

Resistance to Root-knot, Reniform, and Soybean Cyst Nematodes in Selected Soybean Breeding Lines¹

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Abstract: Soybean breeding lines and reported sources of nematode resistance were evaluated in repeated greenhouse tests for resistance to North Carolina populations of the soybean cyst nematode *Heterodera glycines*, reniform nematode *Rotylenchulus reniformis*, and the root-knot nematode species *Meloidogyne incognita*, *M. arenaria*, and *M. javanica*. Lines from the soybean breeding program in Missouri that had 'Hartwig' soybean as a parent were the most resistant to races 1-4 of the soybean cyst nematode and the population of reniform nematode evaluated here. Numerous cysts of an inbred soybean cyst nematode race 4 population were produced on several of these Hartwig descendants, however, and accession S92-1603 had a cyst index of 29.2%. These accessions were also susceptible to *M. arenaria* and *M. javanica*. Soybean lines N87-539 and N91-245 from the breeding program in North Carolina had strong resistance to an inbred soybean cyst nematode race 1 population and to *M. javanica*, respectively. Soybean germplasm from the Georgia breeding program demonstrated the strongest resistance to the root-knot nematode species tested. Lines from the Georgia program, including G80-1515, G83-559, G93-9106, and G93-9223, that incorporated both root-knot and soybean cyst nematode resistance had the best overall resistance to the nematode populations evaluated. Resistance reported in the soybean lines was generally upheld. In a few cases, differences in the origin and culture of the nematode populations used in this study may have led to discrepancies between reported and observed resistance.

Key words: *Glycine max*, *Heterodera glycines*, *Meloidogyne arenaria*, *Meloidogyne incognita*, *Meloidogyne javanica*, nematode, reniform nematode, resistance, root-knot nematode, *Rotylenchulus reniformis*, soybean cyst nematode.

Nematodes are primary pathogens of soybean throughout the world (Wrather et al., 1997). The soybean cyst nematode, *Heterodera glycines* Ichinohe, causes the most soybean yield loss of any pathogen, with an estimated U.S. yield loss of 1,990,000 metric tons in 1994 alone (Wrather et al., 1997). In the southern United States, root-knot and other species of nematodes have ranked second behind the soybean cyst nematode as the most significant pathogens causing yield loss in soybean (Wrather and Sciumbato, 1995). Breeding soybean cultivars that are resistant to the soybean cyst nematode has been a primary component in management tactics to reduce crop damage, but the development of races of the soybean cyst

nematode that can overcome available sources of resistance remains a threat to profitable soybean production (Riggs and Schmitt, 1988). The soybean cultivar, Hartwig, was developed from a cross between PI 437654 and Forrest soybean, and it is reported to have resistance to all races of soybean cyst nematode tested (Anand, 1992). Hartwig is being used as a parent in the soybean breeding programs in many public and private institutions to develop agronomically superior soybean cultivars with broad resistance to the soybean cyst nematode. However, since there are reports that some populations of the soybean cyst nematode can produce cysts on Hartwig and PI 437654, these sources of resistance may not be durable (Davis et al., 1996; Dias et al., 1998; Young, 1998).

In a 1976 survey, race 1 was the predominant race of the soybean cyst nematode detected in North Carolina (D. P. Schmitt, pers. comm.), but the frequency of races 2 and 4 has been increasing in this state (Koenning and Barker, 1998; Schmitt and Barker, 1988). This increased incidence may be due in part to cropping of soybean cultivars with resistance derived from Peking and PI 88788 sources of resistance to the soy-

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bean cyst nematode (Koenning and Barker, 1998). In addition, cultivation of soybean cyst nematode-resistant soybean cultivars in North Carolina may enhance selection for other nematode species that damage soybean, particularly root-knot (*Meloidogyne* species), Columbia lance (*Hoplolaimus columbus*), and reniform (*Rotylenchulus reniformis*) nematodes (Koenning and Barker, 1998; Schmitt and Barker, 1988). *Meloidogyne incognita*, *M. arenaria*, and *M. javanica* are the species of root-knot nematodes important in soybean in North Carolina and many other southern states. The Hartwig source of soybean cyst nematode resistance appears to be susceptible to root-knot nematodes, especially *M. arenaria* and *M. javanica* (Davis et al., 1996). Sources of resistance to different species of root-knot nematodes have been identified in soybeans, and these are being combined with resistance to the soybean cyst nematode in the soybean breeding program at the University of Georgia (Boerma et al., 1991; Luzzi et al., 1987, 1996a, 1996b, 1997). The late-maturing soybean cultivar, 'Bryan', has resistance to races 1 and 3 of the soybean cyst nematode, plus resistance to *M. incognita*, *M. arenaria*, and *M. javanica* (Boerma et al., 1991).

Although soybean genotypes grown in the southern United States have been evaluated for resistance to cyst, root-knot, and reniform nematodes in several studies (Davis et al., 1996; Hussey et al., 1991; Kinloch et al., 1985; Riggs et al., 1988, 1991, 1995; Robbins et al., 1994), breeding programs generally use local populations for screening. Nematode populations of the same species in different geographic locations may vary in virulence. The following study was designed to evaluate soybean breeding lines from three geographic sources for resistance to North Carolina populations of root-knot, reniform, and soybean cyst nematodes in two greenhouse tests.

MATERIALS AND METHODS

Soybean lines tested: The soybean breeding lines and plant introductions (PIs) that were evaluated for nematode resistance are listed

in Table 1. These soybean lines were obtained from the breeding programs of J. W. Burton at North Carolina State University, H. R. Boerma and R. S. Hussey at the University of Georgia, and S. C. Anand at the University of Missouri. Asgrow 5979 and Bryan soybean were included as susceptible and resistant checks, respectively, in all root-knot nematode tests. Hartwig and PI 437654 soybean also were tested for root-knot resistance. Lee 68, Bryan, Hartwig, PI 437654, and three of the soybean cyst nematode differential soybean hosts, Peking, PI 88788, and PI 90763 (Riggs and Schmitt, 1988), were included in reniform nematode tests. Bryan, Hartwig, and PI 437654 were included in all soybean cyst nematode tests, and Lee 68 soybean also was included to facilitate calculation of cyst indices.

Test procedures: All soybean lines were tested for resistance to nematodes in 150-ml Cone-tainers (Stuewe and Sons, Corvallis, OR) that contained a 1:1 pasteurized mixture of coarse sand and field soil (loamy sand: 88.9% sand, 8.3% silt, and 2.8% clay). Soybean seeds were germinated directly in the Cone-tainers containing the sand-soil mixture, and nematode inoculum was injected into the soil with a syringe at the base of each plant 2 weeks after seedling emergence. Initial inoculum in each cone consisted of 10,000 eggs for root-knot and soybean cyst nematodes, and 10,000 mixed eggs and vermiform life stages for reniform nematode.

