Inheritance of Resistance of Soybeans to the Cyst Nematode, *Heterodera Glycines*[1]

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SYNOPSIS. The F_1, F_2, and testcross generations from crosses involving resistant × susceptible soybeans were evaluated for ability to inhibit reproduction of the soybean cyst nematode. These data indicate that resistance is the result of three independently inherited recessive genes.

THE soybean cyst nematode, *Heterodera glycines* Ichinohe, 1952, was first identified (6) on soybeans in the United States at Castle Hayne, North Carolina, in 1954. Subsequently infestations were reported in Arkansas, Mississippi, Missouri, Kentucky, Tenessee, Virginia, and Illinois. Losses due to the soybean cyst nematode have ranged from little or no reduction in yield to almost total crop failure.

The use of nematocides (1), although effective in reducing population level of the nematode, is economically impractical as a control measure in soybean production at present. Crop-rotation experiments in North Carolina (Ross, unpublished data) indicate that rotations with a nonsusceptible crop for at least two years are necessary for reducing soybean losses. The use of resistant varieties appears to be the most practical control measure. This study was undertaken in an attempt to determine the inheritance of resistance of soybeans to *H. glycines*.

Ross and Brim (3) using the double-row method evaluated 2800 plant introductions and varieties of soybeans for reaction to the cyst nematode. Three strains, Peking, P.I. 90763, and P.I. 84751 had high resistance as measured by the absence of white females on the roots at the end of one month. None of these resistant strains is adapted for soybean production in the southeastern United States.

Ichinohe (2) and Skotland (5) made extensive studies of the life history of the soybean cyst nematode. Their results indicate that after entering the roots, second stage larvae of the nematode assume a sedentary feeding position in the pericyclic region and subsequently undergo three molts. Host giant cells are developed during the sedentary feeding period. Ross (4) ascribed the type of resistance found in Peking as the failure of the host plant to form giant cells.

MATERIALS AND METHODS

F_1, F_2, and testcross plants from crosses involving various combinations of resistant and susceptible parents were classified for reaction to the soybean cyst nematode. The resistant parents, Peking, P.I. 90763, and P.I. 84751, are introductions from China and were chosen on the basis of field reaction to the nematode (3). The varieties Lee and Hill and an experimental line (D53-354), which are adapted to the southeastern United States, were used as susceptible parents. Hill and D53-354 were derived from crosses having a common parent, a sister selection of the variety Lee.

The F_1 crosses were made in the field in 1957 and were advanced to the F_2 generation in the greenhouse during the winter 1957–1958. Testcross seed from the cross of Peking with Peking × Lee and with Peking × D53-354 were obtained in the field in 1958.

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[1] Joint contribution from Crops Research Division, ARS, USDA, and the Departments of Field Crops and Plant Pathology, North Carolina State College, Raleigh, N. C. Journal Paper No. 1113, North Carolina Agr. Exp. Station. Portion of a thesis submitted by the senior author for the M. S. degree, North Carolina State College.

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In the F_1 and segregating generations flower color or pubescence or both were observed so that nonhybrid plants could be discarded. In the testcross generation only purple-flowered plants were classified for resistance, since white-flowered plants could have resulted from either a cross or a self.

Plants of the various generations were evaluated in the greenhouse by growing them in sterilized soil artificially infested with cyst nematodes. Two F_1 plants of each of the crosses Peking × Hill and Peking × P.I. 90763 and 1 F_1 plant of the cross P.I. 84751 × P.I. 90763 were grown in separate pots containing sterilized soil for 2 weeks. Peking and Hill were included as checks. The plants were then placed in 3-inch pots containing sterilized soil after the root system had been washed free of soil. Crushed cysts were placed in the root area during transplanting. The crushed cysts were obtained by screening infested soil through a 60-mesh sieve and crushing the cysts retained on the sieve. The crushed residue was examined under a microscope to insure that no intact cysts remained. After 30 days soil was washed from the roots and screened through a 60-mesh sieve. Cysts in the residue and on the roots were counted. Since plants were inoculated with crushed cysts, any intact cysts found would have developed on the test plant root system.

F_2 plants from resistant × resistant crosses were evaluated both in the field and in the greenhouse. Plants grown in the field were removed from the soil with a spade 30 days after emergence and classified. Greenhouse studies on F_2 plants from resistant × resistant crosses were conducted in the same manner as those on plants from the resistant × susceptible crosses.

