Journal of Nematology 16(3):304–309. 1984.

Changes in the Reproduction of *Heterodera glycines* on Different Lines of *Glycine max*[1]

L. D. YOUNG[2]

Abstract: Selection for ability of soybean cyst nematode (SCN), *Heterodera glycines*, to reproduce on soybeans with different sources of resistance divides some SCN race 4 field populations into two distinct subpopulations. These subpopulations reproduce well on 'Bedford' and plant introduction (PI) 88788 or PI 89772 and PI 90763 but not on both pairs of soybean lines. The ability of these subpopulations to reproduce on the four soybean lines was reversed by changing the soybean line used as a host during a second cycle of selection. When SCN populations previously selected for reproduction on Bedford and PI 88788 were selected for their ability to reproduce on D72-8927 and J74-88, the ability of these populations to reproduce on Bedford and PI 88788 decreased significantly and their ability to reproduce on PI 89772 and PI 90763 increased significantly. Conversely, when SCN populations, previously selected for reproduction on PI 89772 and PI 90763, were selected for their ability to reproduce on Bedford, the reproduction of these populations on Bedford increased significantly and reproduction on PI 89772 and PI 90763 decreased significantly. Selection for ability of a SCN race 4 field population to reproduce on soybean lines derived from SCN race 4 resistant PIs resulted in the same division of the field population into two distinct subpopulations. These data substantiate earlier proposals to rotate cultivars with different genes for SCN resistance as a means of managing SCN populations.
Key words: races, resistance, soybean, soybean cyst nematode.

Planting resistant soybean cultivars and rotating soybeans (*Glycine max* [L.] Merr.) with nonhosts are the primary methods of limiting yield losses caused by the soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe. Nematicide use is less efficient than planting resistant cultivars (2). Four races of SCN have been distinguished in the United States (3). Several soybean cultivars in maturity groups III thru VIII are available with resistance to SCN races 1 and 3. Several cultivars in maturity groups III, V, and VI have resistance to SCN races 3 and 4. Most public and private soybean cultivar development programs have SCN resistance as a major trait to incorporate into new cultivars.

Triantaphyllou (9) demonstrated culturing SCN populations on resistant soybean lines ('Peking,' 'Pickett,' and PI 88788) increased the ability of the populations to reproduce on these lines. The ability to reproduce on PI 88788 was inherited independently of the ability to reproduce on Pickett. Riggs et al. (8) demonstrated culturing SCN races 1, 2, 3, and 4 on resistant soybean lines increased the ability of the races to reproduce on the resistant soybeans. Anand and Brar (1), McCann et al. (7), and Young (10) demonstrated that culturing field populations of SCN race 4 on 'Bedford,' 'Cloud,' PI 87631-1, PI 88788, and PI 209332 resulted in populations which reproduced well on these soybean lines, but not on PI 89772 and PI 90763. Culturing populations of SCN race 4 on Peking, PI 89772, and PI 90763 resulted in populations which reproduced well on these soybean lines, but not on Bedford, Cloud, PI 87631-1, PI 88788, and PI 209332. Luedders (5) proposed two genetic groups with Cloud, PI 87631-1, PI 88788, and PI 209332 in one and Peking, PI 89772, and PI 90763 in another. Changes in the ability of SCN populations to reproduce on resistant soybean lines were assumed to be accompanied by changes in gene frequencies for parasitism.

Rotating soybean cultivars with different genes for SCN resistance has been proposed as a means of maintaining yields and lessening the risks of developing new virulent populations of SCN (5,10). A proposed rotation would be to grow cultivars with Bedford resistance in fields infested with race 4 of SCN until a virulent population developed and yield reduction was imminent and then plant a cultivar with genes for SCN resistance from PI 89772 or PI 90763. If after several years of utilizing cultivars with one of these sources

Received for publication 31 October 1983.
[1] The author thanks D. L. Boykin and M. A. Brown, Stoneville, Mississippi, for their assistance in the analysis and interpretation of the data.
[2] Research Plant Pathologist, Agricultural Research Service, U.S. Department of Agriculture, West Tennessee Experiment Station, Jackson, TN 38301.

