Journal of Nematology 16(3):289–296. 1984.

Tolerance to *Heterodera glycines* in Soybean[1]

H. R. Boerma and R. S. Hussey[2]

Abstract: Fifty-four susceptible soybean, *Glycine max*, cultivars or plant introductions were evaluated for tolerance to *H. glycines*, the soybean cyst nematode (SCN). Seed yields of genotypes were compared in nematicide-treated (1,2-dibromo-3-chloropropane, 58 kg a.i./ha) and nontreated plots at two SCN-infested locations over 3 years. Distinct and consistent levels of tolerance to SCN were observed among soybean genotypes. PI 97100, an introduction from Korea, exhibited the highest level of tolerance with an average tolerance index ([yield in nontreated plot ÷ yield in nematicide-treated plot] × 100) of 96 over 2 years. Coker 156 and Wright had moderate levels of tolerance (range in index values 68 to 95) compared to the intolerant cultivars Bragg and Coker 237 (range in index values 33 to 68). Most of the soybean genotypes evaluated were intolerant to SCN. The rankings of five genotypes for tolerance to SCN and *Hoplolaimus columbus* were similar. Tolerance for seed yield was more consistently correlated with tolerance for plant height ($r = 0.55$ to 0.64) than for seed weight ($r = 0.23$ to 0.65) among genotypes.

Key words: soybean cyst nematode, *Glycine max*, seed yield, *Hoplolaimus columbus*.

The soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe, is a major pathogen of soybean, *Glycine max* (L.) Merrill, in the United States (7,15). Crop rotation and resistant cultivars are the principal control strategies for limiting yield losses from this nematode. However, the effective use of resistant cultivars is complicated by the variability in SCN populations (11,20,24). Although five races of this pest have been identified (6,9,23), its genetic variability is much greater. Riggs et al. (16) separated 38 SCN populations into 25 distinct groups (races) based on their reaction on 13 soybean genotypes. This wide range of genetic variation for parasitism emphasizes the need to exploit control measures which minimize the selection pressure on SCN populations.

The following terms and meanings, defined by Cook (3), will be used in this article to characterize nematode–host relationships: *resistance* (low nematode reproduction) and *susceptibility* (high nematode reproduction) characterize host efficiency, whereas *tolerance* (little suppression of yield) and *intolerance* (high suppression of yield) delineate host sensitivity. The use of tolerance is a method to limit soybean yield losses from SCN without providing selection pressure on the nematode for the development of more aggressive races as occurs with the use of resistant cultivars.

Although tolerance to plant-parasitic nematodes has received less attention than resistance, potato genotypes tolerant to po-

Received for publication 21 October 1983.

[1] Research was supported by State and Hatch funds allocated to the Georgia Agricultural Experiment Stations and by grants provided by the Georgia Agricultural Commodity Commission for Soybeans. The authors thank Steve Finnerty, Dale Wood, and George Barrett for technical assistance.

[2] Professors, Departments of Agronomy and Plant Pathology, respectively, University of Georgia, Athens, GA 30602.

tato cyst nematode, *Globodera rostochiensis,* and sugarbeet genotypes tolerant to the beet cyst nematode, *H. schachtii,* have been reported (5,8,21). Tolerance has also been described for other nematode species (18).

Tolerance has not been widely used in soybean as a strategy to control diseases. Soybean genotypes with tolerance to phytophthora root rot, *Phytophthora megasperma* Drecks. var. *sojae,* have been identified (19), and differences among soybean genotypes for tolerance to *Hoplolaimus columbus* also have been detected (12).

The objectives of our research were 1) to determine the amount of genotypic variation for tolerance to SCN among susceptible soybean cultivars and plant introductions, 2) to identify superior sources of tolerance to SCN for use in soybean improvement programs, and 3) to determine if genotypes tolerant to SCN had tolerance to *H. columbus.*