Root-knot nematodes: The root-knot nematode inocula included one population each of races 3 and 4 of *Meloidogyne incognita*, races 1 and 2 of *M. arenaria*, and a population of *M. javanica* that were isolated from North Carolina field samples and maintained in pure greenhouse culture on roots of 'Rutgers' tomato (*Lycopersicon esculentum*). Eggs of root-knot nematode populations were extracted from roots of greenhouse cultures with a 0.5% NaOCl solution (Hussey and Barker, 1973). Soybean plants were harvested at 56 days after inoculation and rated visually for the percentage of root system galled and percent of root system exhib-

TABLE 1. Sources of soybean germplasm, parents of selected lines, potential resistance to nematodes, and reference citations for the soybean breeding lines evaluated for resistance to North Carolina populations of root-knot, reniform, and soybean cyst nematodes.

Soybean sources, lines	Parents	Potential resistance ^a	Reference
North Carolina			
N91-207	Forrest × (N73-40 × N74-511)	Hg R3; Mi, Ma	Kenty and Mosley, 1993
N91-245	Forrest × (N73-40 × N74-511)	Mi, Ma	Kenty and Mosley, 1993
N87-539	Gasoy 17 × N79-491	Hg R3; Mi	Hartwig, 1989
N90-541	Hutcheson × N80-1014	Hg R3; Mi	Kenty and Mosley, 1993
N91-386	Braxton × N85-4085	Mi	Kenty and Mosley, 1993
N91-404	Braxton × N85-4085	Hg R3; Mi	Kenty and Mosley, 1993
Georgia			
PI 96354	—	Mi	Luzzi et al., 1987
PI 200538	—	Ma	Luzzi et al., 1987
PI 230977	—	Mj	Luzzi et al., 1987
G80-1515	Pickett 71 × Bedford	Hg R3; R14	Luzzi et al., 1997
G83-559	D77-6103 × F77-6903	Hg R3; R14	Luzzi et al., 1997
G93-9009	G83-559 × (G80-1515 ² × PI 96354)	Hg R3; R14; Mi	Luzzi et al., 1996a
G93-9027	G83-559 × (G80-1515 ² × PI 96354)	Hg R3; R14; Mi	Luzzi et al., 1996a
G93-9106	G83-559 × (G80-1515 ² × PI 200538)	Hg R3; R14; Ma	Luzzi et al., 1996b
G93-9223	G83-559 × (G80-1515 ² × PI 230977)	Hg R3; R14; Mj	Luzzi et al., 1997
Missouri			
PI 437654	—	Hg all races	Myers and Anand, 1991
Hartwig	Forrest × PI 437654	Hg all races	Anand, 1992
S91-1661	Pioneer 9571 × Hartwig	Hg all races	Anand, 1992
S92-1403	Pioneer 9581 × Hartwig	Hg all races	Anand, 1992
S92-1603	Asgrow 5403 × Hartwig	Hg all races	Anand, 1992

^a Reported or expected resistance to races (R) of the soybean cyst nematode *Heterodera glycines* (Hg) and three species of the root-knot nematodes *Meloidogyne incognita* (Mi), *Meloidogyne arenaria* (Ma), and *Meloidogyne javanica* (Mj).

iting necrosis. Root fresh weights also were recorded at harvest. Eggs of root-knot nematodes from infected soybean roots were extracted from a random 5-gram sample of each root system with 0.5% NaOCl. Total eggs per root system was calculated based upon total root fresh weight.

Reniform nematode: The reniform nematode population was isolated from a soybean field sample in North Carolina and subsequently maintained in greenhouse culture on roots of 'Deltapine 16' cotton (*Gossypium hirsutum*). A mixture of both eggs and vermiform life stages of the reniform nematode was extracted from soil by flotation and sieving from greenhouse cultures and used as inoculum for soybean tests (Davis, et al., 1996). Soybean plants were harvested at 90 days after inoculation with reniform nematodes, and eggs and vermiform life stages were extracted from total soil (150 ml) in individual Cone-tainers as described above. The percentages of the total root system showing necrosis and total fresh root weight were recorded at harvest.

Soybean cyst nematodes: The soybean cyst nematode populations, from greenhouse cultures reared on susceptible 'Lee 68' soybean, included three highly homozygous, inbred lines that corresponded to races 1, 3, and 4 of the soybean cyst nematode (Dong and Opperman, 1997). The term "inbred races" is used here for convenience, but the inbred soybean cyst nematode lines actually do not represent field "races" because they are derived from individual nematode crosses and sibling matings (Dong and Opperman, 1997). A field population of race 2 of the soybean cyst nematode from a North Carolina soybean field was cultured on Lee 68 soybean and included in resistance screening. The race identity of each soybean cyst nematode population was confirmed on differential soybean hosts (Riggs and Schmitt, 1988). Cysts were collected from roots and soil of greenhouse cultures using spray from a high-pressure water hose in combination with floating and sieving. The cysts were then crushed with a Ten-Brock homogenizer to release eggs for use as in-

oculum (Davis et al., 1996). At 50 days after inoculation, plants were harvested and cysts were extracted from soil and roots of individual plants as described for soybean cyst nematode inoculum preparation above. Visual assessments of percent root system necrosis and the fresh weight of each root system also were recorded at harvest.

Statistics: All treatments (cultivar plus nematode population) were replicated four times in each test, and all tests were repeated once. Each test was arranged in a randomized complete block design with cultivar and nematode population as the main treatments. All data were subjected to analysis of variance with the SAS General Linear Models procedure (SAS Institute, Cary, NC), and interaction main effects were analyzed for all dependent variables. The Waller-Duncan k -ratio t -test (k -ratio = 50) was used to compare treatment means.

RESULTS

Cultivar effects were significant ($P \leq 0.05$) among all nematode species for all dependent variables except percent necrosis ($P \leq 0.21$) and total cysts ($P \leq 0.10$) for soybean cyst nematode race 1 in Test 1, percent necrosis for *M. arenaria* race 1 in Test 1 ($P \leq 0.45$) and Test 2 ($P \leq 0.09$), total eggs for *M. arenaria* race 2 ($P \leq 0.09$) and *M. incognita* race 3 ($P \leq 0.71$) in Test 1, and percent necrosis for reniform nematode in Test 1 ($P \leq 0.08$). Significant interactions for the dependent variables presented in Tables 2–6 occurred between Tests 1 and 2; hence, values for both tests are listed separately. No other significant interactions were observed.

Soybean cyst nematodes: Differential resistance to the populations of soybean cyst nematode tested was observed among the soybean germplasm evaluated, and the data were mostly consistent between Tests 1 and 2 (Tables 2 and 3). Cyst numbers were generally higher in Test 2 than in Test 1. In most cases, PI 437654, Hartwig, and soybean lines from Missouri that were descendants of crosses with Hartwig were resistant to races 1–4 of soybean cyst nematode. Up to an average of 70 cysts of race 2, however, devel-

oped on soybean accession S91-1661, and inbred race 4 produced an average of 68, 313, and 499 cysts on accessions S91-1661, S92-1403, and S92-1603, respectively, in Test 2. Soybean accession N87-539 from the North Carolina selections was resistant to the inbred race 1 population in both tests, and both Bryan and G93-9106 soybean were resistant to this population in Test 2. The soybean lines from Georgia were relatively resistant to the inbred race 3 and 4 populations, but the plant introductions from Georgia and all soybean lines from North Carolina were susceptible to these populations. Percent necrosis of soybean root systems ranged from an average of 2.5% to 70.0% in both tests, and root necrosis was generally more severe in Test 2 than in Test 1. The plant introductions from Georgia generally had the highest percentage of root necrosis observed in both tests, although descendants from crosses with these plant introductions had considerably lower overall root necrosis.

