grown on potato-dextrose agar; 14-day-old cultures were flooded with a solution containing two drops of Tween-20 per 100 ml of distilled water and then scraped to release the conidia. The conidial suspensions were filtered through two layers of cheesecloth, and spore concentrations were determined in a hemacytometer (Spiers-Levy Eosinophil Counter, C. A. Hausser and Son, Philadelphia, PA 19104).

After inoculation, the plants were incubated in a mist chamber in the greenhouse for 16 hr. Five days after inoculation the lesions on

the fifth leaf were measured. The mean length of lesions produced by the 25 isolates of *C. graminicola* that were screened ranged from 1.75 to 5.43 mm (Fig. 1). Four isolates, CgA, CgB, Cg11, and Cg106, with mean lesion lengths of 1.8, 3.6, 5.0, and 4.8 mm, respectively, were chosen for use in the experiments at different illuminances.

Illuminance. Six inbred lines from the open-pollinated corn cultivar Jarvis were grown as described (5) in the air-conditioned greenhouse of the phytotron at the Southeastern Plant Environmental Laboratory, Raleigh, NC, at day/night temperatures of 26/22 C for 2 wk. Cultivar Jarvis consists of a randomly mating population that has been shown to be genetically heterogeneous for agronomic traits as well as for levels of resistance to *C. graminicola* and *Bipolaris maydis* (5,6). After 2 wk, the plants were thinned to one per pot and then transferred to walk-in controlled-environment chambers kept at 30/26 C. The illuminance levels were 455, 228, or 114 hlx (592, 296, or 148 $\mu mol \cdot m^{-2} \cdot sec^{-1}$ photosynthetic photon flux density, respectively) during the 9-hr day period. The night period in the chambers was interrupted for 3 hr at 41, 21, or 10 hlx, respectively, for the three chambers. Regulation of temperature, relative humidity, air flow, and carbon dioxide concentration was as described by Jenns and Leonard (5).

Plants were inoculated 21 days after planting when they were in the six-leaf stage. Inoculum was prepared as in the screening experiment. The fifth leaf of each plant was sprayed to run-off with a spore suspension containing 100,000 conidia per milliliter applied with an atomizer attached to a pressure pump at 1.03 kPa (15 psi). Ten 5-μl drops of an aqueous conidial suspension of the same concentration were applied to the fourth leaf of each plant by using a 100-μl syringe.

After inoculation, the plants were incubated in a controlled-environment chamber at 30 C in the dark for 18 hr. During the incubation period a fine mist of deionized water was sprayed for 26 sec every 3 min at a rate of about 10.6 L/hr from each of four nozzles near the ceiling. The mist was turned off and the plants were left in the chamber for 3 hr while the humidity returned to normal, then the plants were returned to the controlled-environment chambers at the three illuminance levels. Three days after inoculation, the lesions on the fifth leaf were counted and the length and width (at the widest part) of this leaf were measured.

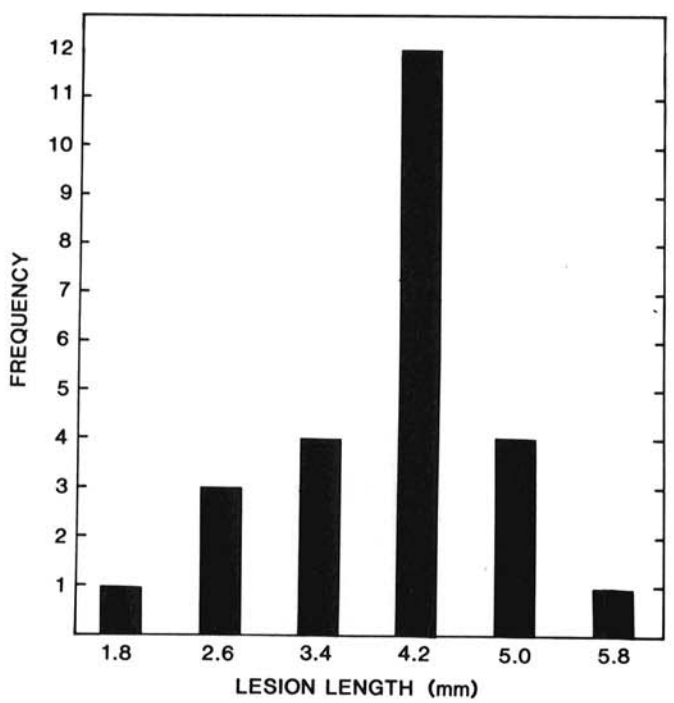

Fig. 1. Frequency distribution of the mean length of lesions produced on plants of an inbred line of the open-pollinated corn cultivar Jarvis by 25 isolates of *Colletotrichum graminicola*.