Materials and Methods

Field experiments: Experiments with natural infestations of *H. glycines* (Race 3) were conducted from 1980 to 1982 at the Plant Sciences Farm near Athens, Georgia (14), and the Southeast Branch Experiment Station near Midville, Georgia (13). At Athens, the soil was an Appling coarse sandy loam (Typic Hapludult, clayey, kaolinitic, thermic) and at Midville a Dothan loamy sand (Plinthic Paleudult, fine-loamy, siliceous, thermic). At Midville, we also used a Tifton loamy sand soil (Plinthic Paleudult, fine-loamy, siliceous, thermic) infested with *Hoplolaimus columbus* Sher. The experimental areas were fertilized according to soil test analyses; rates varied from 0 to 76, 0 to 37, and 56 to 140 kg/ha for N, P, and K, respectively. Trifluralin (ααα-trifluoro-2,6-dinitro-N,N-dipropyl-p-toluidine, Treflan, 0.56 kg a.i./ha) was applied preplant at all locations, and bentazon (3-isopropyl-1H-2,1,3-benzothiadiazin-4[3H]-one 2,2-dioxide, Basagran, 0.6 kg a.i./ha) was applied postplant at Athens for weed control. Plots were irrigated (2.5 cm water per application) at Athens when needed. Plots at Midville were not irrigated.

A split-plot treatment design with a randomized complete block experimental design was used in all field experiments. The main plots were the soybean genotypes (cultivars or plant introductions); subplots consisted of a fumigant nematicide or no nematicide. Each subplot consisted of one row, with the exception of the 1982 five-cultivar experiment at Athens (two rows) and Midville (four rows). The nematicide (DBCP, 1,2-dibromo-3-chloropropane, 58 kg a.i./ha) was applied at planting 20 cm deep 12.5 cm on each side of the row. Rows were 5.2 m long, spaced 96 cm apart. Plots were planted at a rate of 30–35 seeds/m.

Data were collected from a 4.2-m section of plants after removing 0.5 m of plants from each end of a plot at maturity. Maturity was determined as the date on which 95% of the pods were their mature pod color (measured only at Athens). Seed yield was obtained by mechanically harvesting and weighing seed that had been air dried and adjusted to 13% moisture. Plant height was measured from the ground level to the tip of the mainstem on three plants per plot at maturity. Seed weight was determined on a sample of 100 seeds.

Soil samples for nematode assays were collected from the top 20 cm of soil (ten 2.5-cm cores per row) of each plot during August of each year. Nematodes were extracted with a combination of elutriation (2) and centrifugal flotation (10). Eggs were extracted from *H. glycines* cysts collected on a 250-μm pore sieve from 500 cm^3 of soil during elutriation by grinding cysts in 50 ml of tap water in 100 ml polypropylene centrifuge tubes for 1 minute at 3,500 rpm with a stainless steel pestle having 1-mm ridges (J. A. Fox, pers. comm.). *H. columbus* was extracted from soybean roots by a shaker incubation method (1) in addition to soil assays.

The soybean genotypes and the number of replications varied among experiments. In 1980, 27 SCN-susceptible cultivars in Maturity Groups (MG) V, VI, VII, and VIII, and SCN-resistant, Bedford (MG V), Centennial (MG VI), and Foster (MG VIII) were planted on 29 May at Athens with four replications. In 1981, 27 SCN-susceptible genotypes (cultivars and plant introductions in MG VI, VII, and VIII) not tested in 1980 and Bragg (MG VII), Centennial, and Foster were planted on 14 May with four replications. In addition, 10 cultivars evaluated in 1980 were retested at Athens. These cultivars were grouped according to maturity into two experiments

TABLE 1. Seed yield and tolerance index of 10 soybean cultivars grown with (+) and without (−) DBCP soil treatment for 2 years in field plots infested with *Heterodera glycines*.

	1980			1981		
	Seed yield (kg/ha)			Seed yield (kg/ha)		
Cultivar	−	+	Tolerance index†	−	+	Tolerance index†
Maturity Group VI						
Centennial	1,825	2,131	86	2,537	2,507	101
Coker 156	1,329	1,945*	68	1,466	2,076*	71
Davis	842	1,788*	47	938	1,641*	57
Lee 74	1,190	1,769*	67	1,071	1,935*	55
McNair 600	912	1,547*	59	418	1,155*	36
LSD (0.05)‡	620	620	29	472	472	31
Maturity Group VII or VIII						
Bragg	765	2,306*	33	761	1,675*	45
Coker 237	833	1,745*	48	634	1,435*	44
Foster	1,248	1,719*	73	2,323*	1,815	128
Semmes	1,215	1,587*	77	1,274	1,905*	67
Wright	1,481	2,209*	67	1,543	2,055*	75
LSD (0.05)‡	620	620	29	329	329	15

* Significant difference between nematicide treated vs. nontreated within a cultivar by LSD ($P = 0.05$).
† Index = (yield of nontreated ÷ yield of treated) × 100.
‡ For comparison of cultivars within a maturity grouping.