TABLE 1. Reaction of soybean lines to races of the soybean cyst nematode, *Heterodera glycines*, and their sources of resistance.

Soybean	Source of resistance	Reaction to SCN races*			
		1	2	3	4
Essex		S	S	S	S
Forrest	Peking	R	S	R	S
Bedford	Forrest, PI 88788		S	R	R
Peking		R	S	R	MR
D72-8927	Peking, PI 90763	R	R	R	MR
J74-87	Forrest, PI 87631-1	S	S	R	R
J74-88	Forrest, PI 89772	R	S	R	R
L77-906	PI 209332			R	R
PI 88788		MR	MR	R	R
PI 89772		R	MR	R	R
PI 90763		R	R	R	MR

* S = susceptible, MR = moderately resistant, R = resistant; compiled from Hartwig (4) and unpublished data.

of resistance, a shift in the population of SCN occurred so that Bedford was again resistant, cultivars with Bedford resistance could be grown once more. In order for the rotation to be effective, the ability of the SCN populations to reproduce on one cultivar must decrease as it increases on another resistant cultivar.

Breeding lines with resistance genes from PI 89772 and PI 90763 are being used in the USDA-ARS germplasm program; however, the breeding lines were selected for resistance to race 2 or race 4 of SCN. These breeding lines, D72-8927 and J74-88, may lack some of the genes for SCN resistance that occur in PI 89772 and PI 90763. Therefore, the interaction between SCN and D72-8927 and J74-88 may not equal the interaction of SCN with PI 89772 and PI 90763.

The objectives of these experiments were to determine 1) if the interaction between enhanced soybean breeding lines and race 4 of SCN equaled the interaction between race 4 of SCN and the parents of these breeding lines, and 2) if SCN populations would undergo a second change in virulence when challenged with SCN-resistant lines with different genes for resistance.

Materials and Methods

Experiment 1: Soil infested with SCN race 4 was collected from a field near Clarkton, Missouri. Eight soybean lines—'Essex,' 'Forrest,' Bedford, Peking, D72-8927, J74-87, J74-88, and L77-906—(Table 1), planted in 10-cm-d pots containing SCN-infested soil with four plants per pot and pots replicated four times, were grown for 30 days in the greenhouse. Washed plant roots were lightly hand rubbed in water to remove cysts which were collected on a sieve with 250-μm pores and counted. One hundred hand-picked white and yellow cysts were added to steam-sterilized soil in 7.5-cm-d pots and the pots planted with the soybean line on which the nematode had reproduced. After 30–35 days, 26–100 hand-picked white and yellow cysts from the roots of each soybean line were used as inoculum for another generation of selection on the same soybean line. After five generations of selection as above, the procedure was changed as follows. Roots screened from the soil with a 6-mm-pore sieve were rubbed gently during the screening to dislodge the cysts. The soil from each pot was mixed with enough sterile soil to fill a 15-cm-d pot, and the same soybean line was again planted. This procedure was repeated for 15 additional generations at 35–40-day intervals.

After 20 generations of selection, reproduction of the selected nematode populations was determined on seven soybean lines—Essex, Forrest, Bedford, Peking, PI 88788, PI 89772, and PI 90763. Seeds were planted in 7.5-cm-d pots and seedlings thinned to two plants per pot; pots were replicated three times. Each pot was infested with 2,500 eggs, and the plants were grown in a greenhouse at 28 ± 4 C for 30 days after which cysts were separated from the soil and roots. The test was repeated after an additional four generations of selection on the original soybean lines. Re-

TABLE 2. Reproduction of eight host-selected populations of *Heterodera glycines* relative to reproduction on Essex. Means of six replicates.

Selection host	Inoculated soybean						
	Essex	Forrest	Peking	PI 89772	PI 90763	Bedford	PI 88788
Essex	456 a*	93 a	64 b	34 c	26 c	8 d	4 d
Forrest	564 a	104 a	80 b	39 c	28 c	6 d	2 d
Peking	567 a	94 a	58 b	51 bc	37 c	6 d	5 d
D72-8927	536 a	118 a	81 b	47 c	49 c	12 d	12 d
J74-88	715 a	97 a	70 b	61 c	44 c	7 d	6 d
Bedford	603 a	53 b	15 c	0 d	0 d	108 a	102 a
J74-87	428 a	60 b	29 c	3 d	1 d	93 a	60 b
L77-906	880 a	47 b	24 c	0 d	1 d	77 a	49 b

* Analysis was performed on rank transformed data; data followed by the same letter within a row do not differ significantly at $P = 0.05$. Data in the Essex column are actual numbers of nematodes, and other data are percentage of reproduction on Essex.

sults of the two tests were combined for analysis, and analysis of variance was performed using data transformed by a nonparametric rank procedure.