Plastic bags were secured over these leaves to induce sporulation. Six days after inoculation, the leaves enclosed in bags were removed and stored at 4 C until sporulation was measured as described by Jenns and Leonard (5). The lengths of lesions on the fourth leaf were measured 5 days after inoculation.

In one experiment, the lengths and widths of detached leaves from all six lines were measured with a ruler and their areas were determined with an Automatic Area Meter Type AAM-5 (Hayashi Denko Co., Ltd., Tokyo, Japan). Leaf area was regressed on length and width, and the following regression equation was used to estimate leaf area from length and width measurements for inoculated leaves:

$$\text{Area}\,(\text{cm}^2) = 0.539\,(\text{length}\,[\text{cm}] \times \text{width}\,[\text{cm}]) + 0.005\,(\text{length}\,[\text{cm}]).$$

In each of the two trials, 12 plants of each of the six lines were inoculated on each of three successive days. Since the 12 plants of each line were from three different illuminance regimes and were inoculated with each of four different isolates, there was no replication in one day's inoculation. The three inoculation days were replications within trials. Thus, in each trial there were three replications of 72 combinations of treatments (six lines $\times$ four isolates $\times$ three illuminance regimes). Treatment and interaction effects were analyzed both for each trial separately and also for the combined data over the two trials. Trial-to-trial variation was greater than within-trial variation, because conditions for growth of plants and production of inoculum varied less within the 3-day time span within trials than over the period of time between trials.

RESULTS

Frequency distributions of the mean lesion length data approached normality, whereas those of lesions per square centimeter and sporulation per lesion were skewed toward the right. The null hypotheses that the data for lesions per square centimeter and sporulation per lesion were random samples from normal distributions were tested by using a modified version of the Kolmogorov-Smirnov D-statistic (14). The null hypothesis was rejected in both cases at $P < 0.01$. Log transformations of these two variables produced data with distributions closer to the normal distribution, so transformed data were used in all analyses of these variables.

Lesion length, lesions per square centimeter, and sporulation per square centimeter decreased with increasing illuminance (Fig. 2). Sporulation per lesion was greatest at 228 hlx, slightly lower at 114 hlx, and lowest at 455 hlx (Fig. 2). Host line effects were significant or highly significant for all four components (Table 1).

Isolate effects were highly significant for lesions per square centimeter, sporulation per lesion, and sporulation per square centimeter (Table 1) but were not significant for lesion length. Mean lesion lengths for isolates over all lines and illuminance levels were 4.11, 4.52, 5.06, and 5.01 mm for isolates CgA, CgB, Cg106, and Cg11, respectively. Thus, the isolates that were selected for differences in lesion length on inbred line 349 showed greater differences in the other components on different host lines under the conditions of the controlled-environment tests. In spite of this, the mean lesion lengths for the four isolates over lines and illuminance levels were highly correlated ($R = 0.99$) with lesion lengths for these isolates in the initial screening test in the greenhouse. Thus, while the range of mean lesion lengths among the isolates in the controlled-environment tests was greatly reduced compared to that of the screening test, the relative ranking order of isolates remained very similar.

Lesion length was significantly correlated with lesions per square centimeter ($R = 0.36$, $P = 0.0002$), sporulation per lesion ($R = 0.34$, $P = 0.0001$), and sporulation per square centimeter ($R = 0.44$, $P = 0.0001$). Line 41 was an exception to the general correlation between lesion length and other components of resistance. Although line 41 had the smallest lesions of any of the six lines tested, it had relatively large numbers of lesions per square centimeter (Table 2). Sporulation per square centimeter was significantly correlated with lesions per square centimeter ($R =$

0.49, $P = 0.0001$) and with sporulation per lesion ($R = 0.77$, $P = 0.0001$). Sporulation per lesion and lesions per square centimeter were not significantly correlated.