(Table 1). Both experiments were planted on 14 May with eight replications.

In 1982, five MG VII genotypes initially tested in 1981 and Wright (MG VII), Bragg, and Foster were retested at Athens (Table 6). The experiment was planted on 14 May with eight replications. In another experiment, five cultivars with five replications were planted in soil infested with SCN at Athens and Midville and in soil infested with *H. columbus* at Midville (Tables 3, 5). Planting dates were 14 May at Athens and 19 May at Midville. Both rows of Athens subplots and the two middle rows of Midville subplots were harvested for seed yield.

Greenhouse experiments: Eleven genotypes were planted in 474-ml styrofoam cups filled with SCN-infested soil obtained from Athens and Midville (Table 4). Soil sources were handled as separate experiments. The cups were planted with five seeds and thinned to one plant per cup. The experimental design was a randomized complete block with five replications. The number of cysts per plant was determined after 48 days by shaking root systems in water for 3 minutes and collecting roots on a 850-μm pore sieve nested in a 250-μm pore sieve. Roots on the 850-μm pore sieve were sprayed with water for 45 seconds twice. Cysts collected on the 250-μm pore sieve were counted.

In a repetition of this experiment, the same procedures were followed except four replicates were used and the experiment was terminated after 29 days.

Data analysis: Data were subjected to analysis of variance. In 1982, the two field experiments on SCN-infested soil were combined over locations, assuming location and replication to be random effects and cultivar and nematicide to be fixed effects. Nematode data were transformed ($\log_{10}[n + 1]$) prior to analysis and are presented as antilogs. Correlation coefficients among traits were calculated on genotype means. A tolerance index was calculated for each strain as (trait in nontreated subplot ÷ trait in treated subplot) × 100.

RESULTS

Distinct and consistent levels of tolerance to SCN were observed among soybean cultivars. The seed yields and tolerance indices for 8 of the 27 SCN-susceptible cultivars and two of the three resistant cultivars grown in 1980 and retested in 1981 illustrated the range of tolerance to SCN found in commercial cultivars (Table 1). In MG VI, the application of DBCP in-

TABLE 2. Populations of *Heterodera glycines* on different soybean cultivars grown in four field experiments.

Cultivar	Location/sampling date							
	Athens/ 22 August 1980		Athens/ 26 August 1981		Athens/ 13 August 1982		Midville/ 10 August 1982	
	Eggs* × 10^3	Juveniles*	Eggs* × 10^3	Juveniles*	Eggs* × 10^3	Juveniles*	Eggs* × 10^2	Juveniles*
Maturity Group VI								
Centennial	2.3 b†	94 b†	2.8 b†	9 a†	1.1 b‡	24 c‡	1.0 c‡	2 a‡
Coker 156	3.3 b	201 ab	10.7 a	9 a	9.9 a	107 a	5.8 b	3 a
Davis	17.3 a	340 a	13.8 a	6 a				
Lee 74	3.0 b	113 ab	13.5 a	15 a				
McNair 600	6.9 b	292 ab	10.5 a	12 a				
Maturity Group VII or VIII								
Bragg	9.1 ab	417 a	10.5 ab	44 a	8.9 a	38 bc	8.5 ab	4 a
Coker 237	12.8 a	243 ab	10.1 ab	44 a	7.8 a	54 abc	9.3 ab	4 a
Foster	3.8 b	131 b	2.8 c	8 b				
Semmes	7.0 ab	168 b	11.7 a	59 a				
Wright	3.9 b	286 ab	5.9 b	30 a	6.4 a	80 ab	18.8 a	3 a

* Eggs per 500 cm^3 and juveniles per 100 cm^3 of soil.

† Means followed by the same letter within a maturity grouping are not significantly different based on LSD ($P = 0.05$) performed on $\log_{10}(n + 1)$ transformed data.

‡ Means followed by the same letter within a column are not significantly different based on LSD ($P = 0.05$) performed on $\log_{10}(n + 1)$ transformed data.

creased yield for all cultivars except Centennial, which is resistant to SCN Race 3 (the predominant race at Athens). Centennial was the highest yielding cultivar in both nematicide treated and nontreated plots. Davis and McNair 600 were the lowest yielding cultivars in nontreated plots both years. Coker 156 was higher in yield than Davis or McNair 600 in the nontreated plots in 1981. Coker 156 had a 2-year mean tolerance index of 70, compared with 48 for McNair 600 and 52 for Davis.

