Resistance of Soybean Cultivars to Field Populations of *Heterodera glycines* in North Carolina

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ABSTRACT

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The soybean cyst nematode (SCN), *Heterodera glycines*, is the most important pathogen of soybean, *Glycine max*, in North Carolina. Cultural practices are the most effective means of managing this pathogen because a majority of cultivars are susceptible to the races of this nematode that predominate in the state. Resistant and susceptible cultivars were evaluated in 14 *H. glycines*-infested fields from 1992 to 1999. Resistance in cvs. Hartwig and Delsoy 5710, and line S92-1603 derived from plant introduction (PI) 437654, was highly effective against all populations of *H. glycines* evaluated in these experiments. Numbers of cysts (cysts and white females) per three plants 28 days after planting and final egg population densities (Pf) were lower than on other cultivars evaluated. Cultivars with SCN resistance derived from PI 90763 were moderately resistant in many of the test fields, but cultivars with Peking-derived resistance were effective at only two locations. Some cultivars with resistance derived from PI 88788 were highly to moderately resistant to races 9 or 14 of SCN, but were not consistently effective against other populations. Hartwig and Delsoy 5710 had low SCN reproductive factors (Rf = egg density at harvest/mean egg density at planting for site) of 0.16 and 0.23 compared with an Rf of 1.9 and 2.19 on the susceptible cvs. Essex and Hutcheson, respectively. In contrast, the Rf on cultivars derived from Peking generally was greater than on susceptible cultivars. Resistant cvs. Hartwig and Delsoy 5710 generally yielded more than susceptible cultivars or cultivars derived from other sources of resistance. The initial inoculum level (Pi) was negatively correlated with soybean seed yield, but cysts 28 days after planting proved to be better at predicting seed yield than Pi. Due to the genetic diversity of *H. glycines* populations with regard to the ability to parasitize resistant cultivars, cultivars with resistance derived from PI 437654 or other genotypes are needed to manage this nematode in North Carolina.

Additional keywords: damage function, host-plant resistance

Worldwide, the most damaging pathogen of soybean (*Glycine max* L.) is the soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe. This parasite is distributed throughout most soybean-growing areas in the United States, and infests a significant portion of the soybean hectarage in Brazil and Argentina (29). Significant soybean yield loss can occur in the absence of visual symptoms (28). Resistant cultivars and cultural practices are the primary means for alleviating yield losses caused by this nematode (6,8,11,14–18,24,34,35).

Cultural practices that may prevent soybean yield losses to *H. glycines* in North Carolina include rotation with nonhost crops, the use of early-maturing cultivars, planting date, and tillage method (14–18). Rotation is an effective means of managing *H. glycines*, especially when this practice is combined with other tactics (16,18). Crop rotation, however, requires sufficient suitable land for nonhost crops that can be grown profitably. Inclusion of resistant cultivars in rotation sequences can shorten the interval needed between soybean crops grown in the cropping system.

Resistant cultivars can be cost-effective in management of SCN (8,12,14,19,34). The use of SCN-resistant cultivars, however, places selection pressure on populations of *H. glycines* that may result in changes in the frequency of alleles for parasitism on resistant cultivars (30–33,35–37,39). This phenomenon has been referred to as a race shift for advisory purposes, and results in populations of *H. glycines* that can parasitize previously resistant cultivars (37,39). Because of the genetic variability of this pathogen, periodic assessments of the ability of field populations to reproduce on resistant cultivars are required (15,21,22). Spatial and temporal deployment of host-plant resistance genes to *H. glycines* have been proposed that may slow race shifts (3,4,30–33,37).

Selection of a resistant cultivar is complicated by several factors. The initial population density of SCN must exceed the damage threshold if a resistant cultivar, often with lower yield potential, is to be used. The race of SCN that is present in the field and the ability of a resistant cultivar to suppress nematode reproduction must be known. The initial race classification scheme for *H. glycines* was based on one resistant cultivar (Pickett) and three resistant plant introductions (PIs) and delineated four host races (20). Subsequently, the classification scheme was expanded to include 16 races, and a revised system of classification of *H. glycines* populations with regard to parasitism on a set of differentials has been proposed (20,22). A female index (female index [FI] = number of females on a resistant cultivar/number of females on a susceptible cultivar × 100) generally is used to describe the ability of a population to reproduce on a cultivar. Initially, cultivars were considered resistant if the FI for a race on a cultivar was less than 10% of that on a susceptible cultivar. A later proposal by Schmitt and Shannon (27) differentiates levels of resistance based on SCN reproduction or FI; with highly resistant (FI < 10), moderately resistant (FI >10 and <30) moderately susceptible (FI >30 and <60), and susceptible (FI > 60) cultivars being delineated. The validity of this approach and its usefulness in SCN management, however, have not been evaluated. Typically, cultivars are considered to be highly resistant, moderately resistant, or susceptible.

Schmitt and Barker (25) found *H. glycines* in 33% of soybean fields in the North Carolina Coastal Plain sampled in 1985 and 1986. The populations at that time were categorized as race 1 (18%), race 2 (21%), race 3 (15%), race 4 (7%), race 5 (16%), and others (23%). A later survey conducted in North Carolina during the years 1994 to 1996 indicated that as much as 60% of the soybean hectarage may be infested with *H. glycines*, and that at least 56% of the populations of SCN could be categorized as either races 2 or 4, with

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only 4% characterized as race 1; no populations of race 3 were found (15). Data from these surveys show that considerable variation occurs with respect to parasitism by this nematode on resistant cultivars, and that resistance to races 1 and 3 derived from Peking no longer would be effective in managing prevalent populations of *H. glycines* in many fields in the state.

Cv. Bedford, with resistance from both PI 88788 and Peking, was released as resistant to races 3 and 4 of SCN in 1977 (10). SCN populations that can reproduce on resistant cultivars derived from Peking but could not reproduce on Bedford now are generally considered to be either race 9 or 14 under the more recent 16-race system (22). Bedford was not used extensively in North Carolina (E. J. Dunphy, *personal communication*), but numerous cultivars with resistance derived from Bedford or its sister lines with resistance to races 3, 9, and 14 have gained acceptance in recent years. Still, these cultivars have only limited resistance to races 2 and 4, which predominate in North Carolina (15,25). Cultivars with resistance to races 9 or 14 have resistance derived from PI 88788, which also is susceptible to race 1 of *H. glycines*. Consequently, cultivars with resistance from sources other than Peking or PI 88788 would be useful in managing other races of *H. glycines.*

The only cultivars in maturity groups V or VI with resistance derived from sources other than Peking or PI 88788 are Cordell, TN5-92; Northrup King S61-89 (all with PI 90763 in their pedigree), Hartwig (Forrest × PI 437654), Delsoy 5710 (Hartwig × Hartz 5164), Anand, and Fowler (Hartwig × Holiday) (1,2,5,9,10,15,38). Hartwig generally is considered resistant to all host races of SCN in the United States, although Young and other researchers have reported populations that can reproduce on Hartwig (36,37). Soybean cultivars derived from PI 90763 or PI 437654 have not been well received by growers because of poor agronomic performance and the difficulty in identifying fields where these types of resistance could be used efficiently. Cvs. Cordell, TN5-92, and Northrup King S61-89 are no longer available to growers. Hartwig has been replaced by Delsoy 5710, but neither cultivar has good yield potential. Cvs. Fowler and Anand were evaluated in the latter portion of this research and have better yield potential than Delsoy 5710, but these cultivars do not have the full compliment of resistance genes present in Delsoy 5710 (1,2,5,38).