Isolate × line interactions were not statistically significant for lesion length, but for lesions per square centimeter, sporulation per lesion, and sporulation per square centimeter the interaction was significant at $P = 0.11$, $P = 0.10$, and $P = 0.07$, respectively. Since the analysis of variance is not a sensitive indicator of specificity in genetic interactions (4,11), we considered these levels of significance as suggestive of a potential for adaptation of *C. graminicola* to quantitative resistance in corn.

When data for each illuminance level in each trial were analyzed separately, only one of six analyses for lesion length and sporulation per square centimeter showed an isolate × line interaction effect that was significant at $P < 0.05$. None of the analyses for lesion number or sporulation per lesion showed an isolate × line interaction effect significant at $P < 0.05$.

Isolate × illuminance and line × illuminance interactions were most pronounced for sporulation per lesion and sporulation per square centimeter (Table 1). Significance levels for these interaction effects involving sporulation ranged from $P = 0.06$ to $P = 0.10$. Among the other interaction effects, only the illuminance × trial and line × illuminance × trial interactions for lesions per square centimeter (Table 1) were significant.

Relative amounts of specific resistance in the corn genotypes were estimated both by regression methods (Ratings 1 and 2) (7) and a variance method (4). Ratings 1 and 2 are based on a modified stability analysis in which the disease reaction of each host line is regressed against the virulence indexes of the pathogen isolates with which it was inoculated. The virulence indexes may be based either on the mean disease severity induced by the isolate over all lines in the test or on the level of disease induced by the isolate on the most susceptible line in the test (ie, the line with the least specific resistance) (7). Rating 1 incorporates the mean disease severity for the line, the slope of the regression of disease severity on a virulence index based on the mean for each isolate, and the deviations from the regression of disease severity on a virulence index based on the host line with the least specific resistance. Rating 2 incorporates only the regression statistics and not the mean.

In the variance method, the variance in disease severity induced by pathogen isolates on a susceptible check cultivar (or the most susceptible line in the test) is assumed to represent error variance and variance in general virulence among the isolates. For other host lines in the test, the disease severity induced by each isolate on the susceptible check is subtracted from the severity induced on the test line, giving negative adjusted disease severity values. The variance among adjusted severity values for isolates on each test line should reflect the amount of matching of specific virulence of the isolates with specific resistance in the line (4).

Rankings of lines for degrees of specificity of resistance by Rating 1 and Rating 2 were highly correlated ($R = 0.70$) (Table 2). Rankings based on the variance method were better correlated with those from Rating 2 ($R = 0.49$) than from Rating 1 ($R = 0.40$). Rankings differed somewhat for different components of resist-

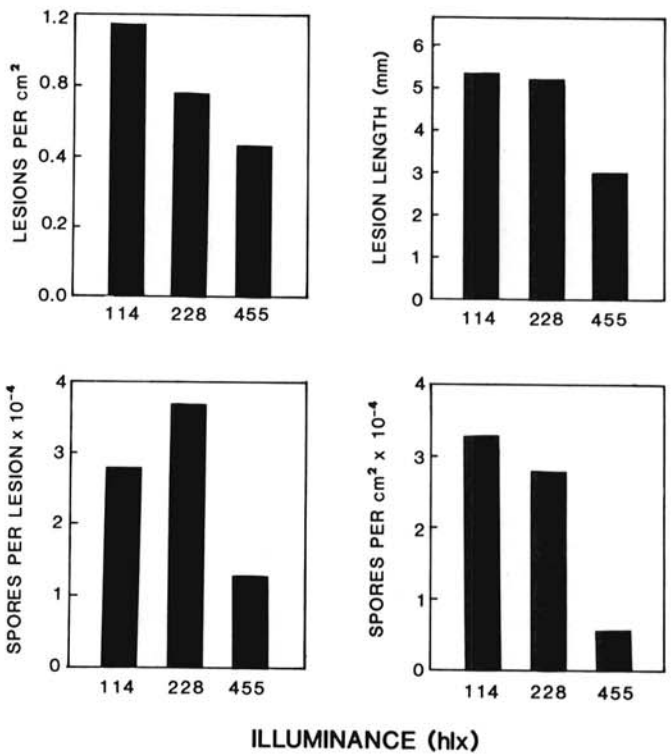

Fig. 2. Mean lesion lengths, lesions per square centimeter, spores per lesion, and spores per square centimeter produced by isolates of *Colletotrichum graminicola* on inbred lines of the open-pollinated corn cultivar Jarvis grown under three levels of illuminance before and after inoculation.