The SCN population levels differed little among susceptible cultivars. In 1980, Davis plots had more SCN eggs than did plots of the other MG VI cultivars, but there were no differences among the susceptible cultivars for the number of juveniles (Table 2). The SCN population levels for the susceptible cultivars did not differ in 1981. Soil from Centennial plots had fewer eggs than did soil from the plots of other cultivars.

DBCP increased yield in MG VII and VIII susceptible cultivars both years (Table 1). In treated plots, Bragg had the highest yield in 1980 and Wright in 1981 (Table 1). In nontreated plots, Bragg and Coker 237 were lower in yield than the other cultivars both years. The tolerance indices for 2 years averaged 39, 46, 71, and 72 for Bragg, Coker 237, Wright, and Semmes, respectively. Foster, which is resistant to SCN Race 3, was higher in yield in the treated plots in 1980 and in the nontreated plots in 1981.

The numbers of SCN eggs or juveniles varied among MG VII and VIII susceptible cultivars (Table 2). Foster, however, had the lowest number of eggs and juveniles both years.

DBCP increased yields of Bragg, Coker 237, and Wright but not Coker 156 or Centennial at two locations in 1982 (Table 3). Centennial, Coker 156, and Wright produced higher yields than Bragg and Coker 237 in both DBCP-treated and nontreated plots. Centennial was resistant to the predominant race (Race 3) of SCN present at both Midville and Athens (Tables 2, 4).

Growth of susceptible cultivars was suppressed by SCN in nontreated plots. The reduction in plant height when compared with plants in treated plots was greater for Coker 237 (24%) and Bragg (22%) than for the other two susceptible cultivars (Table 3). Seed weight of Coker 237 was 7% less in DBCP-treated than in nontreated plots. Seed weight for the other cultivars did not differ between treated and nontreated plots. Although there were no differences

TABLE 3. Mean performance of five soybean cultivars grown with (+) and without (−) DBCP soil treatment in 1982 at two locations in soil infested with *Heterodera glycines.*

Cultivar	Seed yield (kg/ha) −	Seed yield (kg/ha) +	Tolerance index†	Maturity (day/month) −	Maturity (day/month) +	Plant height (cm) −	Plant height (cm) +	Seed weight (g/100 seeds) −	Seed weight (g/100 seeds) +
Bragg	1,540	1,964*	78	14/10	12/10	80	102*	12.2	12.6
Centennial	2,587	2,749	94	13/10	13/10	91	97	12.6	12.1
Coker 156	2,210	2,329	95	2/10	2/10	76	88*	11.2	11.1
Coker 237	1,548	1,905*	81	13/10	11/10	67	88*	12.8*	11.9
Wright	2,082	2,449*	85	15/10	16/10	88	100*	12.5	12.7
LSD (0.05)	496	496	ns	5	5	11	11	0.5	0.5

* Significant difference between nematicide treated vs. nontreated within a cultivar by LSD ($P = 0.05$).
† Index = (yield of nontreated ÷ yield of treated) × 100.

in maturity between plants grown in treated and untreated plots, Coker 156 averaged 10–14 days earlier than the other cultivars in the experiment (Table 3).

Numbers of SCN juveniles or eggs differed little among susceptible cultivars across the two locations (Table 2). In greenhouse reproduction experiments, Centennial had fewer cysts after 29 and 48 days with either soil source than did Bragg, Coker 237, Coker 156, or Wright (Table 4). The susceptible cultivars did not differ in numbers of cysts.

Certain cultivars also exhibited tolerance to *H. columbus*. Application of DBCP to *H. columbus*-infested plots increased the yield of only Coker 237 (80%) and Bragg (73%) (Table 5). Wright and Coker 156 were higher in yield than Coker 237 and Bragg in nontreated plots, although there were no differences among these cultivars in treated plots. The tolerance index was at least 30 units greater for Centennial, Coker 156, and Wright than for Bragg and Coker 237.

Only Coker 237 had greater plant height in treated than in nontreated plots (Table 5). Seed weight of Bragg and Coker 237 averaged 1 g/100 seeds greater in treated than in nontreated plots. There were no differences in seed weight between nematicide treatments for Wright, Coker 156, or Centennial. Root and soil populations of *H. columbus* differed little among cultivars within treated or nontreated plots. DBCP, however, reduced nematode populations on all cultivars (Table 5).