Root-knot nematodes: Significant differences ($P \leq 0.05$) in percent galling were observed among the soybean lines tested for resistance to different populations of root-knot nematodes in two tests (Tables 4 and 5). Galling ranged from an average of 1.3% to 57.5% of root system galled and was generally higher in Test 2, but galling was usually less than 25% of the total root system in both tests. Differences in the level of resistance to the populations of root-knot nematodes were observed. Results were generally consistent among the soybean lines between Tests 1 and 2, although total eggs produced by races 1 and 2 of *M. arenaria*, and *M. javanica*, were generally higher in Test 2. All soybean lines were resistant to race 3 of *M. incognita*. A higher number of eggs of *M. incognita* race 3 (4,271 eggs per root system) were produced on PI 437654 and PI 96354 compared to other lines in Test 2, but Hartwig and its descendants were resistant to *M. incognita* race 3. Bryan and PI 96354 from Georgia were highly resistant to race 4 of *M. incognita*, and the other Georgia lines also were generally resistant to *M. incognita* race 4. Egg production by *M. incognita* race 4

TABLE 2. Production of cysts^a and associated root necrosis in Test 1 of inbred lines^b ("races") of the soybean cyst nematode *Heterodera glycines* and a greenhouse-cultured North Carolina field population of race 2 of the soybean cyst nematode on selected soybean germplasm from breeding programs in North Carolina, Georgia, and Missouri.

Soybean	Inbred Race 1				Race 2				Inbred Race 3				Inbred Race 4			
	Percent necrosis	Total cysts	Cyst index	Rating ^c	Percent necrosis	Total cysts	Cyst index	Rating ^c	Percent necrosis	Total cysts	Cyst index	Rating ^c	Percent necrosis	Total cysts	Cyst index	Rating ^c
Lee 68 (check)	62.5 a	80 a	100.0	S	22.5 e-j	217 ab	100.0	S	52.5 ab	680 abc	100.0	S	20.0 de	1093 a	100.0	S
North Carolina																
N87-539	62.5 a	7 a	8.8	R	10.0 ij	232 ab	106.9	S	27.5 c-i	496 d	72.9	S	8.8 e	600 cd	54.9	S
N90-541	40.0 a	127 a	158.8	S	30.0 c-h	315 a	145.1	S	30.0 c-g	593 bcd	87.2	S	20.0 de	659 bcd	60.3	S
N91-207	50.0 a	28 a	35.0	MS	42.5 bcd	254 ab	117.0	S	35.0 cde	533 cd	78.4	S	20.0 de	758 bc	69.4	S
N91-245	40.0 a	100 a	125.0	S	12.5 hij	333 a	153.5	S	20.0 e-k	644 bcd	94.7	S	8.8 e	856 b	78.3	S
N91-386	57.5 a	242 a	302.5	S	32.5 c-g	138 bcd	63.6	S	28.8 c-h	762 ab	112.1	S	21.3 cdc	677 bcd	61.9	S
N91-404	65.0 a	34 a	42.5	MS	26.3 c-j	201 abc	92.6	S	35.0 cde	589 bcd	86.6	S	18.8 de	661 bcd	60.5	S
Georgia																
Bryan	45.0 a	61 a	76.3	S	26.3 c-j	275 ab	126.7	S	20.0 e-k	269 e	39.6	MS	13.8 de	338 ef	30.9	MS
PI 96354	55.0 a	64 a	80.0	S	25.0 d-j	151 bcd	69.6	S	40.0 bc	550 cd	80.9	S	13.8 de	662 bcd	60.6	S
PI 200538	55.0 a	124 a	155.0	S	40.0 b-e	332 a	153.0	S	57.5 a	837 a	123.1	S	41.3 ab	1140 a	104.3	S
PI 230977	32.5 a	71 a	88.8	S	65.0 a	148 bcd	68.2	S	36.3 cd	266 e	39.0	MS	40.0 abc	464 de	42.5	MS
G80-1515	40.0 a	81 a	101.3	S	30.0 c-h	205 abc	94.5	S	10.0 kl	31 f	4.5	R	17.5 de	174 fg	15.9	MR
G83-559	50.0 a	29 a	36.3	MS	8.8 j	328 a	151.2	S	10.0 kl	27 f	4.0	R	10.0 e	69 g	6.3	R
G93-9009	32.5 a	81 a	101.3	S	20.0 f-j	185 abc	85.3	S	2.5 i	46 f	6.8	R	10.0 e	138 fg	12.6	MR
G93-9106	50.0 a	60 a	75.0	S	28.8 c-i	279 ab	128.6	S	13.8 h-l	21 f	3.0	R	13.8 de	75 g	6.9	R
G93-9223	62.5 a	31 a	38.8	MS	37.5 c-f	281 ab	129.5	S	16.3 g-l	17 f	2.5	R	16.3 de	69 g	6.3	R
Missouri																
PI 437654	60.0 a	2 a	2.5	R	23.8 d-j	1 d	0.5	R	11.3 jkl	12 f	1.8	R	11.3 de	13 g	1.2	R
Hartwig	30.0 a	2 a	2.5	R	32.5 c-g	1 d	0.5	R	21.3 d-k	4 f	0.6	R	18.8 de	14 g	1.3	R
S91-1661	37.5 a	3 a	3.8	R	35.0 c-g	19 d	8.8	R	26.3 c-j	4 f	0.6	R	20.0 de	29 g	2.7	R
S92-1403	60.0 a	2 a	2.5	R	16.3 g-j	3 d	1.4	R	13.8 h-l	8 f	1.8	R	17.5 de	28 g	2.6	R
S92-1603	57.5 a	2 a	2.5	R	16.3 g-j	6 d	2.8	R	12.5 i-l	7 f	1.0	R	11.3 de	10 g	0.9	R

Table values represent the mean of four replicate treatments. Means followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, $k = 50$). Analysis of variance for each dependent variable was significant ($P \leq .05$) by treatment (cultivar) except for the percent necrosis value ($P \leq 0.21$) and total cyst value ($P \leq 0.1$) of SCN Inbred Race 1.

^a Total number of cysts per root system is reported. Cyst indices were calculated as the percent number of cysts per root system as compared to susceptible 'Lee 68' soybean. Percent root necrosis values are based upon observations of total root systems. Initial inoculum was 10,000 eggs per plant.

^b "Race 1," "Race 3," and "Race 4" are inbred lines developed from crosses of single soybean cyst nematode individuals and subsequent sib matings (Dong and Opperman, 1997).

^c Rating is based upon scale presented by Schmitt and Shannon (1992), where cyst index 0-9 is resistant (R), cyst index 10-30 is moderately resistant (MR), cyst index 31-60 is moderately susceptible (MS), and cyst index >60 is susceptible (S).