TABLE 1. Analysis of variance of lesion lengths, lesions per square centimeter,[a] spores per lesion,[b] and spores per square centimeter[c] obtained in two trials with isolates of *Colletotrichum graminicola* on corn lines at three illuminance levels[d]

	Lesion length		Lesions per cm²		Spores per lesion		Spores per cm²	
Source	df	Mean square	df	Mean square	df	Mean square	df	Mean square
Trial (random)	1	15.988***	1	0.485***	1	0.465*	1	0.000
Isolate (fixed)	3	6.494	3	2.499***	3	1.331***	3	6.917***
Line (fixed)	5	55.913***	5	1.030***	5	0.648**	5	1.752***
Illuminance (fixed)	2	5.011*	2	1.824*	2	2.686**	2	7.878**
Isolate × Line	15	2.870	15	0.052	15	0.137	15	0.118*
Isolate × Illuminance	6	2.942**	6	0.040	6	0.161*	6	0.234*
Line × Illuminance	10	2.477	10	0.120	10	0.145*	10	0.216*
Isolate × Trial	3	2.942	3	0.020	3	0.022	3	0.054
Line × Trial	5	0.995	5	0.018	5	0.109	5	0.136
Illuminance × Trial	2	0.418	2	0.140	2	0.070	2	0.238
Isolate × Line × Trial	15	2.838	15	0.052	15	0.071	15	0.054
Isolate × Illuminance × Trial	6	0.381	6	0.040	6	0.047	6	0.115
Line × Illuminance × Trial	10	1.485	10	0.120**	10	0.052	10	0.092
Isolate × Line × Illuminance	30	1.318	30	0.032	30	0.129	30	0.110
Error	26[e]	3.204	29	0.034	29	0.120	29	0.151

[a] Lesions per square centimeter transformed to $\log_{10}$ (lesions per square centimeter) prior to analysis.
[b] Spores per lesion transformed to $\log_{10}$ (spores per lesion) prior to analysis.
[c] Spores per square centimeter transformed to $\log_{10}$ (spores per square centimeter) prior to analysis.
[d] Plants were grown at illuminance levels of 455, 228, of 114 hlx for 1 wk before or after inoculation.
[e] Differences in degrees of freedom for error are due to missing values. Asterisks *, **, and *** indicate effect significance at $P < 0.10$, $P < 0.05$, and $P < 0.01$, respectively.

ance, but the rankings based on lesion length and sporulation per lesion were more similar to each other than to the rankings based on lesions per square centimeter (Table 2). With the exception of line 26, the rankings for degree of specificity of resistance for a given component were quite similar over the three illuminance levels. The resistance of line 26 appeared to have a high degree of isolate specificity for lesion length and sporulation per lesion at 455 and 228 hlx but a low level of specificity at 114 hlx. The reverse was true for lesions per square centimeter on line 26.

Line 41, which had the smallest lesions and least sporulation per lesion, appeared relatively susceptible in terms of numbers of lesions per square centimeter (Table 2). The value of the resistance of line 41 may be suspect for this reason and also because it ranked relatively high for isolate specificity for all components under all illuminance levels. Line 56 appeared to have the best combination of moderate resistance in all components with low rankings for isolate specificity for lesion length and sporulation under all illuminance levels. Thus, its resistance should be relatively stable.

DISCUSSION

In general, the reactions of the six inbred lines of corn to *C. graminicola* in these controlled-environment tests correlated well with those of the same six lines in our earlier greenhouse tests (6). The coefficient of correlation between mean lesion lengths over all isolates and illuminance levels in the phytotron and mean lesion lengths over all isolates and trials in the greenhouse was $R = 0.88$.