Evaluation of additional susceptible genotypes in 1981 and 1982 indicated DBCP was not providing complete protection for

TABLE 4. Reproduction (number of cysts) of two populations (Athens and Midville) of *Heterodera glycines* on 11 soybean genotypes in two greenhouse experiments.

Genotype	Experiment 1 (48 days) Athens	Experiment 1 (48 days) Midville	Experiment 2 (29 days) Athens	Experiment 2 (29 days) Midville
Bragg	98 a*	1,098 a	318 ab	186 a
Centennial	7 b	41 b	54 c	3 c
Coker 237	70 a	1,062 a	184 b	132 a
Coker 156	71 a	630 a	169 b	63 a
Foster	2 b	5 c	1 d	19 b
Woods Yellow	42 a	1,055 a	291 ab	94 a
Wright	73 a	922 a	185 b	134 a
PI 97100	138 a	1,095 a	353 ab	63 a
PI 159096	86 a	1,420 a	406 ab	108 a
PI 200462	129 a	1,418 a	169 b	169 a
PI 200531	182 a	1,453 a	600 a	75 a

* Means followed by the same letter within a column are not significantly different based on LSD ($P = 0.05$) performed on $\log_{10}(n + 1)$ transformed data.

TABLE 5. Performance of and nematode population level on five soybean cultivars grown in 1982 with (+) and without (−) DBCP soil treatment in soil infested with *Hoplolaimus columbus* at Midville, Georgia.

Cultivar	Seed yield (kg/ha) −	Seed yield (kg/ha) +	Tolerance index†	Plant height (cm) −	Plant height (cm) +	Seed weight (g/100 seeds) −	Seed weight (g/100 seeds) +	*H. columbus* No. per 100 cm³ soil −	*H. columbus* No. per 100 cm³ soil +	*H. columbus* No. per 1 g root −	*H. columbus* No. per 1 g root +
Bragg	1,710	2,960*	58	89	98	11.5	12.5*	320* a‡	2 a	318* a	8 a
Centennial	2,553	2,864	89	81	86	12.1	11.8	144* a	2 a	267* a	8 a
Coker 156	3,077	3,456	89	74	85	10.6	10.7	41* a	3 a	327* a	1 a
Coker 237	2,000	3,604*	56	78	101*	12.1	13.2*	144* a	1 a	227* a	1 a
Wright	2,874	3,251	88	92	93	11.9	12.0	52* a	2 a	72* b	6 a
LSD (0.05)	853	853	24	15	15	0.8	0.8				

* Significant difference between nematicide treated vs. nontreated within a cultivar by LSD ($P = 0.05$).
† Index = (yield of nontreated ÷ yield of treated) × 100.
‡ Means followed by the same letter within a column are not significantly different based on LSD ($P = 0.05$) performed on $\log_{10}(n + 1)$ transformed data.

some SCN-intolerant cultivars. For example, Bragg yielded 39% less than Foster in 1981 and 62% less in 1982 in nematicide-treated plots (Table 6). Yield data for 3 years (1980–82) from Athens on soil not infested with SCN indicated Bragg yielded only 6% less than Foster (4).

Among the susceptible strains initially tested in 1981, PI 97100 showed a relatively high yield in nontreated plots and a high tolerance index for yield compared with other plant introductions (Table 6). PI 97100 was higher in yield than Bragg in 1981 and 1982. PI 159096, PI 200462, and Woods Yellow had moderate to high tolerance indices but lower yields than PI 97100 in nontreated plots.

Greenhouse experiments indicated PI 97100 was susceptible to both field populations of SCN (Table 4). None of the SCN-Race 3 susceptible genotypes appears to have partial resistance, since there were no differences among these genotypes in the number of cysts after 29 or 48 days.

DISCUSSION

The high levels of tolerance found in certain susceptible soybean genotypes have potential for stabilizing yields on SCN-infested land. Although most of the genotypes evaluated were intolerant to this nematode, Wright and Coker 156 were shown to have a moderate level of tolerance and PI 97100, a plant introduction from Korea, exhibited a high level of tolerance. Even though the above normal rainfall early in the 1982 growing season at both Athens and Midville resulted in less SCN damage for all susceptible cultivars than in the previous 2 years, the ranking of the cultivars for tolerance remained the same as in the previous years.