The effective use of resistant cultivars in cropping systems is dependent on two factors: (i) their ability to lower the population density of the nematode pathogen, and (ii) profitable yield in the presence of the nematode pathogen (23). The primary objective of this research was to evaluate the effectiveness of resistant soybean cultivars and lines in limiting reproduction of *H. glycines* field populations and determining their yield potential in infested fields in North Carolina.

MATERIALS AND METHODS

All experiments were conducted between 1992 and 1999 in fields naturally infested with the SCN (Table 1). Fields were in soybean–corn rotations prior to initiation of this study. Soybean breeders from various university experiment stations and private companies provided seed of soybean lines from maturity groups (MGs) V and VI with resistance to SCN each year (Table 2). Cvs. Essex (MG V), Hutcheson (MG V), Deltapine 105 (MG V), Young (MG VI), or Brim (MG VI) were susceptible controls. Cv. Centennial (MG VI) was used because it has resistance to races 1 and 3 of SCN, and was useful in evaluating resistance derived solely from Peking.

Cultivars were arranged in a randomized complete block design with four to six replications at each location. There were two locations each year, with the exception of 1995. Cultivars differed between years, but all lines were included at both locations within a year. Results of experiments conducted in 1996 are not included because of severe hurricane damage to plots. Conventional tillage was used at all experimental sites. All plots consisted of four rows, 6.1 m long with 0.91-m row spacing and 3.0-m alleys between plots. The center two rows of each plot were harvested with a plot combine and seed yield was adjusted to 13% moisture.

Soil samples for assays of *H. glycines* eggs and cysts were collected at planting in May or June (mean preplant population density for the field [Pi]) and at soybean harvest in October (final egg density [Pf]). Each soil sample consisted of a composite of 8 to 10 2.5-cm-diameter cores taken to a depth of 15 cm. A 500-cm^3 subsample was processed by elutriation and centrifugation (7,13). Eggs were extracted from cysts using a Ten-broeck homogenizer (Fisher Scientific, Pittsburgh, PA). Additional samples were taken by collecting three plants from each plot 28 days after planting (DAP) that were transported to the lab to count cysts and white females. Soil from these plants was removed gently by soaking in a bucket, and the number of cysts per three plants was determined in order to assess the level of resistance of each cultivar or line.

Reproductive factors (Rf) of *H. glycines* were calculated for each cultivar by dividing Pf by Pi. The mean and standard deviation for each cultivar across sites was calculated from the mean for each site. Similarly, mean yields for all locations in which the cultivar or line was included were calculated (Table 2) and relative yield was calculated by dividing the yield by the mean yield for each site. At sites where MG VI cultivars yielded significantly more ($P \leq 0.10$) than MG V cultivars, the mean for the MG was used rather than the site mean.

Statistical analysis for individual sites used the PROC GLM procedure of

Table 1. Site designation, planting date, *Heterodera glycines* races, soil type, particle size distribution, initial population density (Pi) of *H. glycines* eggs plus juveniles per 500 cm^3 of soil, and standard deviation (SD) of mean density

							Soybean cyst nematode		
Site	Location	Planting date	Soil type	Sand (%)	Silt (%)	Clay (%)	Race[a]	Mean Pi	SD
1	Hoke	20 May 1992	Fuquay sand	90	9	1	2	2,747	2,662
2	Robeson	19 May 1992	Norfolk sandy loam	87	11	2	2	5,614	4,874
3	Pitt	2 June 1993	Goldsboro sandy loam	83	14	3	2	803	956
4	Cumberland	25 May 1993	Fuquay sand	89	10	1	2	26,827	37,162
5	Pasquotank	18 May 1993	Bayboro loam	75	21	4	2	1,144	1,804
6	Tyrrel	24 May 1994	Weeksville sandy loam	71	24	5	14	804	959
7	Martin	26 May 1994	Goldsboro fine sandy loam	86	13	1	9	3,353	3,994
8	Washington	24 May 1995	Arapahoe fine sandy loam	92	7	1	2	1,719	1,906
9	Johnston	6 June 1997	Norfolk sandy loam	84	10	6	1	4,891	2,561
10	Washington	28 May 1997	Portsmouth fine sandy loam	75	21	4	14	2,296	2,138
11	Chowan	2 June 1998	Tomotley fine sandy loam	74	25	1	4	256	426
12	Washington	1 June 1998	Portsmouth fine sandy loam	76	23	1	4	1,041	1,241
13	Wilson	20 May 1999	Norfolk sandy loam	85	12	3	5	834	1,137
14	Currituck	29 June 1999	Roanoke fine sandy loam	73	23	4	2	3,138	2,790

[a] Race determined from a composite of preplant soil samples (22).

Table 2. Cultivars or lines evaluated for resistance to *Heterodera glycines* (soybean cyst nematode [SCN]), company or university program, reported resistance to SCN races, source of resistance, maturity group (MG), sites tested (Table 1), resistance rating at specific site based on number of cysts 28 days after planting (DAP), mean and standard deviation (SD) of average reproductive factor (Rf) over sites tested from 1992 to 1999, average yield over all sites tested, and relative yield