Both Hammerschmidt and Nicholson (3) and Schall et al (13) had previously shown that resistance of corn to anthracnose caused by *C. graminicola* is reduced in plants exposed to low light intensity. Hammerschmidt and Nicholson (3) found that the lesions on one susceptible, and four resistant, lines of corn were significantly smaller on plants grown at 376 hlx than on plants grown at 96 hlx. Our results with corn lines grown at 455, 228, and 114 hlx were similar; on the average, the lesions were smaller at the higher than at the lower illuminance levels. In addition, we found that the number of lesions per square centimeter of leaf area was also reduced at higher illuminance levels. Schall et al (13) reported that the percentage of corn leaf tissue affected by anthracnose symptoms was increased when plants were exposed to low illuminance during the day after inoculation with *C. graminicola*. They did not distinguish whether the effect was due to increased size of lesions, increased numbers of lesions, or both. We also measured sporulation per lesion and found it to be affected by illuminance as well, being greatest at 228 hlx, slightly less at 114 hlx, and least at 455 hlx.

Our results for *C. graminicola* differ from those we obtained in a similar study with *Bipolaris maydis* (5). With *B. maydis*, illuminance had no effect on the number of lesions per square centimeter, whereas for *C. graminicola*, reduced illuminance had a greater effect on number of lesions than on lesion length. This suggests that infection occurred rapidly from conidia of *B. maydis* so that the length of the period of leaf wetness was not limiting regardless of the resistance of the host plants in the test. With *C. graminicola*, however, infection proceeds more slowly so that any delay in the establishment of infections from genetic resistance or environmental preconditioning of the plants could result in reduced numbers of lesions. Schall et al (13) found that illuminance affected percent anthracnose lesion coverage when corn genotypes were incubated in the dark for 18 hr after inoculation, but it had no effect if the incubation period was increased to 42 hr. It seems probable that at least some of the response that they measured was due to an effect on lesion number as well as on lesion size for the 18-hr incubation period.

Another contrast between our results with *C. graminicola* and those we obtained with *B. maydis* was in sporulation per lesion. With *B. maydis*, sporulation per lesion was greatest at 114 hlx, whereas for *C. graminicola* sporulation per lesion was greater at 228 hlx. This may be because at 114 hlx, anthracnose lesions often coalesced and killed the leaf, limiting the size to which individual lesions could grow. Since lesion size and sporulation per lesion were significantly correlated, the number of spores produced per lesion was less for small, crowded lesions. It seems clear, however, that for both diseases, the pathogen will cause more damage and reproduce more abundantly during periods of reduced light

TABLE 2. Ranking of corn lines according to the specificity of components of resistance to *Colletotrichum graminicola*

Light regime[a] (hlx)	Line	Lesion length (mm)				Lesions per cm^2				Spores per lesion × 10^3			
			Rank[b] by rating:				Rank[b] by rating:				Rank[b] by rating:		
		Mean	Var.[c]	1[d]	2[e]	Mean	Var.	1	2	Mean	Var.	1	2
455/41	41	2.3	5	5	5	0.96	6	3	4	8.1	4	5	5
	26	3.7	6	4	4	0.23	1	5	1	23.4	2	6	6
	56	4.2	1	1	1	0.29	5	6	6	20.9	1	1	1
	20	6.0	2	2	2	0.96	3	1	2	20.5	5	2	2
	72	5.6	3	3	3	0.85	2	4	3	20.1	3	4	4
	80	6.1	4	6	6	0.76	4	2	5	25.0	6	3	3
228/20	41	2.8	4	3	3	1.03	3	3	3	19.3	4	6	6
	26	4.3	5	4	4	0.36	1	1	2	46.7	3	5	5
	56	3.8	1	1	2	0.50	5	5	6	55.7	2	2	1
	20	5.8	2	2	1	1.71	4	6	4	37.6	1	4	3
	72	6.9	6	5	5	1.39	2	2	1	84.7	5	3	4
	80	7.8	3	6	6	1.38	6	4	5	61.1	6	1	2
114/10	41	4.1	4	6	6	1.23	4	4	3	33.7	4	5	5
	26	4.3	2	1	1	0.95	5	5	4	38.8	5	2	2
	56	4.0	1	3	3	1.33	6	6	5	39.7	1	1	1
	20	6.5	3	4	4	1.28	3	3	2	35.8	2	4	4
	72	5.8	6	2	2	1.71	1	2	1	64.5	6	6	6
	80	7.2	5	5	5	1.94	2	1	6	37.3	3	3	3

[a] Daytime/interrupted night light intensities.

[b] Ranking 1 = least specific resistance; 6 = most specific resistance.

