The Effect of C and S Group Cytoplasms on Resistance to Southern Corn Leaf Blight

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ABSTRACT

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Quantitative differences in disease resistance to randomly selected isolates of *Bipolaris maydis* occurred among C and S group male-sterile cytoplasms *(cms)*. *Cms*-pathogen isolate interactions were observed among 18 isolates of *B. maydis*, and 17 male-sterile cytoplasms within the 38-11 × FR37[2] corn genotype. Greater average disease development associated with several cytoplasmic male-steriles indicated that *cms*-H, *cms*-I, *cms*-EK, *cms*-RB, and *cms*-VG may be less desirable than others as alternatives to *cms*-T. *Cms*-EK, *cms*-IA, and *cms*-TA in the Ky-21 line, and the R6-24 and R6-35 lines with normal cytoplasm, were reciprocally crossed in all combinations. The progeny were inoculated with *B. maydis* isolate Ch-448. Significant differences in disease reactions confirmed the association of cytoplasm source with quantitative differences in disease resistance. *Cms*-EK conferred lower resistance, and *cms*-IA and *cms*-TA conferred higher resistance to *B. maydis* isolate Ch-448 in the 38-11 × FR37[2] and Ky-21 genotypes.

The quantitative differences in disease resistance and *cms*-pathogen isolate interactions observed, indicate that cytoplasms differ in reaction to isolates of *B. maydis*, and that isolates of the pathogen differ in their response to *cms*. The potential for large-scale use of a single male-sterile cytoplasm to cause selection of pathogen strains more aggressive on plants with that cytoplasm is indicated.

Additional key words: Helminthosporium maydis, race T, race O.

The southern corn leaf blight epiphytotic of 1970 is an example of the hazards of cytoplasmic monoculture. The widespread use of a single cytoplasmic male-sterility source in corn *(Zea mays* L.), and the occurrence of a virulent pathogen, *Bipolaris maydis* (Nisikado) Shoemaker race T, resulted in extensive economic losses during 1970. With evidence that susceptibility is inherited with Texas male-sterile cytoplasm (*cms*-T), disease evaluation of alternative cytoplasmic male-steriles is needed. Field observations indicate that most steriles in corn are resistant to *B. maydis* race T (2, 10, 11, 14). The resistant male-sterile cytoplasms have been categorized into two groups: the C and S (1). Individual cytoplasms included in the C and S groups may have originated independently, but have been grouped on the basis of restoration of pollen production in specific inbred lines. Although all have a common identifying characteristic of male sterility, they are not believed to be identical (8, and V. E. Gracen, and C. O. Grogan, *unpublished*). Responses to genetic restoration of fertility differ between the C and S groups, and within the S group cytoplasms. Susceptibility to *B. maydis* race T is associated with male-sterile cytoplasms of the T-group which includes *cms*-T, -Q, -HA, and -P (2, 4, 7, 10, 11, 14, 16).

Male-sterile cytoplasms that confer resistance to race T also confer insensitivity to the race T toxin (6, 9, 11, 16, 17). Lack of sensitivity to the toxin is apparently the basis of their resistance. Qualitative resistance of *cms* to *B. maydis* is well documented. This study was undertaken to determine whether quantitative differences in disease resistance exist among the C and S groups of male-sterile cytoplasms to randomly selected isolates of *B. maydis*.

MATERIALS AND METHODS.—*Inoculum.*—Monoconidial cultures were established from isolates of *B. maydis* race T and race O that had been collected in 1970 and 1971 from different geographic areas. The cultures were grown on potato-dextrose agar, and spores from the cultures were used to inoculate corn seedlings of inbred line B37 with *cms*-T and N cytoplasm. Leaves infected with different isolates were collected separately, dried, and stored at room temperature. These leaves were used as a source of conidia for all inoculations in this investigation.