Experiment 2: In another experiment (10) 10 SCN populations—WTES BED, WTES 88, WTES 89, WTES 90, LAKE BED, LAKE 88, LAKE 90, WM BED, WM 89, and WM 90—were established from three race 4 populations of SCN by selecting for 12 generations for reproduction on Bedford, PI 88788, PI 89772, and PI 90763. WTES, LAKE, and WM were in reference to the location of the three SCN race 4 populations (West Tennessee Experiment Station, Lake County, and Woodland Mills, respectively). The second set of letters and numerals designated the soybean line on which each population was selected; Bedford, PI 88788, PI 89772, and PI 90763 were abbreviated BED, 88, 89, and 90, respectively.

Cysts from WTES 89 and WTES 90, LAKE 89 and LAKE 90, and WM 89 and WM 90 populations were combined to form WTES 89+90, LAKE 89+90, and WM 89+90 populations, respectively, and each of the latter populations were used to infest soil planted to Bedford. Cysts from WTES BED and WTES 88 and from LAKE BED and LAKE 88 populations were combined to form WTES BED+88 and LAKE BED+88 populations, respectively, and each of the latter populations, along with WM BED population, were divided and used to infest sterile soil in two 10-cm-d pots for each population. D72-8927 was planted in one pot and J74-88 was planted in the other pot. After 30 days of plant growth, cysts separated from roots and soil (5–100 hand-picked cysts) were used to inoculate the same soybean line on which the nematode had reproduced; thus the new SCN populations WTES 89+90-BED, LAKE 89+90-BED, WM 89+90-BED, WTES BED+88-D72, WTES BED+88-J88, LAKE BED+88-D72, LAKE BED+88-J88, WM BED-D72, and WM BED-J88 were established. These SCN populations were designated, using the convention of Luedders and Dropkin (6), by adding a hyphen and an abbreviation for the soybean line on which they were selected to the former SCN population designation. BED, D72, and J88 were the abbreviations for Bedford, D72-8927, and J74-88, respectively. Selection for reproduction on these three soybean lines was continued using the procedure outlined in experiment 1. LAKE BED+88-J88, LAKE 89+90-BED, and WM BED-J88 reproduced poorly and were lost before completion of five generations of selections. Selected populations were evaluated for ability to reproduce on Essex, Forrest, Bedford, Peking, PI 88788, PI 89772, and PI 90763 after 12, 19, and 21 generations of selection. Each soybean line was replicated four times at each evaluation and was inoculated with 2,500 eggs/7.5-cm-d pot, except 1,000 eggs/pot were used for some of the populations selected on D72-8927 with the data adjusted to account for the lower inoculum. Data from the three eval-

TABLE 3. Reproduction of *Heterodera glycines* after exposure to soybean lines with different genes for resistance, relative to Essex. Means of 10 replicates.

	Inoculated soybean						
Nematode population	Essex	Forrest	Peking	PI 89772	PI 90763	Bedford	PI 88788
LAKE BED*	179 a†	78 a	19 bc	1 c	1 c	110 a	44 b
LAKE 88	190 a	82 ab	26 c	1 c	1 c	90 ab	66 b
LAKE BED+88-D72	592 a	95 a	73 b	61 bc	46 c	17 d	12 d
WM BED	153 a	74 ab	17 c	1 c	1 c	78 ab	41 bc
WM BED-D72	826 a	103 a	55 b	57 b	57 b	6 c	7 c
WTES BED	316 a	92 ab	16 c	4 c	3 c	116 a	47 bc
WTES 88	663 a	67 b	14 c	2 c	2 c	74 b	49 b
WTES BED+88-D72	733 a	80 ab	72 b	53 bc	41 c	10 d	9 d
WTES BED+88-J88	585 a	97 a	80 ab	82 ab	63 b	21 c	22 c
WM 89	179 a	115 a	82 a	89 a	85 a	11 b	12 b
WM 90	447 a	106 a	49 b	29 c	57 b	5 d	1 d
WM 89+90-BED	592 a	90 a	53 c	1 d	1 d	92 a	66 b
WTES 89	938 a	75 b	25 de	28 d	42 c	10 e	10 e
WTES 90	946 a	75 b	30 cd	18 de	43 c	7 e	3 e
WTES 89+90-BED	601 a	79 a	50 b	26 c	43 b	75 a	43 b