[c] Variance among isolates of lesion length, lesions per square centimeter, or spores per lesion adjusted by subtraction of value for line with lowest variance among isolates.

[d] Rating 1 = [(Deviation mean square for regression on Virulence Index based on line with least specific resistance/mean deviation mean square) + line mean/overall mean] × 2 + slope of regression on Virulence Index based on the mean disease severity (7).

[e] Rating 2 = (Deviation mean square for regression on Virulence Index based on line with least specific resistance/mean deviation mean square) + slope of regression on Virulence Index based on the mean disease severity (7).

intensity during cloudy weather than during periods of clear weather with full sunlight.

Correlations between components of resistance in this test were rather low. In fact, the correlation between lesion length and sporulation per lesion ($R = 0.34$) was much lower than the correlation found in the earlier greenhouse study (6). In two tests in the greenhouse involving 16 isolates of *C. graminicola* on a single corn line, correlations of $R = 0.74$ and $R = 0.60$ were obtained between lesion length and sporulation per lesion. In a third test involving 10 isolates and five corn lines, the correlation was $R = 0.56$ (6).

In addition to the different numbers of isolates and lines in the tests, there were two important differences between the results of the greenhouse tests and of the phytotron studies. First, the lesions chosen for study of sporulation in the greenhouse tests were from leaves with only 10 lesions, each of which had been initiated from droplets of spore suspension applied individually to the leaves, whereas the lesions used in the phytotron study were from leaves that were sprayed with a spore suspension and that had large numbers of lesions per leaf. Second, each greenhouse test was done once in a single environment, whereas the correlations calculated from the phytotron data were based on lesion size and sporulation over three different illuminance regimes. Variation in numbers of lesions per leaf might account for part of the loss of correlation between lesion size and sporulation per lesion in this study. Another important source of variation that reduced the correlation between lesion size and sporulation was the interaction of these variables with illuminance level.

The statistical significance of the isolate × illuminance interaction effect for lesion length suggests that isolates of *C. graminicola* differ in virulence mechanisms. That is, illuminance is unlikely to affect isolates directly but may act indirectly through its effect on host resistance. Line × illuminance interaction effects were not significant for lesion length. This differs from results obtained with *B. maydis*, in which interactions of lines with illuminance and temperature were often statistically significant, but interactions of isolates with illuminance or temperature were not (5). This suggests that isolates of *C. graminicola* may be more variable than those of *B. maydis* in their response to environmentally induced changes in host resistance. The lack of a significant line × isolate interaction effect for length of anthracnose lesions in our study also indicates that the six lines that we tested did not differ greatly in the extent to which reduced illuminance affected lesion size. In contrast, Hammerschmidt and Nicholson (3) found that all four resistant lines they tested became significantly less resistant in reduced light, but three of four susceptible lines showed no significant effect of light intensity on the size of anthracnose lesions that developed.

For sporulation per lesion, both the line × illuminance and isolate × illuminance interactions were statistically significant for *C. graminicola* at $P < 0.10$. With *B. maydis* only the line × illuminance interaction effect was significant for sporulation per lesion (5). Since sporulation per lesion depends on the size of lesions, part of the interaction should be determined by the same factors that influence line × illuminance interactions for lesion size. Illuminance might also affect the sporulation of pathogen isolates directly, because the sporulation occurs on the exposed surface of host leaves.

The isolate × line interaction effects were significant at $P = 0.07$, $P = 0.10$, and $P = 0.11$ for sporulation per square centimeter, sporulation per lesion, and lesions per square centimeter, respectively, in our experiments in controlled-environment chambers. As in a previous study conducted in the greenhouse (6), no significant isolate × line interaction effect was found for lesion length when data were analyzed over all environments. Johnson and Taylor (8) suggested that spore production of a pathogen per unit area of host tissue inoculated may be the most sensitive measure for detecting differences in resistance. Although the isolate × line interactions that we observed in the controlled-environment studies were not significant at $P < 0.05$, given the conservative nature of the analysis of variance for detecting specificity, it should not be concluded that there is no specificity in the resistance of these corn lines to these isolates of *C. graminicola*. As shown by Parlevliet and Zadoks (11), a great deal of potential specificity can exist in interactions of polygenic resistance and virulence even when the interaction mean square in the analysis of variance is low. Therefore, we believe that it is reasonable to attempt to estimate relative degrees of specificity of the resistance of host lines involved in the interaction.