The stored leaf sections that served as a source of inoculum were incubated in a moist chamber for 1 week at room temperature. Spores were washed from leaves with 0.0001% Tween-20 (20% polyoxyethylene sorbitan monolaurate) solution, and filtered through two layers of cheesecloth to remove mycelium and leaf fragments. Spores were counted with a hemacytometer, and suspensions of each isolate were adjusted to a concentration of 5,000 spores/ml. Spore suspension (20 ml) was sprayed onto eight corn seedlings in the four- to six-leaf stage with a hand sprayer held about 0.5 m above

the seedlings and attached to an air pump delivering air at 350-700 g per cm^2. The hand sprayer was moved uniformly back and forth over the seedlings. After inoculation, the seedlings of the 17 *cms* in the 38-11 × $FR37^2$ lines were placed in a mist chamber for 12 hours. The progeny of the reciprocal crosses of the Ky-21 lines and the Ky-21 lines crossed with R6 lines were placed in the mist chamber for only 8 hours, in an attempt to accentuate the differences in the number of successful infections in host genotypes of differing susceptibility.

Host plants.—Seventeen male-sterile cytoplasms had been incorporated into the 38-11 line and then crossed twice to FR37 (i.e. 38-11 × $FR37^2$) by Illinois Foundation Seeds, Inc., of Champaign, IL. Except for male-sterile cytoplasms, the hybrids were similar, with 25% germ plasm from the 38-11 line and 75% from the FR37 line. The B37N (normal) and the B37Trf (Texas *cms* with restorer gene) cytoplasms were obtained from Clyde Black and Son, Inc., Ames, IA.

Inbred lines Ky-21 *cms*-EK, Ky-21 *cms*-IA, and Ky-21 *cms*-TA were obtained from D. L. Thompson, North Carolina State University. The seeds were from the 1971 ARS leaf blight-rating tests (13).

Normal cytoplasm inbreds R6-24 and R6-35 were derived from single plants of the open-pollinated cultivar Indian Chief at North Carolina State University.

Since normal or near normal fertility is exhibited by Ky-21 with the three *cms* (1), all possible reciprocal crosses were made among the Ky-21 lines, and progeny from each of these were crossed reciprocally with the R6 lines. At least three plants were used for each reciprocal cross between Ky-21 lines, and the seeds from these plants were bulked. For each of the reciprocal crosses between the three Ky-21 *cms* and R6 lines one plant was used. The cross Ky-21 *cms*-EK × R6-35 and its reciprocal yielded too few seeds for adequate tests. The reciprocal crosses tested are listed in Table 2.

Seedlings for inoculation were grown in loam:sand mixture (2:1, v/v) in 10-cm diameter clay pots (1 seedling per pot) in the greenhouse at about 22 C. One week before inoculation, about 3 g of slow-release fertilizer, Osomocote 18-9-9 (Sierra Chemical Co., Newark, CA) was placed on the surface of the soil. Variations among progeny from reciprocal crosses were observed for both seed germination and seedling vigor. Disease reactions were evaluated only on plants that appeared vigorous and healthy before inoculation.

Experimental design.—A confounded design (3) was used for the investigation of interaction of the 17 C and S group cytoplasms and 18 *B. maydis* isolates. The cytoplasms were randomly assigned to three groups, with B37Trf and B37N used in each group of cytoplasms. The *B. maydis* isolates were randomly assigned to three groups, and a group of isolates was paired with a group of cytoplasms. The means of each cytoplasm-isolate combination within a group were compared using Duncan's multiple range test.

An analysis of variance was used to determine the significance of differences among progeny of the reciprocal crosses of the Ky-21 and R6 lines.

Disease evaluation.—Disease resistance ratings were made on the third leaf, which was the last fully extended leaf present at the time of inoculation. The number of days after inoculation that the third leaf survived was a measure of disease severity. A leaf was considered to have survived until a continuous area greater than one-half the area of the leaf appeared yellow or brown from enlarging and coalescing lesions. At the end of 3 weeks, all leaves with less than 50% necrotic and chlorotic area received a survival rating of 21 days.

Five additional disease-resistance ratings were used for the Ky-21 lines and the progeny from reciprocal crosses. The numbers of lesions on the third leaf of each plant were counted 4-5 days after inoculation. Numbers of lesions per square centimeter of leaf area were calculated from the approximate leaf area determined as length × width × a correction factor of 0.702, as suggested by Williams et al. (18). The mean length of the five largest lesions on the third leaf was recorded at 4-5 and 8 days after inoculation. The third leaves were also rated visually at the end of the 21-day test period. A disease rating scale was based on sample leaves, with 0 = 1%-9%, 1 = 10%-40%, 2 = 41%-60%, 3 = 61%-90%, and 4 = 91%-100% necrotic area.