						Rating at site[a]		Rf[b]		Yield[c]	
Cultivar	Company[d]	Resistance[e]	Source[f]	MG	Sites tested	HR	MR	Mean	SD	Mean (kg/ha)	Relative
Hartwig	MO	1–16	Pk, 437	V	1–14	1-14	…	0.16	0.16	1,764	1.12
Delsoy 5500	MO	3,14	Pk, 88	V	9,10	…	…	2.86	1.49	1,437	0.82
Delsoy 5710	MO	1–16	Pk, 437, 88	V	9–14	9-14	…	0.23	0.36	1,875	1.05
Anand	MO	1,2,3,5,14	Pk, 437	V	11,12	11	…	2.24	2.63	2,303	1.00
Fowler	TN	1,2,3,5,14	Pk, 437	V	11–14	11,13,14	12	1.90	3.68	2,365	1.29
S84-1876	MO	3,14	Pk, 88	V	1–5	…	1	1.89	2.54	751	0.94
S92-1603	MO	1–6	Pk, 437	VI	8	8	…	0.19	…	2,828	1.10
Cordell	TN	1,3,5 (MR 2,14)	Pk, 88, 90	V	3–7	…	3,5,7	2.13	3.38	1,604	0.94
TN 5-92	TN	1,3,5 (MR 2,14)	Pk, 88,90	V	3–12	9,10	3,4,7,8,12	2.12	3.22	1,890	1.00
TN 5-95	TN	3,14	Pk, 88	V	8–14	…	9	2.10	2.15	1,823	0.95
A5979	Asgrow	3,4	Pk, 88	V	1–8	6	1	1.84	0.90	1,481	0.93
A5843	Asgrow	3,14	Pk, 88	V	6–14	6,10,11	…	2.48	3.09	2,004	1.01
A5848	Asgrow	1,3, 14 (MR 2)	Pk, 88	V	9–14	10,11	12	1.99	2.00	1,917	1.07
A5545	Asgrow	3	Pk	V	6,7	…	6	1.03	0.04	1,935	0.88
A5547	Asgrow	3,14	Pk, 88	V	8–10	10	…	1.47	0.85	2,086	1.04
Dp 415	Deltapine	1,3	Pk	V	1–5	…	…	1.62	0.75	843	0.76
Dp 3519	Deltapine	3,9,14	Pk, 88	V	8–14	…	9,10	2.87	3.58	1,869	0.95
Dp 3571	Deltapine	3,14	Pk, 88	V	8	…	…	1.57	…	2,739	1.06
Dp 3588	Deltapine	3	Pk, 88	V	9,10	…	9	4.47	5.00	1,790	1.03
Dp 5354	Deltapine	3	88	V	11,12	…	11	5.35	6.57	2,061	0.90
DPX4090	Deltapine	ND	NA	V	3–5	…	…	1.18	0.63	1,169	0.74
H5164	Hartz	3,9,14	Pk, 88	V	1–8	…	1,6	1.84	0.97	1,459	0.95
H5164RR	Hartz	3,9,14	Pk, 88	V	9,10	…	9,10	3.29	3.90	1,749	1.01
H5566	Hartz	3,9,14	Pk, 88	V	6–8	…	6	3.05	1.27	2,237	1.02
Hartz 5350	Hartz	3,14	88	V	8–10	…	9,10	2.06	1.99	1,807	0.86
S57-11	Syngenta	3 (MR 14)	Pk, 88	V	6,7,9–14	6	7,10	2.28	2.26	1,890	1.00
S59-95	Syngenta	3,4	Pk, 88	V	8	…	…	2.97	…	2,951	1.14
S57-A4	Syngenta	3,9,14	88	V	13,14	…	…	1.70	1.78	1,334	1.00
x9851	Syngenta	ND	NA	V	11,12	…	12	6.74	9.44	2,399	1.07
x9855	Syngenta	ND	NA	V	11,12	…	…	6.47	7.97	2,297	0.99
x 9955	Syngenta	ND	NA	V	13,14	…	…	1.43	1.08	1,296	0.96
9521	Pioneer	3,14	NA	V	3–5	…	…	0.66	0.30	1,247	0.80
96B01	Pioneer	3,14	Pk, 88	VI	13,14	…	…	0.99	0.87	1,335	0.95
Robin 5	Riverside	3,5,9	NA	V	11,12	…	…	10.07	13.02	1,978	0.84
Essex	VA	S	…	V	1–7	…	…	1.90	1.74	924	0.67
Hutcheson	VA	S	…	V	3–14	…	…	2.19	1.58	1,518	0.83
DP105	Deltapine	S	…	V	1–7	…	…	2.64	2.27	1,317	0.98
DP566	Deltapine	S	…	VI	1,2	…	…	2.30	1.66	388	0.71
Centennial	TN	1,3	Pk	VI	1–14	9	…	5.47	6.28	1,668	0.91
NC 93-54	NC	3,14	Pk, 88	V	11,12	…	11	4.26	5.76	2,185	0.96
NC 96-223	NC	3,14	Pk, 88	V	13,14	13	…	0.73	0.89	1,283	0.92
A6711	Asgrow	3	Pk	VI	6,7	…	…	5.17	4.30	2,363	1.09
DP726	Deltapine	1,3	Pk	VI	8	…	…	3.03	…	2,380	0.92
DP6200RR	Deltapine	3 (MR 14)	Pk, 88	VI	11–14	…	…	9.44	15.13	1,897	1.03
DP3640	Deltapine	3,9 (MR 14)	Pk, 88	VI	9–14	9	14	7.02	11.98	2,064	1.10
DP3681	Deltapine	1,3	Pk	VI	9–12	…	9,10	11.15	15.83	2,228	1.01
DPX6-4821	Deltapine	ND	NA	VI	8	…	…	4.97	…	2,665	1.03
H 6104	Hartz	3	Pk	VI	9,10	9	10	2.38	3.30	2,415	1.15
HX 613219	Hartz	ND	NA	VI	6,7	…	…	5.24	5.34	2,002	0.92
HX 615389	Hartz	ND	NA	VI	8	…	…	2.34	…	2,787	1.08
S61-89	Syngenta	3,4,5	Pk, 90	VI	1–8	…	1,4	1.85	0.90	1,609	0.91
S62-62	Syngenta	3,4	Pk, 88	VI	9,10	10	…	2.00	1.83	1,596	0.79
S62-66	Syngenta	3,4	Pk, 88	VI	1–8	1,6	4,7	1.99	1.17	1,546	0.99
S66-90	Syngenta	3,4	Pk, 88	VI	6–8	…	6	1.90	0.20	2,395	1.01
S65-50	Syngenta	3,9 (MR 14)	Pk, 88	VI	9–14	…	10,11,12	4.40	5.39	2,085	1.08
S60-E4	Syngenta	3,14	Pk, 88	VI	9,10	…	10	2.99	2.82	1,817	0.89
Brim	NC	S	…	VI	3–7	…	…	3.47	2.35	1,856	0.93
Young	NC	S	…	VI	1–14	…	…	3.37	3.49	1,695	0.99

[a] Resistance rating is based on (number of cysts on roots of three plants 28 DA/number of cysts on susceptible cultivars 28 DAP) × 100. Highly resistant (HR) is defined as <10 and moderately resistant (MR) as >10 and <30 (27).

[b] Reproductive factor (Rf) = mean egg density at harvest/mean preplant density for site.

[c] Mean yields for all locations in which the cultivar or line was included, and relative yield was calculated by dividing the yield by the mean yield for each site. At sites where MG VI cultivars yielded more ($P \leq 0.10$) than MG V cultivars, the mean for the MG was used rather than the site mean.