TABLE 3. Production of cysts^a and associated root necrosis in Test 2 of inbred lines^b (“races”) of the soybean cyst nematode *Heterodera glycines* and a greenhouse-cultured North Carolina field population of race 2 of the soybean cyst nematode on selected soybean germplasm from breeding programs in North Carolina, Georgia, and Missouri.

Soybean	Inbred Race 1				Race 2				Inbred Race 3				Inbred Race 4			
	Percent necrosis	Total cysts	Cyst index	Rating ^c	Percent necrosis	Total cysts	Cyst index	Rating ^c	Percent necrosis	Total cysts	Cyst index	Rating ^c	Percent necrosis	Total cysts	Cyst index	Rating ^c
Lee 68 (check)	65.0 a	808 a	100.0	S	60.0 a-d	2,165 ab	100.0	S	55.0 ab	2,386 b	100.0	S	62.5 ab	1,712 cde	100.0	S
North Carolina																
N87-539	55.0 a-d	5 g	0.6	R	60.0 a-d	956 d-g	44.2	MS	45.0 a-d	1,059 e	44.4	MS	50.0 b-c	2,416 abc	141.1	S
N90-541	41.3 b-h	119 efg	14.7	MR	45.0 c-h	1,510 bcd	69.8	S	37.5 b-e	2,278 b	95.5	S	37.5 c-g	2,294 bcd	134.0	S
N91-207	60.0 ab	323 de	40.0	MS	52.5 a-e	1,534 bcd	70.9	S	30.0 c-g	1,692 cd	70.9	S	67.5 ab	1,853 b-e	108.2	S
N91-245	42.5 b-g	200 d-g	24.8	MR	50.0 b-f	1,624 a-d	75.0	S	37.5 b-e	2,264 b	94.9	S	57.5 a-d	2,692 ab	157.2	S
N91-386	57.5 abc	116 efg	14.4	MR	57.5 a-e	1,848 abc	85.4	S	60.0 a	2,492 b	104.4	S	60.0 abc	3,186 a	186.1	S
N91-404	52.5 a-c	140 efg	17.3	MR	42.5 d-i	1,020 d-g	47.1	MS	60.0 a	3,314 a	138.9	S	76.7 a	2,208 bcd	129.0	S
Georgia																
Bryan	45.0 a-g	0 g	0.0	R	40.0 e-j	1,631 a-d	75.4	S	32.5 c-f	724 e	30.3	MS	50.0 b-e	1,524 de	89.0	
PI 96354	50.0 a-f	648 ab	80.2	S	70.0 a	2,284 a	105.5	S	60.0 a	2,083 bc	87.3	S	62.5 ab	2,018 b-e	117.9	S
PI 200538	33.3 e-j	424 bcd	52.5	MS	62.5 abc	1,308 cde	60.4	S	47.5 abc	2,270 b	95.1	S	48.3 b-e	1,220 ef	71.3	S
PI 230977	37.5 c-i	325 de	40.2	MS	40.0 e-j	230 hi	10.6	MR	37.5 b-e	1,568 d	65.7	S	60.0 abc	2,232 bcd	130.4	S
G80-1515	31.3 f-j	197 d-g	24.4	MR	21.7 j	686 e-i	31.7	MS	17.5 efg	121 f	5.1	R	17.5 g	93 g	5.4	R
G83-559	26.3 g-j	596 abc	73.8	S	26.3 hij	1,077 def	49.7	MS	15.0 fg	62 f	2.6	R	22.5 fg	129 g	7.5	R
G93-9009	21.3 hij	356 cde	44.1	MS	26.3 hij	545 f-i	25.2	MR	13.8 fg	115 f	4.8	R	31.7 efg	425 fg	24.8	MR
G93-9106	50.0 a-f	52 fg	6.5	R	42.5 d-i	315 ghi	14.5	MR	42.5 a-d	75 f	3.1	R	33.8 d-g	264 g	15.4	MR
G93-9223	55.0 a-d	313 def	38.7	MS	67.5 ab	738 e-h	34.1	MS	25.0 d-g	80 f	3.4	R	45.0 b-f	27 g	1.6	R
Missouri																
PI 437654	16.3 j	4 g	0.5	R	27.5 hij	6 i	0.3	R	8.75 g	1 f	0.1	R	35.0 d-g	1 g	0.1	R
Hartwig	35.0 d-j	1 g	0.1	R	30.0 g-j	2 i	0.1	R	31.3 c-f	0 f	0.0	R	23.8 fg	9 g	0.5	R
S91-1661	40.0 b-h	6 g	0.7	R	32.5 f-j	70 hi	3.2	R	37.5 b-e	3 f	0.1	R	55.0 a-e	68 g	4.0	R
S92-1403	18.8 ij	5 g	0.6	R	31.3 f-j	4 i	0.2	R	35.0 b-f	0 f	0.0	R	23.8 fg	313 g	18.3	MR
S92-1603	42.5 b-g	2 g	0.2	R	27.5 hij	4 i	0.2	R	33.3 b-f	7 f	0.3	R	52.5 a-c	499 fg	29.2	MR

Table values represent the mean of four replicate treatments. Means followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, *k* = 50).

^a Total number of cysts per root system is reported. Cyst indices were calculated as the percent number of cysts per root system as compared to susceptible ‘Lee 68’ soybean. Percent root necrosis values are based upon observations of total root systems. Initial inoculum was 10,000 eggs per plant.

^b “Race 1,” “Race 3,” and “Race 4” are inbred lines developed from crosses of single soybean cyst nematode individuals and subsequent sib matings (Dong and Opperman, 1997).

^c Rating is based upon scale presented by Schmitt and Shannon (1992), where cyst index 0–9 is resistant (R), cyst index 10–30 is moderately resistant (MR), cyst index 31–60 is moderately susceptible (MS), and cyst index >60 is susceptible (S).

TABLE 4. Root galling,^a percent root necrosis, and egg production in greenhouse Test 1 of North Carolina populations^b of the root-knot nematodes *Meloidogyne incognita* races 3 and 4, *M. arenaria* races 1 and 2, and *M. javanica* on selected soybean germplasm from breeding programs in North Carolina, Georgia, and Missouri.