RESULTS.—*C and S group cms.*— Of 240 pairs of *cms*-isolate combinations tested in the 38-11 × $FR37^2$ genotype, 13 combinations showed differences in leaf survival that were significant ($P = 0.05$) when analyzed with Duncan's multiple range test (15). Based on leaf survival, the *cms*-I plants were significantly more susceptible than *cms*-L plants to isolate Ch-449 (Fig. 1). Plants with *cms*-EK were more susceptible than were *cms*-G plants to isolate Ch-400 (Fig. 2). With isolate Ch-530, *cms*-R and *cms*-TA plants were more susceptible than *cms*-M plants. Plants with *cms*-EK or *cms*-K were more susceptible to Ch-270 than were plants with either *cms*-M or *cms*-R; plants with *cms*-G and *cms*-TA were less resistant than *cms*-M. *Cms*-VG plants were more susceptible to Ch-80 than were *cms*-IA plants (Fig. 3). *Cms*-H plants were more susceptible to Ch-187 than were *cms*-IA and *cms*-MY plants. Some apparent *cms*-isolate interaction was observed. *Cms*-M plants were significantly more resistant than *cms*-K plants to Ch-270. The *cms*-K plants appeared to be more resistant than *cms*-M plants to Ch-115, although the difference was not significant (Fig. 2).

The mean of leaf survival times of all cytoplasm-isolate combinations for each cytoplasm of the C and S groups was significantly greater than the mean leaf survival of the B37Trf. Mean leaf survival for *cms*-I, *cms*-RB, *cms*-EK, *cms*-H, and *cms*-VG was significantly less than the mean leaf survival of inbred B37N (Fig. 4, 5, 6).

Progeny from reciprocal crosses.—Isolate Ch-448 was selected for evaluation of disease resistance among inbred lines and progeny from reciprocal crosses with *cms*-EK, -IA, and -TA (Table 1, 2). Lesions on the 38-11 × $FR37^2$ lines with *cms*-EK, -IA, and -TA were significantly smaller than were lesions on the Ky-21 lines with those cytoplasms. Leaves of 38-11 *cms*-EK × $FR37^2$ did not survive as long as those of 38-11 *cms*-TA × $FR37^2$ (Table 1). Similar trends were observed in inbred line Ky-21 (Table 2). Leaf survival of *cms*-EK was significantly less than *cms*-IA.

In reciprocal crosses of Ky-21, *cms*-IA and *cms*-TA conferred significantly more resistance then *cms*-EK as measured by leaf survival. The *cms*-IA progeny had longer leaf survival, and smaller lesions, than did *cms*-EK progeny. Numbers of lesions in the Ky-21 line were