[d] MO = University of Missouri Agricultural Experiment Station, NC = North Carolina Agricultural Experiment Station, TN = University of Tennessee Agricultural Experiment Station, VA = Virginia Polytechnical Agricultural Experiment Station. Syngenta is used for companies formerly known as Novartis, and Northrup King.

[e] Specific resistance to races of *H. glycines* as reported by companies, soybean breeders, or university experiment stations (10). Cultivars listed as resistant to races 3 and 4 are likely resistant to races 3, 9, or 14 according to a later classification system (22). ND indicates not determined and S indicates susceptible.

[f] Resistance source: Pk = Peking, 88 = plant introduction (PI) 88788, 90 = PI 90763, 437 = PI 437654, and NA = not available.

PC/SAS software (SAS Institute, Cary, NC) for a randomized complete block design for each year and location, because locations and years differed (Table 3). Orthogonal contrasts were used to evaluate the effects of MG. Based on 28-DAP samples (cysts and white females), cultivars were considered to be highly resistant if the number of cysts on a cultivar was less than 10% of the mean on susceptible cultivars, moderately resistant if the number of cysts was >10% but <30% of those found on susceptible cultivars, and susceptible if the number of cysts was >30% (27). Orthogonal contrasts were used to separate differences between highly resistant, moderately resistant, and susceptible cultivars. Nematode numbers were transformed ($\log_{10}$ [x + 1]) to normalize variances. Untransformed data are presented in tables for clarity. Regression models were developed using the PROC MIXED procedure of PC/SAS with year and location nested in year as random variables. A stepwise procedure eliminating terms that were not significant ($P \leq 0.05$) was used to simplify the model and discriminate between quadratic versus linear models. Approximate 99% confidence limits were estimated from this procedure.

RESULTS

Analyses across all locations. Reproductive factors on cultivars or lines derived from PI 437654 (Hartwig, Delsoy 5710, and S92-1603) were 0.16, 0.23, and 0.19, respectively (Table 2). In comparison, the average Rf for susceptible MG V cvs. Essex, Hutcheson, and DP 105 were 1.90, 2.19, and 2.64, respectively, or approximately 10-fold greater. Susceptible MG VI cultivars generally had greater Rf values than susceptible MG V cultivars (Table 3). Population densities of *H. glycines* generally were higher at soybean harvest than at soybean planting on susceptible cultivars or lines at most locations (Table 4). Final population densities did not increase over initial populations on susceptible cultivars at the Robeson County site in 1992 and the Cumberland County site in 1993, because of extensive damage to soybean due to high initial population density, resulting in severe stunting of soybean (Tables 1 and 4). Final SCN population development also was limited at three sites (Pasquotank County in 1993 and Currituck and Wilson counties in 1999) because of saturated soils in the latter portions of the growing season. A linear model best described the relationship ($P \leq 0.0001$) between the number of cysts on a cultivar 28 DAP with *H. glycines* Rf, but a quadratic model adequately ($P \leq 0.0001$) described the relationship between cysts 28 DAP and the final egg population density/500 cm^3 of soil (Figs. 1 and 2).

Highly resistant cultivars yielded more ($P \leq 0.10$) than susceptible cultivars at 64% of the sites evaluated, and moderately resistant cultivars yielded more ($P \leq 0.10$) than susceptible cultivars at 36% of the locations. MG VI cultivars yielded more ($P \leq 0.10$) than MG V cultivars at 7 of the 14 sites (Table 5). MG V cultivars out yielded MG VI soybean cultivars only at the Currituck location in 1999. Soybean seed yield was related ($P \leq 0.0001$) to the number of cysts per three plants 28 DAP by a linear relationship (Fig. 3). Although preliminary analysis indicated that the pre-plant number of *H. glycines* eggs/500 cm^3 of soil was negatively related to soybean yield, further analysis with PROC MIXED of SAS with locations and years as random factors showed that Pi was not a significant factor in determining yield when the variable cysts 28 DAP was included in the model (Table 3).

Table 3. Partial analysis of variance main effects on mean values for each soybean cultivar or line at a location in experiments performed in 1992 to 1999

			F value[a]		
Source	**DF**	**Rf[b]**	**Pf[b]**	**Yield**
Year	6	17.71**	29.02**	171.95**
Location (year)	7	33.95**	15.80**	71.21**
Maturity group	1	19.70**	52.0**	17.33**
Pi	1	0.58	0.14	1.49
Cysts 28 DAP[c]	1	19.70**	255.37**	39.82**

[a] Values followed by ** are significant at $P \leq 0.01$. Rf is the reproductive factor (Rf = mean egg density at harvest/initial inoculum level for site), Pf is the final egg population density per 500 cm^3 of soil, and yield is soybean seed yield (kg/ha).
[b] Analysis performed on transformed values ($\log_{10} X + 1$).
[c] DAP = days after planting.

Table 4. Number of cultivars per resistance class (resistance class based on cysts 28 days after planting [DAP]), population densities of *Heterodera glycines*, mean number of cysts per three plants 28 DAP, number of eggs per 500 cm^3 of soil at soybean harvest (Pf), and orthogonal contrasts (OC) for comparisons at 28 DAP, based on resistance class at 14 sites from 1992 to 1995 and 1997 to 1999 in North Carolina

								***P* value**						***P* value**		
		Class[a]			**Mean no. cysts**			**OC for cysts**			**Mean Pf for class**			**OC for Pf**		
Year, site	**County**	**HR**	**MR**	**S**	**HR**	**MR**	**S**	**HR vs MR**	**HR vs S**	**MR vs S**	**HR**	**MR**	**S**	**HR vs MR**	**HR vs S**	**MR vs S**
1992																
1	Hoke	2	4	6	20	53	238	0.01	0.01	0.01	3,066	3,008	8,005	0.84	0.01	0.01
2	Robeson	1	0	11	6	…	419	…	0.01	…	900	…	4,796	…	0.01	…
1993																
3	Pitt	1	2	14	7	14	75	0.62	0.02	0.06	433	4,883	6,002	0.92	0.03	0.54
4	Cumberland	1	4	12	0	24	102	0.51	0.01	0.01	2,733	9,825	12,623	0.10	0.01	0.08
5	Pasquotank	1	1	15	0	1	9	0.12	0.15	0.45	200	66	1,481	0.86	0.09	0.04
1994																
6	Tyrrel	5	5	10	8	34	106	0.09	0.01	0.01	1,250	3,550	4,993	0.03	0.01	0.11
7	Martin	1	4	15	2.0	20	68	0.60	0.01	0.04	200	4,633	6,345	0.05	0.01	0.13
1995																
8	Washington	2	1	19	0.25	15	46	0.38	0.01	0.03	529	1,675	5,070	0.72	0.05	0.22
1997																
9	Johnston	6	7	9	0.41	8.3	21	0.04	0.01	0.01	483	3,328	6,342	0.01	0.01	0.01
10	Washington	7	10	5	1.97	14.9	50.4	0.02	0.01	0.01	3,242	8,123	8,520	0.01	0.01	0.71
1998																
11	Chowan	4	6	12	1.50	6.5	23.7	0.01	0.01	0.01	812	2,593	4,861	0.01	0.01	0.03
12	Washington	2	4	16	3.0	17.2	59.2	0.38	0.01	0.01	276	1,406	1,120	0.02	0.05	0.35
1999																
13	Wilson	4	4	10	1.4	22.4	75.0	0.01	0.01	0.22	319	1,320	1,875	0.01	0.01	0.22
14	Currituck	3	0	15	0.23	…	53.7	…	0.01	…	33	…	1,211	…	0.01	…