Soybean	<i>M. incognita</i> race 3			<i>M. incognita</i> race 4			<i>M. arenaria</i> race 1			<i>M. arenaria</i> race 2			<i>M. javanica</i>		
	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs
Asgrow 5979	22.5 cd	6.3 b-f	240 a	35.0 b-g	11.3 bcd	2,820 b	25.0 a	13.8 c-g	3,399 cd	47.5 b-c	31.3 a	3,855 a	55.0 bcd	23.3 a	2,131 bcd
North Carolina															
N87-539	50.0 ab	7.5 a-e	719 a	60.0 abc	10.0 cde	935 bc	45.0 a	17.5 a-e	3,681 bcd	52.5 bcd	20.0 a-e	7,605 a	55.0 bcd	16.3 bc	3,202 bcd
N90-541	32.5 bcd	7.5 a-e	201 a	25.0 efg	6.3 efg	950 bc	17.5 a	10.0 e-i	992 d	47.5 b-e	21.3 a-d	3,853 a	45.0 cde	21.3 ab	4,953 bcd
N91-207	20.0 d	7.5 a-e	374 a	25.0 efg	2.5 gh	1,049 bc	40.0 a	8.3 f-i	9,331 a-d	35.0 b-c	21.3 a-d	17,850 a	55.0 bcd	22.5 a	16,054 a
N91-245	25.0 cd	6.3 b-f	151 a	35.0 b-g	3.8 fgh	383 bc	20.0 a	8.8 f-i	4,075 a-d	30.0 de	13.8 b-f	3,659 a	55.0 bcd	3.8 ef	480 d
N91-386	50.0 ab	6.3 b-f	254 a	30.0 d-g	2.5 gh	2,100 bc	52.5 a	18.3 a-d	4,189 a-d	37.5 b-c	21.3 a-d	5,596 a	60.0 abc	16.3 bc	15,870 a
N91-404	22.5 cd	8.8 a-d	0 a	60.0 abc	16.7 a	0 c	62.5 a	22.5 ab	332 d	40.0 b-e	11.3 c-f	1,186 a	50.0 bcd	12.5 cd	7,149 bc
Georgia															
Bryan	25.0 cd	2.5 ef	87 a	20.0 fg	3.8 fgh	0 c	25.0 a	5.0 hi	4,552 a-d	42.5 b-e	6.3 f	2,063 a	30.0 de	3.8 ef	116 d
PI 96354	45.0 abc	10.0 abc	152 a	57.5 a-d	2.5 gh	0 c	45.0 a	20.0 abc	13,662 a	60.0 b	28.8 a	19,825 a	57.5 abc	20.0 ab	5,920 bcd
PI 200538	25.0 cd	1.3 f	37 a	62.5 ab	7.5 def	96 c	42.5 a	6.7 ghi	927 d	60.0 b	11.7 c-f	10,009 a	47.5 b-e	5.0 ef	1,477 bcd
PI 230977	60.0 a	11.7 ab	282 a	32.5 c-g	7.5 def	213 c	37.5 a	16.3 b-f	1,485 d	52.5 bcd	11.7 c-f	2,081 a	55.0 bcd	6.3 ef	1,826 bcd
G80-1515	25.0 cd	5.0 c-f	719 a	30.0 d-g	2.5 gh	26 c	21.3 a	3.8 hi	2,384 d	25.0 e	10.0 def	7,479 a	52.5 bcd	13.8 cd	95 d
G83-559	25.0 cd	2.5 ef	290 a	22.5 fg	1.3 h	292 c	32.5 a	10.0 e-i	3,038 cd	32.5 cde	6.3 f	8,922 a	72.5 ab	2.5 f	418 d
G93-9027	25.0 cd	5.0 c-f	0 a	20.0 fg	1.3 h	53 c	30.0 a	11.3 d-h	6,102 a-d	37.5 b-e	8.8 ef	1,609 a	55.0 bcd	22.5 a	517 d
G93-9106	40.0 a-d	3.3 def	112 a	47.5 a-f	6.7 d-g	121 c	17.5 a	2.5 i	2,520 d	32.5 cde	3.8 f	—	42.5 cde	6.3 ef	155 d
G93-9223	22.5 cd	3.8 def	151 a	35.0 b-g	2.5 gh	0 c	25.0 a	13.8 c-g	4,348 a-d	57.5 bc	3.3 f	1,633 a	22.5 e	1.3 f	1,715 bcd
Missouri															
PI 437654	30.0 bcd	1.3 f	751 a	72.5 a	15.0 ab	16,452 a	67.5 a	25.0 a	13,337 ab	100.0 a	—	—	82.5 a	20.0 ab	7,432 b
Hartwig	20.0 d	3.8 def	27 a	17.5 g	3.8 fgh	78 c	37.5 a	16.3 b-f	3,118 cd	27.5 de	20.0 a-e	7,718 a	42.5 cde	17.5 abc	4,548 bcd
S91-1661	25.0 cd	7.5 a-e	63 a	52.5 a-e	10.0 cde	1,624 bc	45.0 a	5.0 hi	6,205 a-d	37.5 b-e	23.8 ab	16,520 a	30.0 de	8.8 de	1,030 cd
S92-1464	22.5 cd	12.5 a	818 a	27.5 efg	3.8 fgh	370 bc	32.5 a	17.5 a-e	8,217 a-d	25.0 e	20.0 a-e	11,451 a	50.0 bcd	16.3 bc	3,581 bcd
S92-1603	50.0 ab	8.8 a-d	0 a	47.5 a-f	13.8 abc	2,178 bc	32.5 a	16.3 b-f	12,867 abc	50.0 b-e	22.5 abc	8,523 a	62.5 abc	8.8 de	724 d

Values are the mean of four replicate treatments. Means followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, *k* = 50). Analysis of variance for each dependent variable was significant ($P \leq .05$) by treatment (cultivar) with the exception of percent necrosis for *M. arenaria* race 1 ($P \leq .45$), and egg production for *M. arenaria* race 2 ($P \leq .09$) and *M. incognita* race 3 ($P \leq .71$).

^a Table values of galling and necrosis represent the percent of total root system galled or necrotic, respectively, and egg production is represented as total eggs extracted per root system. Asgrow 5979 is included as a susceptible check.

^b Field isolates of root-knot nematodes from North Carolina were identified and maintained in pure culture on roots or 'Rutgers' tomato in the greenhouse for use as inoculum in this experiment. Initial inoculum was 10,000 eggs per plant.

TABLE 5. Root galling,^a percent root necrosis, and egg production in greenhouse Test 2 of North Carolina populations^b of the root-knot nematodes *Meloidogyne incognita* races 3 and 4, *M. arenaria* races 1 and 2, and *M. javanica* on selected soybean germplasm from breeding programs in North Carolina, Georgia, and Missouri.