The similar ranking of cultivars for tolerance in the SCN- and *H. columbus*-infested areas indicates the plant characteristic(s) responsible for tolerance to one nematode species may provide tolerance to other species. If this relationship for tolerance among nematode species holds with additional nematode species, the value of a tolerant cultivar would be greatly enhanced. This possibility is especially interesting when considering the increasing frequency of soybean fields with damaging levels of several plant-parasitic nematodes. Tolerance to *H. columbus* has been observed in other soybean genotypes (12).

There was an association between tolerance for seed yield and tolerance for plant height in most of our experiments. The correlation coefficients were 0.64 ($P < 0.01$) in 1980 and 0.55 ($P < 0.01$) in 1981 in the initial screening experiments with 30 genotypes. The same trends were observed in the other experiments with fewer genotypes. The association between tolerance for yield and tolerance for seed weight was less consistent. In 1980 the correlation coefficient was 0.65 ($P < 0.01$), but it was only 0.23 ($P > 0.05$) in the 1981 experiment. The dependency of seed weight on the number of pods set by the

TABLE 6. Seed yield and tolerance index of eight soybean genotypes grown with (+) and without (−) DBCP soil treatment for 2 years in field plots infested with *Heterodera glycines*.

	1981			1982		
	Seed yield (kg/ha)			Seed yield (kg/ha)		
Strain	−	+	Tolerance index†	−	+	Tolerance index†
Bragg	569	1,273*	45	1,152	1,338	86
Foster	1,992	2,070	96	2,482	2,812*	88
Woods Yellow	1,122	1,343	84	869	1,044	83
Wright				1,869	2,539*	74
PI 97100	1,715	1,679	102	1,592	1,779	90
PI 159096	1,177	1,651*	71	914	1,311*	70
PI 200462	1,229	1,502	82	907	953	95
PI 200531	967	1,641*	59	869	1,329*	65
LSD (0.05)	595	595	34	354	354	ns

* Significant difference between nematicide treated vs. nontreated within a cultivar by LSD ($P = 0.05$).
† Index = (yield of nontreated ÷ yield of treated) × 100.

plant would suggest the timing of the stress caused by the nematode and subsequent environmental factors (moisture, temperature, etc.) would determine if the seed of stressed plants would be larger or smaller than seed of nonstressed plants.

The damage caused by SCN to intolerant genotypes, such as Bragg in 1982, in nematicide-treated plots presents a problem with the current method of measuring tolerance. Two alternatives can be considered: 1) applying higher rates of nematicide at planting and additional nematicide applications during the growing season, and 2) comparing the yield and other traits of the same genotypes in SCN-infested and SCN-free fields. Of the alternatives, the use of additional nematicide is the most desirable to obtain an unbiased estimate of tolerance for a large number of genotypes. The desirability of using a noninfested area depends on how similar its physical soil properties and environmental conditions are to the SCN-infested area. The use of field microplots would allow paired comparisons of infested and noninfested plots but would limit the number of genotypes that could be evaluated. With currently grown susceptible cultivars, tolerance can be roughly estimated by their yield in SCN-infested soil, since the yield potential among these cultivars within the same maturity group in noninfested soil should be within a range of 15% with adequate testing over environments. We are currently evaluating greenhouse screening methods for selecting SCN-tolerant genotypes. An effective greenhouse screening method has been developed for selecting *G. rostochiensis*-tolerant potato genotypes (22).

Control of SCN is primarily achieved with crop rotation and resistant cultivars (7). The use of tolerant cultivars can enhance the value of these control measures and provide a supplemental control option. Most rotation schemes recommend a varying number of years of a nonhost crop, a resistant soybean cultivar, and a susceptible soybean cultivar. The role of the susceptible cultivar is to stabilize the SCN population by providing all variants of the population an equal opportunity for reproduction. The susceptible cultivar relieves the selection pressure imposed on the SCN population by the resistant cultivar and prevents the resistance-breaking race from becoming dominant in the field population. The role of the susceptible cultivar can be better fulfilled by a tolerant, susceptible cultivar which would be damaged less by SCN.