[a] Number of cultivars in class. Density classes are based on cyst numbers at 28 DAP; resistance rating is based on (number of cysts on roots of plants 28 DAP/number of cysts on susceptible cultivars 28 DAP) × 100. Highly resistant (HR) is defined as <10 and moderately resistant as >10 and <30 (27).

Reproduction of *H. glycines* and impact on soybean yield in Hoke and Robeson counties, 1992. Cvs. Hartwig and S62-66 were highly resistant at the Hoke County site, whereas four cultivars were moderately resistant at this location (A5979, S84-1876, H5164, and S61-89), based on samples taken 28 DAP. Highly resistant cultivars differed from moderately resistant cultivars in numbers of cysts at 28 DAP, and moderately resistant cultivars differed from susceptible cultivars ($P \leq 0.01$; Table 4). Highly resistant and moderately resistant cultivars had lower numbers of *H. glycines* eggs at soybean harvest at this location ($P \leq 0.01$), but highly resistant cultivars did not have lower egg population densities than moderately resistant cultivars. Soybean seed yield of highly resistant (Hartwig and S62-66), and moderately resistant (A5979, S84-1876, H5164, and S61-89) cultivars were greater ($P \leq 0.10$) than susceptible cultivars at the Hoke County location. Yields of highly resistant and moderately resistant cultivars did not differ at this location.

The only cultivar resistant to the race 4 population at the Robeson County site was Hartwig, which had lower numbers of cysts 28 DAP, and a lower ($P \leq 0.01$) final population density than the mean for all other cultivars evaluated. Centennial and DP 415 with resistance to SCN races 1 and 3 did not have lower numbers of cysts 28 DAP or final population density than susceptible cultivars (*data not included*). Hartwig, the only resistant cultivar at this location, yielded more than susceptible cultivars ($P \leq 0.10$).

Reproduction of *H. glycines* and impact on soybean yield in Cumberland, Pasquotank, and Pitt counties, 1993. Only Hartwig was highly resistant to the race 2 populations of SCN present at the three locations used in 1993. Hartwig differed ($P \leq 0.02$) in numbers of cysts 28 DAP from susceptible cultivars at both the Cumberland and Pitt County sites. Cyst numbers at 28 DAP for moderately resistant cultivars were not different from Hartwig at the Cumberland or Pitt sites, but cyst numbers for both highly and moderately resistant cultivars were lower than on susceptible cultivars at theses locations ($P \leq 0.10$). Cultivars S61-89, S62-62, Cordell, and TN5-92 were moderately resistant to SCN at the Cumberland County site, but only Cordell and TN5-92 were moderately resistant at the Pitt County site. TN5-92 was moderately resistant compared with susceptible cultivars at the Pasquotank County site in 1993. Highly resistant cv. Hartwig was effective in limiting the final population density of *H. glycines* eggs at all three locations ($P \leq 0.10$) compared with susceptible cultivars. Moderately resistant cultivars had lower ($P \leq 0.10$) levels of SCN eggs at harvest than susceptible cultivars at the Pitt and Cumberland County sites, but not at the Pasquotank County site. The lack of difference between final population densities at the Pasquotank County site is probably because of generally low *H. glycines* reproduction at this location, possibly a result of excessive rainfall.

Highly and moderately resistant cultivars yielded more ($P \leq 0.01$) than susceptible cultivars at the Cumberland County location, but moderately and highly resistant cultivars did not differ in yield ($P \leq 0.10$). Moderately resistant cvs. Cordell and TN5-92 had greater yields than highly resistant cv. Hartwig or the susceptible cultivars ($P \leq 0.07$ and 0.05, respectively) at the Pitt County site, and cultivars did not differ with respect to soybean yield at the Pasquotank County site.

Reproduction of *H. glycines* and impact on soybean yield in Martin and Tyrell counties 1994. Hartwig, A5979, A5843, S57-11, and S62-66 all were highly resistant to the SCN race 14 population at the Tyrell County site compared with susceptible cultivars. Five cultivars (A5545, H5164, H5566, S66-90, and S61-89) were moderately resistant, and had lower ($P \leq 0.01$) numbers of cysts 28 DAP than susceptible cultivars. The number of cysts 28 DAP was lower ($P \leq 0.09$)