Soybean	<i>M. incognita</i> race 3			<i>M. incognita</i> race 4			<i>M. arenaria</i> race 1			<i>M. arenaria</i> race 2			<i>M. javanica</i>		
	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs	Percent necrosis	Percent galling	Total eggs
Asgrow 5979	—	—	—	—	—	—	21.3 a	17.5 b-f	34,237 bcd	55.0 a	36.3 ab	61,446 a	35.0 b-f	33.8 b	30,021 bcd
North Carolina															
N87-539	31.3 b-f	3.0 cde	207 c	45.0 abc	5.5 bcd	4,940 b	31.3 a	24.3 abc	53,878 b	38.8 b-c	35.0 ab	28,935 cd	43.8 abc	21.3 cd	7,885 ef
N90-541	25.0 d-g	3.0 cde	478 c	12.5 gh	2.0 f	1,564 b	25.0 a	19.0 b-e	4,787 fg	17.5 gh	30.0 bc	21,758 c-f	17.5 gh	23.8 cd	36,863 bc
N91-207	40.0 bc	4.5 bcd	161 c	30.0 c-g	3.3 def	5,773 b	31.3 a	16.3 b-f	40,617 bc	27.5 c-h	25.0 cd	32,494 c	37.5 a-d	23.8 cd	42,698 bc
N91-245	38.8 bcd	3.3 cde	138 c	17.5 e-h	2.5 ef	2,200 b	15.0 a	7.5 def	20,328 c-g	22.5 fgh	12.5 efg	10,613 efg	18.8 fgh	5.0 fg	440 f
N91-386	45.0 ab	4.8 abc	156 c	32.5 b-f	3.5 def	594 b	35.0 a	20.0 bcd	8,105 efg	40.0 a-d	30.0 bc	14,063 d-g	28.8 c-g	23.8 cd	12,545 ef
N91-404	38.8 bcd	6.8 a	135 c	37.5 a-d	4.5 b-f	1,660 b	23.3 a	36.7 a	15,107 d-g	42.5 abc	35.0 ab	35,043 bc	45.0 abc	26.3 bc	27,315 cd
Georgia															
Bryan	25.0 d-g	1.5 e	92 c	36.3 a-c	2.0 f	230 b	40.0 a	4.8 ef	5,127 fg	22.5 fgh	11.3 e-h	8,787 efg	21.3 d-h	4.0 fg	473 f
PI 96354	26.3 c-g	3.0 cde	4,271 a	38.8 a-d	2.8 ef	120 b	20.0 a	15.0 c-f	30,580 cd	32.5 c-g	25.0 cd	17,666 c-g	20.0 e-h	15.0 de	21,362 de
PI 200538	32.5 b-c	3.8 cd	1,638 b	36.3 a-c	6.3 bc	3,027 b	30.0 a	6.3 def	1,826 g	38.8 b-e	13.8 efg	23,562 cde	36.3 a-e	15.0 de	1,958 f
PI 230977	58.8 a	6.5 ab	382 c	55.0 a	5.0 b-e	364 b	42.5 a	6.3 def	22,317 c-f	53.8 ab	8.8 fgh	1,538 g	52.5 a	21.3 cd	4,070 f
G80-1515	16.3 g	1.5 e	115 c	8.0 h	2.3 f	115 b	32.5 a	7.3 def	3,894 fg	15.0 h	12.5 e-h	5,302 fg	12.5 gh	2.3 fg	220 f
G83-559	16.3 g	1.5 e	138 c	23.8 d-h	2.3 f	120 b	11.3 a	3.5 f	891 g	27.5 c-h	8.0 fgh	12,166 d-g	18.8 fgh	3.3 fg	770 f
G93-9027	—	—	—	—	—	—	28.8 a	4.8 ef	4,756 fg	33.8 c-f	7.5 gh	7,326 fg	12.5 gh	1.3 g	396 f
G93-9106	17.5 fg	2.5 de	2 c	20.0 d-h	2.0 f	112 b	18.8 a	6.8 def	6,411 fg	16.3 h	3.3 h	4,004 fg	22.5 d-h	4.3 fg	1,228 f
G93-9223	23.8 efg	2.8 cde	147 c	36.3 a-e	3.5 def	299 b	25.0 a	3.3 f	5,456 fg	28.8 c-h	4.8 gh	4,963 fg	25.0 d-h	4.8 fg	3,564 f
Missouri															
PI 437654	13.8 g	3.8 cd	4,271 a	15.0 fgh	6.8 b	41,860 a	25.0 a	31.3 ab	140,888 a	25.0 d-h	40.0 a	63,250 a	47.5 ab	57.5 a	141,812 a
Hartwig	23.8 efg	3.0 cde	161 c	31.3 c-g	4.0 c-f	2,519 b	43.8 a	15.0 c-f	27,782 cde	32.5 c-g	40.0 a	50,490 ab	26.3 d-h	21.3 cd	13,222 ef
S91-1661	25.0 d-g	4.0 cd	287 c	30.0 c-g	10.0 a	368 b	30.0 a	18.8 b-e	6,640 fg	30.0 c-h	17.5 def	10,292 efg	10.0 h	11.3 ef	9,900 ef
S92-1464	—	—	—	—	—	—	32.5 a	7.5 def	7,656 efg	15.0 h	10.0 fgh	3,564 g	12.5 gh	3.3 fg	188 f
S92-1603	18.8 efg	3.5 cde	130 c	51.3 ab	3.5 def	1,472 b	45.0 a	13.8 c-f	6,168 fg	23.8 e-h	20.0 de	3,153 g	20.0 e-h	6.8 efg	5,586 f

Table values are the mean of four replicate treatments. Means followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, *k* = 50). Analysis of variance for each dependent variable was significant ($P \leq .05$) by treatment (cultivar) with the exception of percent necrosis for *M. arenaria* race 1 ($P \leq .09$).

^a Table values of galling and necrosis represent the percent of total root system galled or necrotic, respectively, and egg production as total eggs extracted per root system. Asgrow 5979 is included as a susceptible check. Data not available where indicated (—).

^b Field isolates of root-knot nematodes from North Carolina were identified and maintained in pure culture on roots or 'Rutgers' tomato in the greenhouse for use as inoculum in this experiment. Initial inoculum was 10,000 eggs per plant.

TABLE 6. Final populations^a and percent root necrosis of a North Carolina population of the reniform nematode^b *Rotylenchulus reniformis* on selected soybean germplasm from breeding programs in North Carolina, Georgia, and Missouri in two greenhouse tests.

Soybean	Percent necrosis		Total eggs and vermiform stages	
	Test 1	Test 2	Test 1	Test 2
Checks				
Lee 68	70 a	45 b-e	21,770 bc	9,914 c-h
PI 88788	75 a	45 b-e	5,890 bcd	2,842 fgh
PI 90763	35 a	40 c-g	23,030 b	392 h
Peking	48 a	53 bc	6,680 bcd	3,799 d-h
North Carolina				
N87-539	40 a	43 b-f	1,510 cd	3,691 d-h
N90-541	24 a	29 f-i	7,176 bcd	13,370 bcd
N91-207	44 a	53 bc	60,520 a	29,170 a
N91-245	24 a	44 b-f	4,363 bcd	11,220 c-f
N91-386	40 a	50 bcd	4,901 bcd	22,670 ab
N91-404	34 a	39 c-h	19,120 bcd	7,810 c-h
Georgia				
Bryan	35 a	35 d-i	12,580 bcd	3,355 e-h
PI 96354	48 a	73 a	4,210 bcd	17,260 bc
PI 200538	63 a	34 e-i	18,830 bcd	8,930 c-h
PI 230977	44 a	58 ab	12,950 bcd	13,290 b-e
G80-1515	40 a	23 i	3,330 bcd	945 h
G83-559	45 a	23 i	2,430 bcd	3,591 d-h
G93-9009	55 a	40 c-g	6,070 bcd	11,016 c-g
G93-9106	43 a	23 i	3,709 bcd	1,075 gh
G93-9223	48 a	29 f-i	739 d	5,929 d-h
Missouri				
PI 437654	45 a	24 hi	684 d	1,558 fgh
Hartwig	68 a	36 d-h	11,400 bcd	7,040 d-h
S91-1661	50 a	26 ghi	1,210 cd	40 h
S92-1403	48 a	25 ghi	2,130 cd	1,414 fgh
S92-1603	53 a	29 f-i	5,350 bcd	1,228 fgh

Table values represent the mean of four replicate treatments. Means followed by the same letter are not significantly different (Waller-Duncan *k*-ratio *t*-test, *k* = 50). Analysis of variance for each dependent variable was significant ($P \leq .05$) except for percent necrosis ($P \leq .08$) in Test 1.