* BED, 88, 89, and 90 = nematode populations selected for 12 generations for reproduction on Bedford, PI 88788, PI 89772, and PI 90763 soybeans, respectively; BED+88-D72 and BED+88-J88 = nematode mixtures of populations selected on Bedford and PI 88788 and then selected for reproduction on D72-8927 and J74-88, respectively; 89+90-BED = nematode mixtures of populations selected on PI 89772 and PI 90763 and then selected for reproduction on Bedford.

† Analysis was performed on rank transformed data; data followed by the same letter within a row do not differ significantly at $P = 0.05$. Data in the Essex column are actual numbers of nematodes, and other data are percentage of reproduction on Essex. Data for BED, 88, 89, and 90 populations are from Young (10).

uations were combined, and analysis of variance was performed on rank transformed data for 10 replications.

Results and Discussion

Experiment 1: Populations of SCN selected on Bedford, J74-87, and L77-906 reproduced as well on Bedford as on Essex and moderately well on PI 88788 (Table 2). These populations reproduced only slightly (less than 4% of Essex) on PI 89772 and PI 90763. Populations selected on Bedford, J74-87, or L77-906 reproduced less on Forrest than on Essex. Populations selected on Essex, Forrest, Peking, D72-8927, and J74-88 reproduced moderately well on PI 89772 (34–60% of Essex) and PI 90763 (26–49% of Essex), but reproduced less on Bedford and PI 88788 (12% or less of Essex). Forrest is a parent of Bedford, J74-87, and J74-88, and all three were selected for resistance to race 4 of SCN. However, the SCN populations selected on J74-88 reproduced better on Forrest and Peking than the populations selected on Bedford and J74-87.

Selection using the breeding lines gave populations of SCN that reproduced on test soybean lines as was experienced using the parental PIs (1,7,10). The SCN-infested soil used in this selection experiment came from the same field as the infested soil used in the experiment by Anand and Brar (1). The PIs they used were the resistant parents of the breeding lines used in this experiment, and reproduction of SCN populations selected on the breeding lines was similar to the populations selected on the parents. It should be possible to develop cultivars with the desired genes for SCN resistance for use in rotations from these breeding lines if appropriate selection pressure is applied. The TN-79 population (11) is being used to select productive soybean lines with resistance to SCN populations that reproduce well on Bedford and PI 88788. The parents of these breeding lines are D72-8927, J74-88, and Forrest with an additional gene for resistance from Peking (4).

Experiment 2: Challenging the previously selected SCN populations with a soybean line with different genes for resistance altered their ability to reproduce on Bedford, Peking, PI 88788, PI 89772, and PI 90763. Reproduction of the WM BED-D72

SCN population on Bedford was 6% of the reproduction on Essex compared to 78% for the WM BED population, and reproduction of WM BED-D72 population on PI 89772 and PI 90763 was 57% of the reproduction on Essex compared to 1% for WM BED population (Table 3). The reproduction on Peking was 55% and 17% of reproduction on Essex for WM BED-D72 and WM BED populations, respectively. Similar changes in reproduction on Bedford, Peking, PI 88788, PI 89772, and PI 90763 were experienced for the LAKE BED+88-D72, WTES BED+88-D72, and WTES BED+88-J88 populations. Reproduction of WM 89+90-BED SCN population on Bedford was 92% of the reproduction on Essex compared to 11% and 5% for WM 89 and WM 90 populations, respectively. A similar change in reproduction on Bedford occurred with the WTES 89+90-BED population. Reproduction of the WM 89 and WM 90 populations on PI 89772 was 89% and 29% of the reproduction on Essex, respectively, and the reproduction on PI 90763 was 85% and 57%, respectively, for the two populations. The reproduction on PI 89772 and PI 90763 for the WM 89+90-BED population declined to 1% of the reproduction on Essex. Challenging the WTES 89+90 population with Bedford did not change the ability of the population to reproduce on PI 89772 and PI 90763.