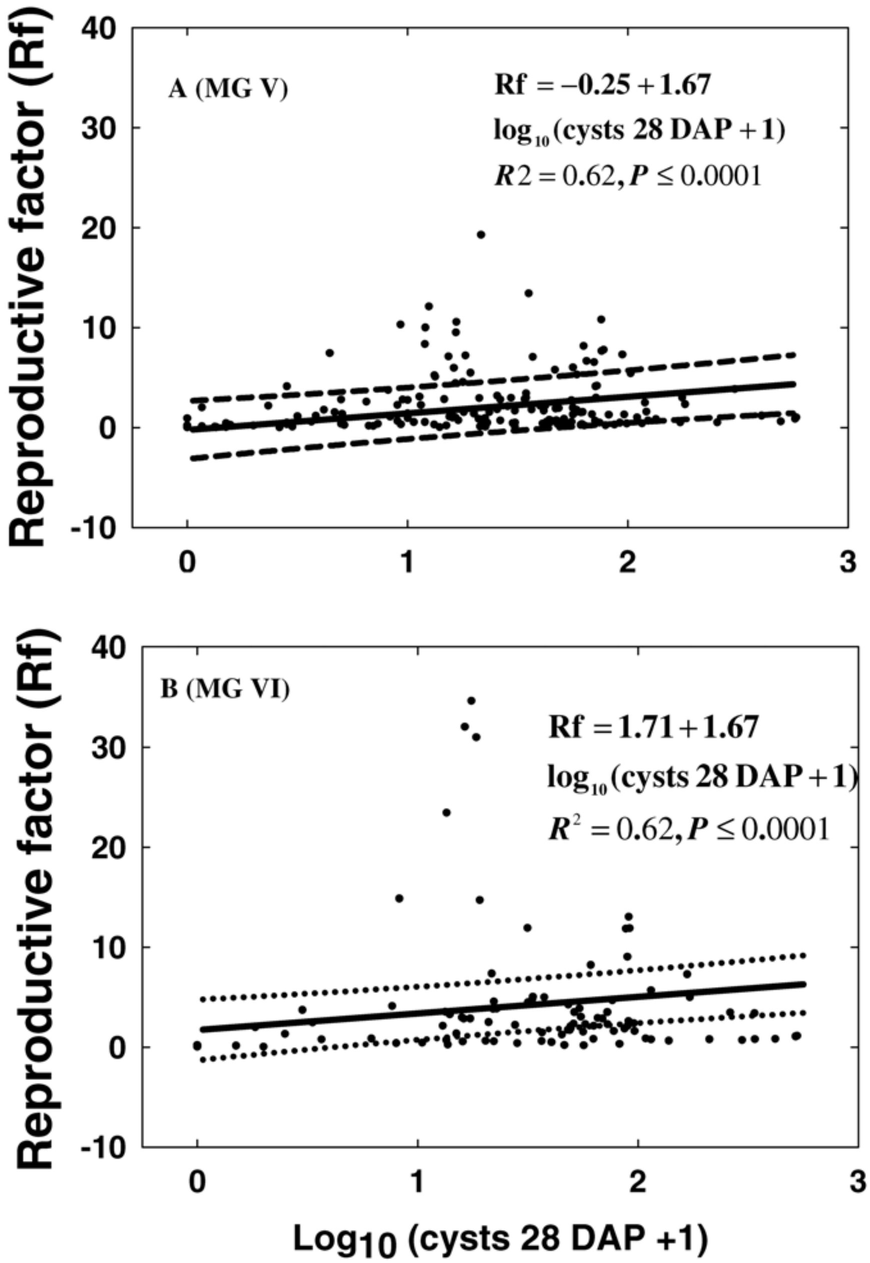

Fig. 1. Relationship of the reproductive factor (Rf = mean egg density at harvest/mean preplant density for site) to the number of *Heterodera glycines* cysts per three plants at 28 days after planting (DAP). Each data point is the mean of six observations per cultivar at each location from 1992 to 1999. Solid line is predicted response and dotted lines are the approximate 99% confidence intervals from the PROC MIXED procedure of SAS. Responses differed ($P \leq 0.0001$) by maturity group (MG); thus, data are reported separately for **A,** MG V and **B,** MG VI. R^2 value is for regression analysis, including both MGs as qualitative variables.

on highly resistant than on moderately resistant cultivars at the Tyrrell County location, and highly resistant cultivars had lower end-of-season egg densities than either moderately resistant or susceptible cultivars ($P \leq 0.03$ and 0.01, respectively) at the end of the season. Final population densities did not differ between moderately resistant and susceptible cultivars. Highly and moderately resistant cultivars yielded more ($P \leq 0.01$) than susceptible cultivars, and highly resistant cultivars yielded more than moderately resistant cultivars ($P \leq 0.04$) at the Tyrell County site. MG did not influence yield at this location.

Only Hartwig was highly resistant to the race 9 SCN population at the Martin County site, whereas five cultivars (A5979, Cordell, TN5-92, N57-11, and S62-66) were moderately resistant. Moderately resistant cultivars did not differ from Hartwig in numbers of cysts 28 DAP, and final egg density of *H. glycines* on the highly resistant Hartwig was less than on moderately resistant or susceptible cultivars ($P \leq 0.05$ and 0.01, respectively). Moderately resistant cultivars did not differ from susceptible cultivars at the Martin County location for Pf. Hartwig yielded more ($P \leq 0.01$) than either moderately resistant cultivars or susceptible cultivars at the Martin County site. Yield of moderately resistant and susceptible cultivars did not differ ($P \leq 0.10$) because four of the five moderately resistant cultivars were in MG V, and MG VI cultivars yielded more ($P \leq 0.01$) than MG V cultivars in the Martin County experiment.

Reproduction of *H. glycines* and impact on soybean yield in Washington County, 1995. One experimental site in 1995 located in Washington County, NC, was infested with race 2 of *H. glycines*. Cv. Hartwig and line S92-1603 were highly resistant, and TN5-92 was moderately resistant to this population. The number of cysts 28 DAP was greater ($P \leq 0.01$ and 0.03) on susceptible cultivars than on either highly or moderately resistant cultivars or lines, respectively, but differences between highly and moderately resistant cultivars ($P = 0.10$) were not observed. Hartwig and S92-1603 had lower ($P = 0.05$) *H. glycines* reproduction at season's end than susceptible cultivars, but SCN reproduction on the moderately resistant TN5-92 did not differ from that on susceptible cultivars. Yields of highly or moderately resistant cultivars did not differ ($P \leq 0.10$) from susceptible cultivars, because MG VI cultivars, all of which were susceptible, yielded more at this location.

Reproduction of *H. glycines* and impact on soybean yield in Johnston and Washington counties, 1997. The population at the Johnston County site was classified as *H. glycines* race 1. Cultivars that were highly resistant to this population included Hartwig, Delsoy 5710, TN5-92, H6104, H5164RR, and DP 3640 based on 28 DAP cyst numbers. Seven cultivars (DP 3519, DP 3588, DP 3681, H5164RR, H5350, S62-62, and TN5-95) were moderately resistant to SCN race 1 at this location. Highly resistant, moderately resistant, and susceptible cultivars differed ($P \leq 0.04$) in numbers of cysts 28 DAP and final population density of nematodes ($P \leq 0.01$). Highly resistant cultivars yielded more ($P \leq 0.01$) than moderately resistant or susceptible cultivars, but the yield of moderately resistant cultivars did not differ from susceptible cultivars. The higher ($P \leq 0.01$) yield of MG VI compared with MG V cultivars accounts for the lack of difference between susceptible cultivars and moderately resistant cultivars because five of the seven moderately resistant cultivars were in MG V.

