Two Genes for Resistance to Race 5 of *Cercospora sojina* in Soybeans

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ABSTRACT

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Crosses were made between the cultivars Lincoln and Davis, which are resistant to race 5 of *Cercospora sojina*, and the susceptible cultivars, Blackhawk and Hood. Evidence from greenhouse inoculations of progeny from F_1, F_2, and F_3 generations indicated that resistance in Lincoln was conditioned by a single dominant gene and that resistance in Davis was conditioned by another dominant gene at a different locus. No cytoplasmic or maternal effect on the expression of resistance was detected. The resistant reaction in Davis was often characterized by small lesions or flecks developing on inoculated leaves, whereas, there seldom were any lesions on Lincoln plants inoculated with race 5.

Additional key words: frogeye leafspot, *Glycine max*, disease resistance, inheritance.

Frogeye leafspot of soybeans (*Glycine max* (L.) Merr.) caused by *Cercospora sojini* Hara was first reported in the U.S. in 1924 (5). Laviolette et al (4) reported yield reductions of up to 21% in a 3-yr study on inoculated Clark soybeans grown in Indiana. Frogeye leafspot has not become a severe problem primarily because it has been controlled by resistant cultivars (1). Five physiological races of the fungus have been reported (2,3,6,9). Athow and Probst (2), Probst and Athow (7), and Probst et al (8) found that two dominant genes, Rcs_1 and Rcs_2 conditioned resistance to races 1 and 2. The inheritance of resistance to races 3 and 4 has not been reported, and cultures of these races are no longer available. Race 5 of *C. sojina* was found in 1978. Many important cultivars are

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susceptible to this race, but resistant cultivars have been identified (6). The present study was undertaken to determine the inheritance of resistance to race 5 of *C. sojina* found in plants of cultivars Lincoln and Davis.

MATERIALS AND METHODS

In 1979, the resistant soybean cultivars, Davis and Lincoln, and the susceptible soybean cultivars, Blackhawk and Hood, were used as parents in the following crosses: Blackhawk × Davis, Blackhawk × Lincoln, Davis × Hood, Lincoln × Hood, and Davis × Lincoln. Plants of the parents and F_1, F_2, and F_3 progeny were grown in the greenhouse and inoculated with race 5 of *C. sojina* (ATCC 42654). Cultures of race 5 were maintained and inoculum was produced on a medium composed of equal parts of soybean stem agar and lima bean agar as previously described (6). A suspension of 6×10^4 conidia per milliliter was atomized onto the plants at the two or three trifoliolate leaf stage (6). After inoculation, F_1 plants were placed in a moist chamber for 72 hr and the inoculated leaves of F_2 and F_3 plants were enclosed in clear plastic bags for 72 hr to maintain high relative humidity. Ratings were made 14 days after inoculation. Plants which showed no lesions or only small lesions were classed as resistant. Plants that showed numerous large spreading lesions were classed as susceptible.

RESULTS AND DISCUSSION

The F_1 plants (total of 24) from the five crosses were all resistant. The F_2 populations from the Blackhawk × Davis, Blackhawk × Lincoln, Davis × Hood, and Lincoln × Hood crosses segregated in a ratio of 3 resistant:1 susceptible as expected assuming monogenic control and complete dominance (Table 1). All the chi-square values for tests for goodness of fit, within individual crosses and pooled over crosses, were acceptable, with probability values greater than 0.4. Since the F_1 plants were resistant and it was impossible to distinguish the heterozygotes among the resistant F_2 plants, it appeared that resistance to race 5 of *C. sojina* was completely dominant to susceptibility. The agreement in classification of the F_2 generation between crosses with a susceptible maternal parent (Blackhawk × Davis, Blackhawk × Lincoln) and crosses with a resistant maternal parent (Davis × Hood, Lincoln × Hood) indicated no cytoplasmic or maternal effect on the expression of resistance.

To confirm the single-gene hypothesis, 107 F_2 plants classified as resistant from the four crosses between resistant and susceptible parents were isolated and grown to maturity. Progeny tests of these plants indicated that 101 were either homozygous resistant or segregating for resistance (Table 2). Six, which either escaped infection or were misclassified, bred true for susceptibility. The F_3 lines (progeny of the correctly classified resistant F_2 plants) occurred as expected with a 1:2 ratio (one-third of the lines homozygous resistant: two-thirds of the lines segregating). There were no significant deviations from the expected 1:2 ratio for any of the four populations of F_3 lines or for the combined data as shown by the chi-square values for goodness of fit. A total of 22 susceptible F_2 plants from the four crosses were grown to maturity. The F_3 progeny from the 22 F_2 plants bred true for susceptibility.

The hypothesis was further substantiated by the ratio of resistant to susceptible plants within segregating F_3 lines (Table 3). The data from the four individual crosses and the pooled data closely fit the expected 3:1 ratio of resistant to susceptible plants.