^a Final populations were measured as the total number of reniform nematode eggs and mixed vermiform life stages (no. eggs and vermiforms) extracted from 150-ml soil.

^b A field isolate of reniform nematode was cultured on roots of 'Deltapine' cotton in the greenhouse for use as inoculum in this experiment. Initial inoculum was a mixture of 10,000 eggs and vermiform nematodes.

on the soybean lines from North Carolina was inconsistent between Tests 1 and 2, but all North Carolina lines were moderately susceptible to *M. incognita* race 4. Total eggs produced by *M. incognita* race 4 on PI 437654 were relatively high, but Hartwig and its descendants were resistant. PI 200538 from Georgia was the most resistant to race 1 of *M. arenaria*. Bryan, N90-541, and the Georgia lines were moderately resistant to *M. arenaria* race 1. The greatest egg production by *M. arenaria* race 1 was observed on PI 437654, and Hartwig and its descendants were also susceptible. All soybean germplasm, with the exception of PI 230977 and

lines G93-9106 and G93-9223, were susceptible to *M. arenaria* race 2. The lines N91-245, G80-1515, G83-559, G93-9027, and cultivar Bryan were the most resistant to *M. javanica*, while PI 230977 and G93-9223 were moderately resistant. The highest egg production by *M. javanica* (141,812 eggs per root system) was observed on PI 437654. Hartwig and its descendants were also susceptible to *M. javanica*. Although no significant interactions among main effects were observed, root necrosis was generally higher in Test 1 than in Test 2. Plant introductions generally had more necrosis compared to other soybean lines in both root-knot tests,

while Georgia accessions G80-1515 and G83-559 had the least necrosis.

Reniform nematode: Different levels of resistance to reniform nematode were observed among the soybean lines in two tests (Table 6). Greater numbers of reniform nematodes generally were collected in Test 1, but results of both tests were comparable. Numbers of reniform nematodes collected from the soybean differentials used for soybean cyst nematode race determination were moderate, with PI 88788 supporting the fewest reniform nematodes overall and reproduction on PI 90763 inconsistent between Tests 1 and 2. PI 437654 and descendants from Hartwig crosses were the most resistant to reniform nematode in both tests. Line N87-539 from North Carolina and most of the lines from Georgia were moderately resistant to reniform nematode. Line N91-207 and the plant introductions from Georgia were the most susceptible to reniform nematodes. Although no significant interactions among main effects were observed, more root necrosis was observed in reniform nematode tests than in tests of the same soybean lines with soybean cyst and root-knot nematodes.

DISCUSSION

Substantial differences in resistance to soybean cyst, root-knot, and reniform nematodes were observed among the soybean germplasm evaluated. The soybean lines from Missouri that included Hartwig as a parent appeared to retain the resistance to the soybean cyst nematode that previously had been reported (Anand, 1992). The inbred race 4 population of soybean cyst nematode produced cysts on the Hartwig descendants, however, similar to previous reports for this population on PI 437654 and Hartwig (Davis et al., 1996). Thus, the potential for selection of a soybean cyst nematode population that overcomes resistance derived from Hartwig must be considered. Attempts in our laboratory to increase a population of the inbred race 4 population on either PI 437654 or Hartwig soybean have not been successful to date. However,

both natural and selected populations of soybean cyst nematode that overcome resistance in Hartwig have been recently reported (Dias et al., 1998; Young, 1998).

Although increases in reniform populations were observed among genotypes, the initial inoculum must be considered as a potential contributing factor to final numbers since the longevity of infective reniform nematodes is considerable (Sivakumar and Seshardi, 1976). PI 437654 had strong resistance to reniform nematode, but Hartwig was moderately susceptible. The lines produced from crosses of Hartwig with higher-yielding soybean cultivars, however, seem to have an increased resistance to reniform nematodes. This also appears to be the case in these lines with resistance to root-knot nematodes, particularly races 3 and 4 of *M. incognita*. Even though the levels of resistance to races 1 and 2 of *M. arenaria* and *M. javanica* were increased in the Hartwig descendants as compared to PI 437654, these lines were still relatively susceptible to these nematode populations.

The soybean germplasm from the North Carolina breeding program were from a diverse background of crosses and sources of resistance to different nematodes. All of the North Carolina lines were resistant to *M. incognita* race 3, and to a lesser extent *M. incognita* race 4, which is consistent with reported resistance (Hartwig, 1989; Kenty and Mosley, 1993). The resistance reported to *M. arenaria* (Kenty and Mosley, 1993) was not observed in lines N91-245 and N91-207, but N91-245 demonstrated strong resistance to *M. javanica* in both tests. Moderate resistance to the reniform nematode, not previously reported, was observed in soybean line N87-539. In addition, line N87-539 was one of the most resistant lines to the inbred race 1 population of the soybean cyst nematode. The North Carolina soybean lines reported to be resistant to race 3 of the soybean cyst nematode were all susceptible to the inbred race 3 population evaluated here. In some instances, the resistance observed using the inbred soybean cyst nematode populations may have differed from results obtained previously using field populations because all

individuals in the inbred lines possessed the same virulence genotype (Dong and Opperman, 1997).

Lines from the Georgia breeding program were resistant to race 3 of the soybean cyst nematode regardless of whether a field or inbred population was used for screening (Luzzi et al., 1996a, 1996b, 1997). The origin of some root-knot nematode populations, however, did appear to influence the resistance observed in the Georgia germplasm. PI 200538 was reported to be resistant to race 2 of *M. arenaria* (Luzzi et al., 1987), but it was susceptible to the *M. arenaria* race 2 population from North Carolina. PI 230977 did not show as high a level of resistance to *M. javanica* as had been previously reported, but it was resistant to *M. arenaria* race 2 (Luzzi et al., 1987). Lines developed from either PI 200538 or PI 230977, however, were resistant to *M. arenaria* race 2 and *M. javanica*, respectively. Although the root-knot nematode-resistant plant introductions were susceptible to reniform nematodes, crosses of these plant introductions with sources of resistance to soybean cyst nematodes produced resistance to reniform nematodes in most of the descendants. This observation is consistent with reports that suggest a linkage between some sources of resistance to soybean cyst nematodes and resistance to reniform nematodes in soybean (Rebois et al., 1970; Robbins et al., 1994).

Although reniform nematodes appeared to produce more root necrosis than soybean cyst and root-knot nematodes, no significant interactions were observed in these tests. Differences in root necrosis were observed among cultivars, but these were not consistent among the nematode populations evaluated. As with root necrosis, gall ratings were not indicative of reproduction by nematodes. In a previous report, soybean yield was negatively correlated with root-knot galling (Kinloch et al., 1985). This stresses the importance of evaluating both nematode populations and plant symptoms when screening for plant resistance and tolerance to nematodes.