Hartwig, Delsoy 5710, A5843, A5848, A5547, S62-62, and TN5-92 were highly resistant to *H. glycines* race 14 at the Washington County site. Moderately resistant cultivars included Delsoy 5500, DP 3519, DP 3681, H6104, H5164, H5350,

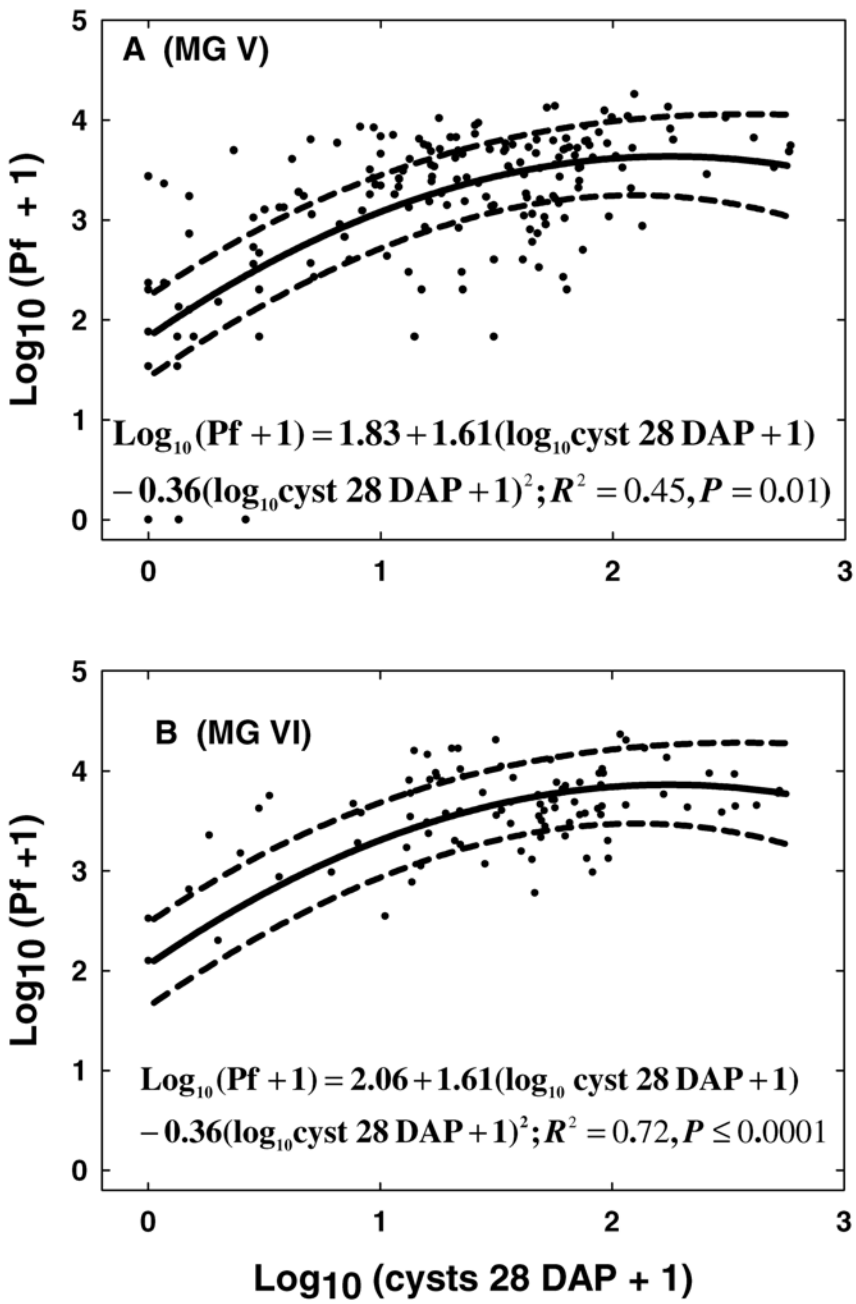

Fig. 2. Influence of the number of *Heterodera glycines* cysts per three plants at 28 days after planting (DAP) on final egg population density (Pf) of *H. glycines* per 500 cm^3 of soil. Each data point is the mean of six observations per cultivar at each location from 1992 to 1999. Solid line is predicted response and dotted lines are the approximate 99% confidence intervals from the PROC MIXED procedure of SAS. Responses differed ($P \leq 0.0001$) by maturity group (MG); thus, data are reported separately for **A,** MG V and **B,** MG VI. R^2 value is for regression analysis, including both MGs as qualitative variables.

TN5-95, S57-11, S65-50, and S60-E4. Highly resistant, moderately resistant, and susceptible cultivars differed ($P \leq 0.02$) in numbers of cysts 28 DAP. Highly resistant cultivars had lower ($P \leq 0.01$) SCN numbers at harvest than moderately resistant or susceptible cultivars, but final egg density for moderately resistant cultivars did not differ from susceptible cultivars. Highly resistant cultivars had greater ($P \leq 0.01$) yields than did moderately resistant or susceptible cultivars at this site, and yield did not differ between moderately resistant and susceptible cultivars.

Reproduction of *H. glycines* and impact on soybean yield in Chowan and Washington counties, 1998. Initial populations of SCN were relatively low at both locations in 1998. Hartwig, Delsoy 5710, Fowler, and Anand were highly resistant to the SCN race 4 population at the Chowan County site, whereas N93-54, A5343, A5348, DP 5554, S65-60, and x9855 were moderately resistant. Highly resistant, moderately resistant, and susceptible cultivars and lines differed in number of cysts 28 DAP ($P \leq 0.01$) and final egg population density at soybean harvest ($P \leq 0.03$). Soybean seed yield of highly resistant, moderately resistant, and susceptible cultivars and lines did not differ ($P \leq 0.10$), because of the low initial inoculum density at this location.

Cultivars highly resistant to the race 4 population at the Washington, County site were Hartwig and Delsoy 5710, and moderately resistant cultivars included A5848, Fowler, S65-50, and TN5-92. Highly resistant and moderately resistant cultivars did not differ in numbers of cysts at 28 DAP, but had lower ($P \leq 0.01$) numbers of cysts than susceptible cultivars. Highly resistant cultivars had lower ($P \leq 0.05$) numbers of SCN eggs at soybean harvest than susceptible cultivars, but egg numbers from plots with susceptible cultivars were not different from moderately resistant cultivars. Moderately resistant cultivars yielded more ($P \leq 0.10$) than highly resistant and susceptible cultivars, and there was no difference ($P \leq 0.10$) in yields of susceptible and highly resistant cultivars.

Reproduction of *H. glycines* and impact on soybean yield in Currituck and Wilson counties, 1999. Hartwig, Delsoy 5710, and Fowler were highly resistant to the race 2 population at the Currituck County site, and no cultivars were moderately resistant. The number of cysts at 28 DAP and Pf was lower ($P \leq 0.01$) on highly resistant cultivars than on susceptible cultivars. The three highly resistant cultivars yielded marginally more ($P \leq 0.06$) than susceptible cultivars at this location. The higher yield of the resistant cultivars may be due to the very late planting date at this site. This was the only experiment in which MG V cultivars yielded more ($P \leq 0.02$) than MG VI cultivars; all resistant cultivars were in MG V.