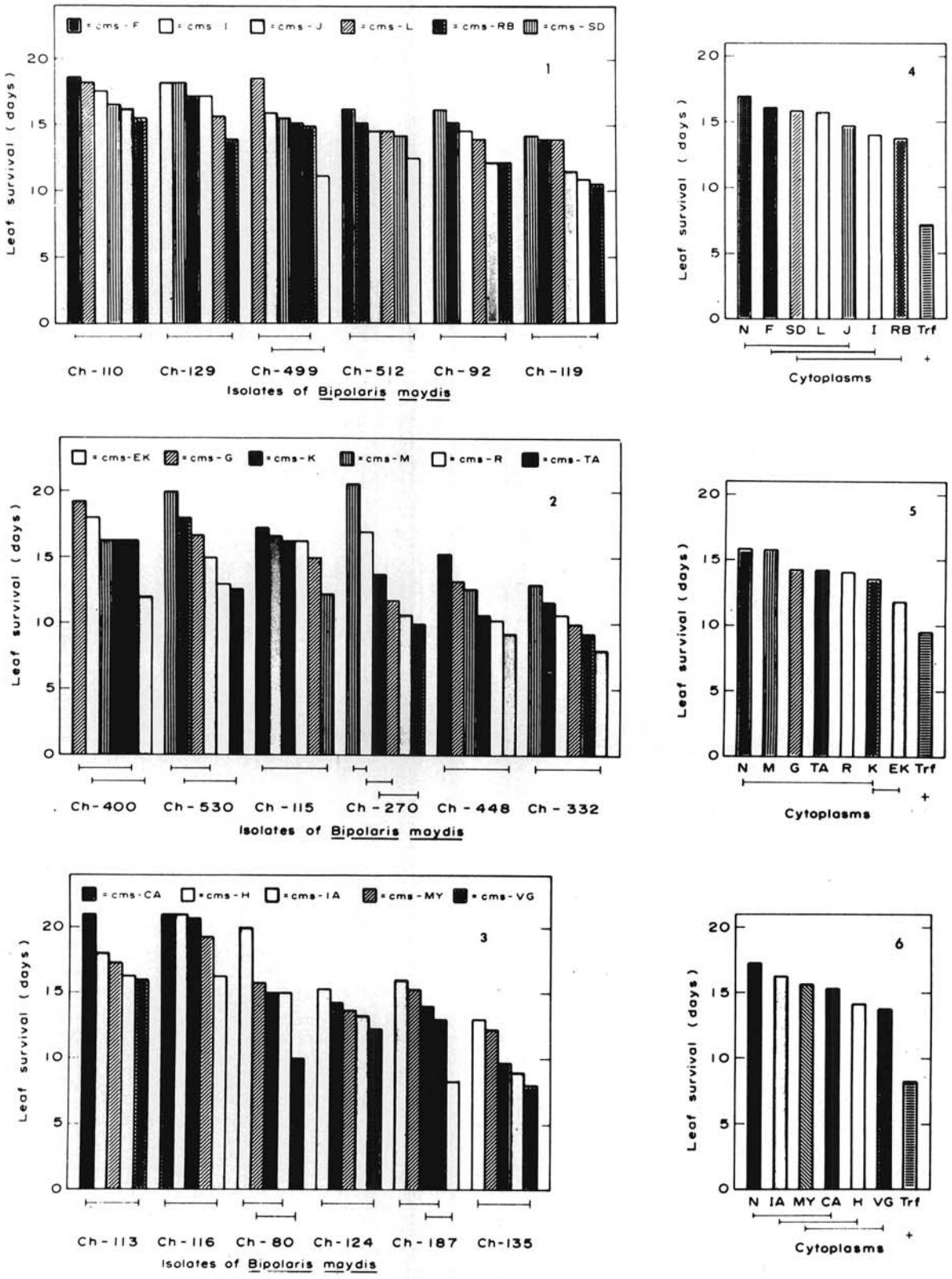

Fig. 1-6. 1-3) Disease reaction of different male-sterile cytoplasms in 38-11 × FR37[2] corn genotypes to isolates of *Bipolaris maydis*. Isolates Ch-119, Ch-332, and Ch-135 are of race O; the other isolates are race T. The values represent the mean of three replications. Cytoplasms underlined by the same line are not considered significantly different by Duncan's multiple range test ($P = 0.05$). **4-6)** Mean disease reaction of different cytoplasms in 38-11 × FR37[2] corn genotypes to six randomly selected isolates of *Bipolaris maydis*. N and Trf (*cms*-T restored) were in the B37 corn inbred line. Cytoplasms underlined by the same line are not considered significantly different by Duncan's multiple range test ($P = 0.05$).

significantly greater for *cms*-EK ♀ × *cms*-IA ♂ than for the reciprocal, but the number of lesions per square centimeter was not significantly different. No significant differences were observed between hybrid *cms*-EK ♀ × R6-24 ♂ and R6-24 ♀ × *cms*-EK ♂. Not enough seeds were obtained from cross R6-35 ♀ × *cms*-EK ♂ to evaluate

TABLE 1. Disease reactions of *cms*-EK, -IA, and -TA in 38-11 × FR37[2] corn lines to *Bipolaris maydis* isolate Ch-448

♀ × ♂	Lesions (no.)[a]	Lesions (no./cm²)[b]	Leaf survival (days)[c]	Disease index[d]	Lesion length (mm)[e] 3-4 days	Lesion length (mm)[e] 8 days
38-11 *cms*-IA × FR37[2]	27.8	0.8	18.6	2.4	2.6	10.4
38-11 *cms*-EK × FR37[2]	28.7	0.6	17.7	2.3	2.4	12.3
38-11 *cms*-TA × FR37[2]	22.4	1.0	19.1	2.3	3.0	12.0
LSD ($P = 0.05$)	10.1	0.6	1.4	0.9	0.9	3.1
LSD ($P = 0.01$)	13.6	0.8	1.9	1.3	1.4	4.8