In many lines, resistance to multiple spe-

cies and populations of nematodes was present. The strongest resistance to races 1–4 of the soybean cyst nematode and to reniform nematodes was from the Missouri lines that contained Hartwig soybean as a parent. Several soybean lines from the North Carolina program had strong resistance to specific species of root-knot nematodes or races of soybean cyst nematodes, depending upon the lineage of the breeding line. Soybean breeding lines from the Georgia program had the strongest resistance to root-knot nematodes. No single soybean genotype, however, was resistant to all of the populations evaluated in these tests. The soybean lines from the Georgia breeding program that incorporated both root-knot and soybean cyst nematode resistance demonstrated the best overall resistance to all of the nematode populations evaluated. The geographic origin and culture of the nematode populations may have had an effect on the reported versus observed resistance demonstrated in this study. For the most efficient use of sources of resistance to multiple nematode populations, soybean breeders and growers should evaluate their local nematode populations.

LITERATURE CITED

- Anand, S. C. 1992. Registration of 'Hartwig' soybean. *Crop Science* 32:1069–1070.
- Boerma, H. R., R. S. Hussey, D. V. Phillips, E. D. Wood, and S. L. Finnerty. 1991. Registration of 'Bryan' soybean. *Crop Science* 31:487.
- Davis, E. L., S. R. Koenning, J. W. Burton, and K. R. Barker. 1996. Greenhouse evaluation of selected soybean germplasm for resistance to North Carolina populations of *Heterodera glycines*, *Rotylenchulus reniformis*, and *Meloidogyne* species. *Journal of Nematology* 28(4S):590–598.
- Dias, W. P., J. F. V. Silva, R. A. S. Kihl, D. M. Hiro-moto, and R. V. Abdelnoor. 1998. Resistance break of Hartwig cultivar by field population of the soybean cyst nematode (*Heterodera glycines*). *Pesquisa Agropecuária Brasileira* 33:971–974.
- Dong, K., and C. H. Opperman. 1997. Genetic analysis of parasitism in the soybean cyst nematode, *Heterodera glycines*. *Genetics* 146:1311–1318.
- Hartwig, E. E. 1989. Uniform soybean tests: Southern states. Stoneville, MS: USDA ARS.
- Hussey, R. S., and K. R. Barker. 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp., including a new technique. *Plant Disease Reporter* 57:1025–1028.
- Hussey, R. S., H. R. Boerma, P. L. Raymer, and B. M.

- Luzzi, 1991. Resistance in soybean cultivars from maturity groups V-VIII to soybean cyst and root-knot nematodes. Supplement to the *Journal of Nematology* 23: 576-583.
- Kenty, M. M., and S. D. Mosley. 1993. Uniform soybean tests: Southern states. Stoneville, MS: USDA ARS.
- Kinloch, R. A., C. K. Hiebsch, and H. A. Peacock. 1985. Comparative root-knot galling and yield responses of soybean cultivars to *Meloidogyne incognita*. *Plant Disease* 69:334-336.
- Koenning, S. R., and K. R. Barker. 1998. Survey of *Heterodera glycines* races and other plant-parasitic nematodes on soybean in North Carolina. Supplement to the *Journal of Nematology* 30: In press.
- Luzzi, B. M., H. R. Boerma, and R. S. Hussey. 1987. Resistance to three species of root-knot nematode in soybean. *Crop Science* 32:258-262.
- Luzzi, B. M., H. R. Boerma, R. S. Hussey, D. V. Phillips, J. Tamulonis, S. L. Finnerty, and E. D. Wood. 1996a. Registration of southern root-knot nematode resistant soybean germplasm line G93-9009. *Crop Science* 36:823.
- Luzzi, B. M., H. R. Boerma, R. S. Hussey, D. V. Phillips, J. Tamulonis, S. L. Finnerty, and E. D. Wood. 1996b. Registration of soybean germplasm line G93-9106 resistant to peanut root-knot nematode. *Crop Science* 36:1423-1424.
- Luzzi, B. M., H. R. Boerma, R. S. Hussey, D. V. Phillips, J. Tamulonis, S. L. Finnerty, and E. D. Wood. 1997. Registration of Javanese root-knot nematode resistant soybean germplasm line G93-9223. *Crop Science* 37: 1035-1036.
- Myers, G. O., and S. C. Anand. 1991. Inheritance of resistance and genetic relationships among soybean plant introductions to races of soybean cyst nematode. *Euphytica* 55:197-201.
- Rebois, R. V., J. M. Epps, and E. E. Hartwig. 1970. Correlation of resistance in soybeans to *Heterodera glycines* and *Rotylenchulus reniformis*. *Phytopathology* 60: 695-700.
- Riggs, R. D., and D. P. Schmitt. 1988. Complete characterization of the race scheme for *Heterodera glycines*. *Journal of Nematology* 20:392-395.
- Riggs, R. D., M. L. Hamblen, and L. Rakes. 1988. Resistance in commercial soybean cultivars to six races of *Heterodera glycines* and to *Meloidogyne incognita*. *Annals of Applied Nematology* (Supplement to the *Journal of Nematology*) 2:70-76.
- Riggs, R. D., L. Rakes, and D. Dombek. 1995. Response of soybean cultivars and breeding lines to races of *Heterodera glycines*. Supplement to the *Journal of Nematology* 27:592-601.
- Riggs, R. D., L. Rakes, and R. Elkins. 1991. Soybean cultivars resistant and susceptible to *Heterodera glycines*. Supplement to the *Journal of Nematology* 23:584-592.
- Robbins, R. T., L. Rakes, and C. R. Elkins. 1994. Reproduction of the reniform nematode on thirty soybean cultivars. Supplement to the *Journal of Nematology* 26:659-664.
- Schmitt, D. P., and K. R. Barker. 1988. Incidence of plant-parasitic nematodes in the coastal plain of North Carolina. *Plant Disease* 72:107-110.
- Schmitt, D. P., and G. Shannon. 1992. Differentiating soybean responses to *Heterodera glycines* races. *Crop Science* 32:275-277.
- Sivakumar, C. V., and A. R. Seshardi. 1976. Longevity of the reniform nematode, *Rotylenchulus reniformis*, in host-free soil. *Indian Journal of Nematology* 6:138-144.
- Wrather, J. A., and G. L. Sciombato. 1995. Soybean disease loss estimates for the southern United States during 1992-1993. *Plant Disease* 79:84-85.
- Wrather, J. A., T. R. Anderson, D. M. Arsyad, J. Gai, L. D. Ploper, A. Porta-Puglia, H. H. Ram, and J. T. Yori-nori. 1997. Soybean disease loss estimates for the top 10 soybean producing countries in 1994. *Plant Disease* 81: 107-110.
- Young, L. D. 1998. *Heterodera glycines* populations selected for reproduction on 'Hartwig' soybean. *Journal of Nematology* 30: Abstract (in press).