Plants of the F_2 and testcross generations involving resistant × susceptible crosses were grown in 3-inch pots which contained a mixture of sterilized soil, sand, and inoculum. The pots were set in sand on the greenhouse bench to prevent rapid drying. One germinating seed was planted in each pot. Susceptible checks were planted at random on the bench and the roots on the outside of the soil-ball were examined frequently to determine when the nematode generation had reached its maximum development. Plants were classified individually by an examination of the roots on the outside of the soil-ball. Since an occasional mature female was found on the roots of resistant parents, plants with 0 or 1 mature female were classified as resistant. Plants with more than 1 mature female were classified as susceptible. To confirm preliminary classification the root systems of plants rated as resistant were washed free of soil and examined. If no more than one adult female was found, the plant was classified as resistant. Of the several hundred susceptible checks grown throughout the investigation all were classified as susceptible.

RESULTS AND DISCUSSION

Adult females on the roots and brown cysts in the soil residue were found when F_1 plants of the cross Peking × Hill were examined. Since the plants were as susceptible as the susceptible checks, it appears that resistance as defined here is inherited as a recessive character.

Neither adult females nor cysts were found on the roots or in the soil residue of F_1 plants of resistant × resistant crosses, Peking × P.I. 90763, or P.I. 84751 × P.I. 90763. These data indicate that the same loci are involved in the resistance of the parents.

Data from segregating F_2 populations were fitted to several of the simpler genotypic models, i.e., 2, 3, and 4 independently inherited genes, by using the chi-square method of analysis. Small and nonsignificant chi-square values were obtained only when the data from each cross were fitted to the 3-factor model (table 1). A small heterogeneity chi-square value ($P = .98$) indicated that the observed data were from a homogeneous population. A probability value of .24 was obtained for the pooled chi-square, signifying satisfactory agreement with a 63:1 segregation ratio.

The data from classifying plants of 2 testcross populations were fitted to a 3-factor model (table 2). A segregation ratio of 7 susceptible to 1 resistant would be expected if 3 recessive genes are involved in the inheritance of resistance. Probability values for each testcross and the pooled chi-square showed good agreement with expected.

Table 1—Reaction of F_1 plants from crosses of resistant × susceptible soybean strains to *Heterodera glycines*.

Cross*	Observed		Expected (63:1)		χ^2	P
	S	R	S	R		
Peking (R) × Lee (S)	242	3	241.2	3.8	0.17	.7
Peking (R) × Hill (S)	329	4	327.8	5.2	0.28	.6
	328	5	327.8	5.2	0.01	.9
Peking (R) × D53-354 (S)	315	3	313.0	5.0	0.81	.4
	346	4	344.5	5.5	0.42	.5
Pooled	1560	19	1554.3	24.7	1.34	.2

*S = susceptible, R = resistant.

Table 2—Reaction of testcross soybean plants to *Heterodera glycines*.

Cross	Observed		Expected (7:1)		χ^2	P
	S*	R	S	R		
Peking × (Peking × Lee)	66	9	65.6	9.4	0.02	.9
Peking × (Peking × D53-354)	57	7	56.0	8.0	0.14	.7
Pooled	123	16	121.6	17.4	0.13	.7

* S = susceptible, R = resistant.

All F_2 plants from resistant × resistant crosses Peking × P.I. 90763, and Peking × P.I. 84751 were found to be resistant. These results further confirm the conclusion that the same loci are involved in the resistance shown by these parents.

The results obtained indicate that resistance is due to three independent recessive genes. However, the reduction in numbers of the resistant class as a result of zygotic and gametic elimination or both cannot be ignored as a possible bias in the results obtained. The extraction and classification of susceptible lines from the F_2 or testcross generations are needed to verify further the genetic hypothesis proposed herein. The symbols Rhg_1rhg_1, Rhg_2rhg_2, and Rhg_3-rhg_3 are proposed for the susceptible and resistant alleles, respectively, of the three loci involved in inheritance of resistance.

SUMMARY

A study was conducted in an attempt to determine the inheritance of resistance to the soybean cyst nematode, *Heterodera glycines*. Included in the study were resistant and susceptible varieties, strains, and plant introductions crossed in various combinations.

F_1 plants from resistant × susceptible matings were susceptible to the cyst nematode, while F_1 plants from resistant × resistant matings were resistant.

Data from the F_2 generation of resistant × susceptible crosses fitted a genetic model of three independently inherited recessive genes for resistance. Satisfactory agreement of observed with an expected ratio of 7 susceptible to 1 resistant was also obtained from classifying testcross plants. The necessity for classifying advanced generations to verify further the genetic hypothesis is discussed.

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