The F_2 population from the cross between the two resistant cultivars, Davis and Lincoln, segregated with resistant and susceptible plants occurring in a 15:1 ratio (Table 1). The F_3 lines from resistant F_2 plants were either homozygous resistant or had resistant and susceptible plants occurring either in a 3:1, or 15:1 ratio (Tables 2 and 3). The susceptible F_2 plants bred true for susceptibility in the F_3 generation. Thus, plants of Lincoln and Davis appeared to have independent dominant genes for resistance.

The F_2 plants from the four crosses of resistant and susceptible plants were also classified for flower, pubescence, and pod wall color. The two genes for resistance in Lincoln and Davis were not linked to W_1 (flower color) or L_2 (pod wall color). The gene for resistance in Lincoln was not linked to T (pubescence color). The possible linkage of T to the gene for resistance in Davis could not be determined with these crosses.

There was a minor difference between the resistant reactions of Lincoln and Davis. When Davis was inoculated with race 5 of *C.*

TABLE 1. Segregation for reaction to *Cercospora sojina* race 5 in the F_2 generation of five soybean crosses

Cross	Plants (no.)			Chi-square probability
	Resistant	Susceptible	Total	
Expected ratio 3:1				
Blackhawk[a] × Davis[b]	152	52	204	0.8–0.9
Blackhawk × Lincoln[b]	104	30	134	0.4–0.5
Davis × Hood[a]	161	49	210	0.5–0.6
Lincoln × Hood	153	56	209	0.5–0.6
Total	570	187	757	0.8–0.9
Expected ratio 15:1				
Davis × Lincoln	218	18	236	0.3–0.4

[a] Susceptible to *C. sojina* race 5.
[b] Resistant to *C. sojina* race 5.

TABLE 2. Segregation for reaction to *Cercospora sojina* race 5 among F_3 soybean lines from resistant F_2 plants

Cross	Lines (no.)			Chi-square probability
	Homozygous resistant	Segregating	Total	
Expected ratio 1:2				
Blackhawk[a] × Davis[b]	5	12	17	0.7–0.8
Blackhawk × Lincoln[b]	7	12	19	0.7–0.8
Davis × Hood[a]	6	12	18	1.0–1.0
Lincoln × Hood	17	30	47	0.6–0.7
Total	35	66	101	0.7–0.8
Expected ratio 7:8				
Davis × Lincoln	11	15[c]	26	0.6–0.7

[a] Susceptible to *C. sojina* race 5.
[b] Resistant to *C. sojina* race 5.
[c] Nine lines segregating 15:1 and six lines segregating 3:1.

TABLE 3. Segregation for reaction to *Cercospora sojina* race 5 among soybean plants in segregating F_3 lines

Cross	Plants (no.)			Chi-square probability
	Resistant	Susceptible	Total	
Expected ratio 3:1				
Blackhawk[a] × Davis[b]	170	52	222	0.5–0.6
Blackhawk × Lincoln[b]	157	61	218	0.3–0.4
Davis × Hood[a]	167	53	220	0.7–0.8
Lincoln × Hood	431	136	567	0.5–0.6
Total	925	302	1,227	0.7–0.8
Expected ratio 3:1				
Davis × Lincoln[c]	228	71	299	0.6–0.7
Expected ratio 15:1				
Davis × Lincoln[d]	387	25	412	0.8–0.9

[a]Susceptible to *C. sojina* race 5.
[b]Resistant to *C. sojina* race 5.
[c]Six lines segregating 3:1.
[d]Nine lines segregating 15:1.

sojina, small lesions or flecks (6) would frequently develop. These small lesions could easily be distinguished from the large spreading lesions of susceptible cultivars. When Lincoln was inoculated there was seldom any lesion development. In the F_3 generation over 60% of the inoculated plants with the Davis gene for resistance had a few small lesions. Fewer than 1% of the inoculated plants with the Lincoln gene for resistance had any lesions. The presence of small lesions on the F_2 plants with the Davis gene was not related to heterozygosity since F_2 plants with small lesions produced F_3 lines that were either homozygous or segregating for resistance.

These data support the hypothesis that Davis and Lincoln each have an independent major gene for resistance to race 5 of *C. sojina*. The relationship of these genes to those for resistance to races 1 and 2 (Rcs_1 and Rcs_2) was not studied due to the unavailability of cultures of race 1 and the erratic results of Kent, the only known source of the Rcs_2 gene, to inoculation with race 2 (3,6,9) and to race 5 in our experiments. Regardless of the genetic relationship between Rcs_1, Rcs_2, and the two genes for race 5 resistance, Lincoln and Davis can be used to develop cultivars with different sources of resistance to race 5 of *C. sojina*. The genetic relationship between these two genes for race 5 resistance and Rcs_2 awaits a complete understanding of the Kent reaction to races 2 and 5. These studies are currently under way.

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