If sufficiently high levels of tolerance to SCN, as in PI 97100, can be combined with high yield and agronomic desirability, this cultivar would provide more stable yields in SCN-infested soils while reducing selection pressure on the nematode. Resistance and tolerance might be combined in one cultivar by selecting soybean genotypes for resistance to one race and for tolerance to a second race or another nematode species. Centennial, which is resistant to SCN Race

3, appears to be moderately tolerant to *H. columbus.*

Tolerance has limitations that necessitate other nematode control measures being used simultaneously. Susceptible, tolerant cultivars allow the buildup of nematode inoculum for the next growing season and the increase of nematodes in the roots that could result in root-rot disease complexes (17). Fortunately, soybean root-rot diseases have not been commonly associated with nematode infections. Currently, we are evaluating tolerance limits of tolerant and moderately tolerant genotypes in field microplots with SCN.

One method to overcome the initial high nematode population levels for tolerant cultivars would be the use of nematicides. The low efficacy of nematicides has limited their use as the sole means of SCN control. However, using a nematicide on a tolerant, susceptible cultivar may be economically feasible. This combination would reduce the initial inoculum density and lessen the danger of developing resistance-breaking races of SCN.

Literature Cited

1. Bird, G. W. 1971. Influence of incubation solution on rate of recovery of *Pratylenchus brachyurus* from cotton roots. Journal of Nematology 3:378–385.

2. Byrd, D. W., Jr., K. R. Barker, H. Ferris, C. J. Nusbaum, W. E. Griffin, R. H. Small, and C. A. Stone. 1976. Two semiautomatic elutriators for extracting nematodes and certain fungi from soil. Journal of Nematology 8:206–212.

3. Cook, R. 1974. Nature and inheritance of nematode resistance in cereals. Journal of Nematology 6:165–174.

4. Cordonnier, M. J. 1983. The 1982 field crops performance tests: Peanuts, soybeans, sorghum, cotton, tobacco, sunflowers, and annual forages. Georgia Agricultural Experiment Stations Research Report 422.

5. Evans, K., and J. Franco. 1979. Tolerance to cyst-nematode attack in commercial potato cultivars and some possible mechanisms for its operation. Nematologica 25:153–162.

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

7. Good, J. M. 1973. Nematodes. Pp. 527–543 *in* B. E. Caldwell, ed. Soybeans: Improvement, production, and uses. Madison, Wisconsin: American Society of Agronomy.

8. Heijbroek, W., J. S. McFarlane, and D. L. Doney. 1977. Breeding for tolerance to beet-cyst eelworm *Heterodera schachtii* Schm. in sugarbeet. Euphytica 26:557–564.

9. Inagaki, H. 1979. Race status of five Japanese populations of *Heterodera glycines.* Japanese Journal of Nematology 9:1–4.

10. Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Disease Reporter 48:692.

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

12. Nyczepir, A. P., and S. A. Lewis. 1979. Relative tolerance of selected soybean cultivars to *Hoplolaimus columbus* and possible effects of soil temperature. Journal of Nematology 11:27–31.

13. Perkins, H. F., R. A. McCreery, G. Lockaby, and C. E. Perry. 1979. Soils of the Southeast Georgia Branch Experiment Station. Georgia Agricultural Experiment Stations Research Bulletin 245.

14. Perkins, H. F., V. Owen, J. E. Hammel, and E. A. Price. 1982. Soil characteristics of the Plant Science Farm of the University of Georgia. Georgia Agricultural Experiment Stations Research Bulletin 287.

15. Riggs, R. D. 1977. Worldwide distribution of soybean-cyst nematode and its economic importance. Journal of Nematology 9:34–39.

16. Riggs, R. D., M. L. Hamblen, and L. Rakes. 1981. Infra-species variation in reactions to hosts in *Heterodera glycines* populations. Journal of Nematology 13:171–179.

17. Roberts, P. A. 1982. Plant resistance in nematode pest management. Journal of Nematology 14: 24–33.

18. Schafer, J. F. 1971. Tolerance to plant disease. Annual Review of Phytopathology 9:235–252.

19. Schmitthenner, A. F., and A. K. Walker. 1979. Tolerance versus resistance for control of phytophthora root rot of soybeans. Proceedings of the Ninth Soybean Seed Research Conference. Pp. 35–44.

20. 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.

21. Trudgill, D. L., and L. M. Cotes. 1983. Differences in the tolerance of potato cultivars to potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*) in field trials with and without nematicides. Annals of Applied Biology 102:373–384.

22. Trudgill, D. L., and L. M. Cotes. 1983. Tolerance of potato to potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*) in relation to the growth and efficiency of the root system. Annals of Applied Biology 102:385–397.

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

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