[a]The mean of 21 plants of each cytoplasm.
[b]The mean of eight plants of each cytoplasm.
[c]The data represents the number of days after inoculation that the third leaf survived. The values are the means of 14 plants of each cytoplasm.
[d]The mean disease index from the third leaf of 12 plants from each cytoplasm. The disease index values are: 0 = 1%-9%, 1 = 10%-40%, 2 = 41%-60%, 3 = 61%-90%, and 4 = 91%-100% necrotic area.
[e]The mean of four plants of each cytoplasm.

TABLE 2. Disease reactions for progeny of reciprocal crosses with *cms*-EK, *cms*-IA, and *cms*-TA cytoplasms in the Ky-21 corn line and normal cytoplasm[a] to *Bipolaris maydis* isolate Ch-448

♀ × ♂	Lesions (no.)[b]	Lesions (no./cm²)[c]	Leaf survival (days)[d]	Disease index[e]	Lesion length (mm)[f] 3-4 days	Lesion length (mm)[f] 8 days
IA × IA	16.7	0.9	17.1	2.7	2.9	15.1
EK × EK	28.9	1.3	14.2*[g]	3.4	3.5	16.3
TA × TA	21.1	0.9	16.3	2.9	2.9	16.7
EK × TA	20.3	1.1	14.7*	3.0	3.1	16.6
TA × EK	27.2	1.1	17.6	3.1	3.2	15.6
EK × IA	34.9*	1.1	15.3*	3.3	3.8	17.4**[g]
IA × EK	15.4	0.6	18.2	2.6	2.9	13.0
TA × IA	11.8	0.9	15.7	3.6	2.4	11.7
IA × TA	25.1	1.0	16.3	2.9	3.4*	15.1**
EK × R6-24	28.9	0.9	17.1	3.3	3.2	13.3
R6-24 × EK	36.9	1.0	16.1	3.5	3.0	13.3
IA × R6-24	37.1	1.7*	15.6	3.3*	3.5	14.0
R6-24 × IA	25.2	0.7	17.4	2.2	2.7	13.6
TA × R6-24	21.6	0.8	17.8	2.3	2.9	13.4
R6-24 × TA	30.7	1.3	15.6	3.5*	3.2	13.1
IA × R6-35	16.5	0.6	19.6	2.0	2.4	11.1
R6-35 × IA	31.3*	1.1	18.7	2.2	2.4	11.7
TA × R6-35	26.4	1.1	18.8	2.7	2.6	13.4
R6-35 × TA	35.0	1.9*	17.3	2.5	2.9	12.5
LSD ($P = 0.05$)	14.0	0.7	2.4	0.9	0.9	2.5
LSD ($P = 0.01$)	18.5	0.9	3.2	1.2	1.1	3.3

[a]Normal cytoplasm R6-24 and R6-35 genotypes were derived from the open-pollinated cultivar 'Indian Chief'.
[b]The mean of 14 plants from each cross.
[c]The mean of eight plants from each cross.
[d]The data represents the number of days after inoculation that the third leaf survived. The values are means of 14 plants from each cross.
[e]The mean disease index from the third leaf of 12 plants from each cross. The disease index values are: 0 = 1%-9%, 1 = 10%-40%, 2 = 41%-60%, 3 = 61%-90%, and 4 = 91%-100% necrotic area.
[f]The mean of four plants from each cross.
[g]Asterisk (*) indicates significant at $P = 0.05$, and asterisks (**) indicate significant at $P = 0.01$.

disease resistance of *cms*-EK in hybrids with line R6-35.