With the exception of one population, SCN populations experienced a second change in virulence when challenged with soybean lines with different genes for SCN resistance. Luedders and Dropkin (6) recently reported reciprocal secondary selection in SCN populations on Cloud or PI 89772 resulted in rapid changes in the populations' ability to reproduce on these two soybean lines. They theorized that at least some of the SCN genes for reproduction on genetically different soybeans probably are alleles, although linkage could exist. Triantaphyllou (9) indicated the ability of SCN populations to reproduce on PI 88788 was inherited independently from the ability to reproduce on Pickett. Data from this experiment and that of Luedders and Dropkin (6) indicate that not all the SCN genes for ability to reproduce on soybean are independent because SCN reproduction on PI 88788 and Cloud increased while it decreased on PI 89772, PI 90763, and Peking. Equal reproduction on PI 89772 and PI 90763 before and after selection of the WTES 89+90-BED population is tentative evidence of linkage. If the genes for the ability of SCN to reproduce on PI 88788, PI 89772, and PI 90763 are linked, rotations including cultivars possessing these different genes for resistance might not be effective. Instead, the two groups of genes would need to be incorporated into a single cultivar. Current field observations indicate that the SCN population shift under continuous culture of Bedford, although slow, is similar to that obtained with selection on Bedford and PI 88788 in Experiment 1 and other studies (1,7,10,12). Although the greenhouse experiments are promising, rotation of soybean cultivars containing different genes for SCN resistance needs to be evaluated in the field before recommending it as a practice to growers.

Literature Cited

1. Anand, S. C., and G. S. Brar. 1983. Response of soybean lines to differentially selected cultures of soybean cyst nematode *Heterodera glycines* Ichinohe. Journal of Nematology 15:120–123.

2. Epps, J. M., L. D. Young, and E. E. Hartwig. 1981. Evaluation of nematicides and resistant cultivars for control of soybean cyst nematode race 4. Plant Disease 65:665–666.

3. Golden, A. M., J. M. Epps, R. D. Riggs, L. A. Duclos, J. A. Fox, and R. L. Bernard. 1970. Terminology and identity of infraspecific forms of the soybean cyst nematode (*Heterodera glycines*). Plant Disease Reporter 54:544–546.

4. Hartwig, E. E. 1981. Breeding productive soybean cultivars resistant to the soybean cyst nematode for the southern United States. Plant Disease 65:303–307.

5. Luedders, V. D. 1983. Genetics of the cyst nematode-soybean symbiosis. Phytopathology 73:944–948.

6. Luedders, V. D., and V. H. Dropkin. 1983. Effect of secondary selection on cyst nematode reproduction on soybeans. Crop Science 23:263–264.

7. McCann, J., V. D. Luedders, and V. H. Dropkins. 1982. Selection and reproduction of soybean cyst nematodes on resistant soybeans. Crop Science 22:78–80.

8. Riggs, R. D., M. L. Hamblen, and L. Rakes. 1977. Development of *Heterodera glycines* pathotypes as affected by soybean cultivars. Journal of Nematology 9:312–318.

9. Triantaphyllou, A. C. 1975. Genetic structure of races of *Heterodera glycines* and inheritance of ability to reproduce on resistant soybeans. Journal of Nematology 7:356–364.

10. Young, L. D. 1982. Reproduction of differentially selected soybean cyst nematode populations on soybeans. Crop Science 22:385–388.

11. Young, L. D. 1982. Reproduction of Tennessee cyst nematode population on cultivars resistant to race 4. Plant Disease 66:251–252.

12. Young, L. D. 1984. Effects of continuous culture of resistant soybean cultivars on soybean cyst nematode reproduction. Plant Disease 68:237–239.