In the greenhouse study (6), significant isolate × line interaction effects were found in the analysis of variance of four of six individual trials (environments) with *C. graminicola*. When data for each illuminance regime in each trial were analyzed separately in the phytotron study, however, only one of six analyses for lesion length and sporulation per square centimeter showed a significant isolate × line interaction effect. None of the analyses for lesion number or sporulation per lesion showed a significant isolate × line interaction effect. Hence, though the analysis of the combined data gave evidence of specificity for three of the variables, significant isolate × line interaction effects were not detected consistently in individual trials.

It is not clear why significant isolate × line effects were not detected in individual trials in the phytotron, whereas significant interactions were detected in individual greenhouse trials. The reason for the difference may be that more isolates and lines (10 each) were used in the greenhouse studies and that there were four replications per trial compared to three replications in the phytotron.

When data from plants grown under each illuminance regime were analyzed separately, no significant isolate × line interaction effects were found. This seems to indicate that illuminance does not greatly influence the expression of specificity of resistance to *C. graminicola* in corn lines. In general, this conclusion is supported by the consistency of estimates of the relative specificity of components of resistance of individual lines over different illuminance regimes. The primary exception was with line 26 in which the estimated relative specificity for all three components was distinctly different at 114 hlx than at 455 or 228 hlx.

Among the three methods used in estimating relative specificity of resistance of lines, Ratings 1 and 2 were previously shown to give consistent results in repeated trials under the same temperature and illuminance conditions in experiments with isolates of *B. maydis* on corn. In those experiments, the coefficient of correlation between rankings of lines for specificity estimated by Rating 2 in two independent tests was 0.94 (5). Thus, Rating 2 is probably the most reliable of the three methods. In the present studies with *C. graminicola*, Rating 2 also gave the most consistent rankings among lines for specificity of resistance in the three illuminance regimes. This is consistent with the conclusion that illuminance levels had little or no effect on the expression of specificity of resistance of corn lines to *C. graminicola*. As in the previous study with *B. maydis*, the rankings based on Rating 1 and Rating 2 were highly correlated, and rankings based on the variance mathod were less well correlated with either those of Rating 1 or Rating 2 (coefficients of correlation were 0.40 and 0.49, respectively). The advantage of the variance method is that it is much less complex and is easier to compute than the other two rating methods. The variance method may suffice to screen out lines with large proportions of specific resistance in breeding trials.

As with the earlier study with *B. maydis* (5), the ratings for relative specificity of resistance of lines varied for the different components of resistance. With resistance to *C. graminicola*, the greatest differences in rankings of lines for relative specificity of resistance occurred between rankings based on numbers of lesions per square centimeter and those based on lesion length or sporulation per lesion. This suggests that the mechanisms of resistance that limit numbers of successful infections may be controlled by a number of genes that differ from those for mechanisms that limit the rate of lesion expansion or sporulation per lesion. If *C. graminicola* has the potential to adapt at least partially to the resistance of corn lines, the degree to which the adaptation can occur may differ for different components of resistance as well as for different corn lines. Confirmation of this prediction would depend upon either long-term field tests or intense selection regimes with populations of the pathogen in greenhouse or growth chamber experiments.

Lines 41 and 26, which developed the smallest lesions at full illuminance (455 hlx), were not the most desirable in terms of overall resistance ratings. Both lines had relatively high rankings for degree of specificity of their resistance in most comparisons, and line 41 developed large numbers of lesions, particularly at high illuminance. Line 56, on the other hand, had good-to-intermediate resistance by all components under all illuminance levels and was consistently low in estimates of isolate-specificity for two of the three components of resistance. Thus, of the limited number of lines tested in this study, we would rate line 56 as superior in terms of level of resistance and the probable durability and environmental stability of the resistance.

The results of these comparisons provide an example of how breeding lines might be evaluated for durability of resistance. Whether such an evaluation is deemed worthwhile will probably depend upon past experience with the adaptibility of pathogen populations and upon the genetic uniformity of the crop in question. For crops in which a few cultivars are likely to be prevalent over large geographical areas for many years, it seems prudent to assume that some pathogen adaptation to resistance is likely to occur and to prepare for it by selecting durable resistance by the best methods available.

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