Progeny from the cross *cms*-TA ♀ × *cms*-IA ♂ had significantly smaller lesions than did progeny of the reciprocal cross. However, the disease index and leaf survival were not significantly different. Progeny from *cms*-TA ♀ × *cms*-IA ♂ grew more slowly than the other genotypes, and were consistently only about three-fourths as large as progeny from the *cms*-IA ♀ × *cms*-TA ♂ crosses. Seed treatment with benomyl [methyl 1-(butylcarbamoyl)-2-benzimidazolecarbamate] did not change the relative growth rates. Plants of *cms*-IA ♀ × R6-24 ♂ had significantly greater disease index and more lesions per square centimeter than the reciprocal cross, whereas plants of *cms*-TA ♀ × R6-24 ♂ had a significantly lower disease index than its reciprocal. Plants of hybrid *cms*-IA ♀ × R6-35 ♂ had significantly fewer lesions than the reciprocal, and progeny of *cms*-TA ♀ × R6-35 ♂ had significantly fewer lesions per square centimeter than the reciprocal.

DISCUSSION.—In this investigation, no new host-specific toxin or toxin-sensitive cytoplasm was discovered, but none was expected. These cytoplasms have been exposed in the field to populations of *B. maydis* more diverse than could be tested in the greenhouse (2, 10, 11, 14). However, the field tests were not designed to detect smaller quantitative differences in resistance among the male-sterile cytoplasms.

Statistically significant differences in leaf survival among the 38-11 × FR37[2] lines occurred for six of the 18 *B. maydis* isolates tested. It may be coincidence that no significant differences were observed with any of the three race O isolates tested. The differences in leaf survival evidently did not result from any inherent weakness to stress associated with a particular cytoplasm because the pattern of response among the cytoplasms differed with the different isolates of *B. maydis*. The most extreme pathogen-by-host-cytoplasm interaction involved *cms*-M and *cms*-K and isolates Ch-115 and Ch-270. *Cms*-M appeared to confer high resistance to Ch-270, but lower resistance to Ch-115. The reverse was true of *cms*-K. The difference in cytoplasms is probably not due to differential sensitivity to race-T toxin, because both Ch-115 and Ch-270 are race T isolates.

Good and Horner (5) studied the effects of normal cytoplasms in corn from different sources. Significant differences in certain agronomic characters, and in resistance to *B. maydis*, were associated with cytoplasm among F_1 and F_2 progeny tested in the field in 1972. However, similar differences were not observed among F_3 progeny tested in the field in 1973. Good and Horner (5) suggested that the differences observed in 1972 probably were due to either sampling variation, or to some maternal seed effects such as undetected *Fusarium* infection. However, they suggested that cytoplasm-by-environment interactions could also have been a factor. They concluded that differences among normal cytoplasms with respect to *B. maydis* resistance either do not occur, or are not large enough or stable enough to be important to corn breeders.

Our results indicate that cytoplasm-by-pathogen interactions can occur. Although Good and Horner (5) used normal cytoplasms, cytoplasm-by-pathogen-isolate interactions may have occurred in their tests. Such interactions might account for their inconsistent results, since they relied on infection by field populations of *B. maydis*. The proportions of races O and T in the southeastern USA changed rapidly during 1972 and 1973 (12). The *B. maydis* isolates to which the F_1 and F_2 corn progeny were exposed must have been quite different from those that infected the F_3 progeny.

Our experiments were conducted in the greenhouse, where environmental stress, pathogen isolates, and inoculum concentration were controlled. The association of *cms*-EK in the 38-11 × FR37[2] genotype with lower resistance to *B. maydis* was confirmed in tests of progeny from reciprocal crosses of the Ky-21 lines. This confirmation adds confidence to the conclusion that the differences observed among other 38-11 × FR37[2] lines are due to their cytoplasmic differences. These results suggest that *cms*-EK, *cms*-H, *cms*-I, *cms*-VG, and *cms*-RB may be less desirable than other male-sterile cytoplasms as alternatives to *cms*-T.

The results of the greenhouse investigations demonstrate that not only do cytoplasms differ quantitatively in their effects on resistance, but also that isolates of *B. maydis* differ in their response to them. These differences increase the importance of cytoplasmic effects, because it indicates a potential of the pathogen population to adapt to a particular cytoplasm if it is used widely. This investigation involved a nonselected pathogen population, so it is likely that adaptation could exceed the levels of interaction observed in this study. If the host population were genetically diverse, however, a high level of host-genotype-by-host-cytoplasm interaction might inhibit adaptation of the pathogen to a particular cytoplasm.

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