Four cultivars (Hartwig, Delsoy 5710, Fowler, and N96-223) were highly resistant and four were moderately resistant (Centennial, DP 3640, NK 57-11, and TN5-95) to the race 5 population at the Wilson County site. Both highly and moderately resistant cultivars had lower ($P \leq 0.01$) numbers of cysts on roots at 28 DAP than susceptible cultivars. Highly resistant cultivars limited SCN final egg densities compared with moderately resistant cultivars and susceptible cultivars ($P \leq 0.01$), but moderately resistant cultivars did not differ from susceptible cultivars. Highly resistant cultivars yielded more ($P \leq 0.01$) than moderately resistant or susceptible cultivars, and the yield of moderately resistant and susceptible cultivars did not differ. Cultivars in MG VI yielded more than MG V cultivars at this location.

DISCUSSION

Significant reproduction of *H. glycines* occurred on most resistant and susceptible cultivars or lines, except those with resistance genes derived from PI 437654 (Hartwig, Delsoy 5710, S92-1603, Fowler, and Anand). The greater Rf values and final SCN density of MG VI cultivars compared with MG V cultivars was not surprising because the tendency for later-maturing cultivars to have higher final *H. glycines* population densities has been documented in other research (16,17,24). Cultivars in both MG V and VI with resistance derived only from Peking often had higher Rf values than susceptible cultivars. The highest Rf values in MG VI cultivars, including Centennial (used in all experiments), A6711, DP726, DP3681, and DP6200RR (Rf = 5.47, 5.17, 3.03, 11.15, and 9.44 respectively), generally were associated

Table 5. Yield (kg/ha) of soybean cultivars highly resistant (HR), moderately resistant (MR), or susceptible (S) to populations of *Heterodera glycines*, orthogonal contrasts (OC) for comparisons of yield by resistance class, and mean yield and OC for cultivars by maturity group (MG) at 14 sites in North Carolina from 1992 to 1995 and 1997 to 1999

								***P* value**					***P* value**
		No. per class[a]			**Yield (kg/ha)**			**OC for yield**			**Yield mean (no.)[b]**		**OC for MG**
Year, site	**County**	**HR**	**MR**	**S**	**HR**	**MR**	**S**	**HR vs MR**	**MR vs S**	**HR vs S**	**MG V**	**MG VI**	**V vs VI**
1992													
1	Hoke	2	4	6	863	744	545	0.14	0.09	0.01	657 (6)	791 (6)	0.01
2	Robeson	1	0	11	497	…	249	…	…	0.01	278 (6)	260 (6)	0.64
1993													
3	Pitt	1	2	14	940	1,298	993	0.07	0.05	0.78	1,057 (11)	1,148 (6)	0.10
4	Cumberland	1	4	12	1,312	1,163	704	0.11	0.01	0.01	1,695 (11)	1,890 (6)	0.06
5	Pasquotank	1	1	15	2,184	2,054	2,151	0.88	0.81	0.16	1,961 (11)	2,557 (6)	0.01
1994													
6	Tyrrel	5	5	10	2,943	2,736	2,298	0.04	0.01	0.01	2,611 (13)	2,671 (7)	0.45
7	Martin	1	4	15	2,047	1,408	1,538	0.01	0.19	0.01	1,405 (13)	1,727 (7)	0.01
1995													
8	Washington	2	1	19	2,624	2,429	2,586	0.48	0.50	0.34 (13)	2,577 (13)	2,587 (9)	0.93
1997													
9	Johnston	6	7	9	2,180	1,750	1,747	0.01	0.98	0.01	1,654 (16)	2,323 (6)	0.01
10	Washington	7	10	5	2,033	1,803	1,425	0.01	0.32	0.01	1,841 (16)	1,887 (6)	0.48
1998													
11	Chowan	4	6	12	3,112	2,770	2,607	0.53	0.49	0.15	2,759 (16)	2,702 (6)	0.75
12	Washington	2	4	16	1,733	1,975	1,788	0.07	0.08	0.70	1,795 (16)	1,958 (6)	0.15
1999													
13	Wilson	4	4	10	1,907	1,631	1,533	0.01	0.25	0.01	1,588 (12)	1,739 (6)	0.02
14	Currituck	3	0	15	1,228	…	1,150	…	…	0.06	1,136 (12)	1,031 (6)	0.02

[a] Number of cultivars in class. Density classes are based on cyst numbers at 28 days after planting (DAP); resistance rating is based on (number of cysts on roots of plants 28 DAP/number of cysts on susceptible cultivars 28 DAP) × 100. Highly resistant (HR) is defined as <10 and moderately resistant as >10 and <30 (27).

[b] Number in parenthesis is number of cultivars in MG.

with defeated resistance genes derived from Peking. Higher levels of reproduction on cultivars with defeated resistance has been demonstrated by other researchers (12). Although cultivars with resistance derived from Peking and PI 88788 (resistance to races 3, 9, or 14) were highly or moderately resistant at some locations, some *H. glycines* reproduction generally occurred on these, and final *H. glycines* population densities frequently were equal to or greater than that on susceptible cultivars.

Reproduction of *H. glycines* based on the number of cysts 28 DAP or final population density of *H. glycines* on Delsoy 5710 did not differ from Hartwig in any of the five experiments where both were tested. These data indicate that Delsoy 5710 has the same compliment of SCN-resistant genes as Hartwig. Fowler, which is derived from Hartwig, was highly resistant at three of the four sites in which it was tested, but was only moderately resistant at one site. Anand, which also is derived from Hartwig, was highly resistant at one site tested but not at a second site. The cultivars with resistance from PI 90763 (Cordell, TN5-92, and NK S61-89) were moderately resistant to populations in many of the fields where they were tested. The most extensively tested of the PI 90763-derived cultivars, TN5-92, was either highly or moderately resistant to *H. glycines* in 7 of 10 fields in which it was tested.

Most SCN-resistant cultivars are marketed as resistant to race 3; race 3 and 14; race 3 and 9; or races 3, 9, and 14. Although the majority of the cultivars or lines evaluated in this research were derived from PI 88788, this resistance generally was not effective in minimizing *H. glycines* reproduction in North Carolina production fields. Only highly resistant cultivars such as Hartwig, Delsoy 5710, Fowler, and possibly Anand will accomplish the dual requirements for the use of a resistant cultivar: acceptable yield in the presence of SCN, and suppression or reduction in levels of SCN such that a susceptible crop can be included in the rotation. Unfortunately, Hartwig and Delsoy 5710 have not been widely accepted by growers because of limited yield potential (14). Fowler and Anand have better yield, but currently are little used because they are not glyphosate resistant (E. J. Dunphy *personal communication*). Additionally, because Anand and Fowler do not include the full compliment of resistance genes present in Hartwig, the durability of these resistant cultivars may be limited (1,5,38).

Cultivars in MG VI yielded more ($P \leq 0.10$) than MG V cultivars at 7 of the 14 locations used in this research, whereas MG V cultivars yielded more than MG VI cultivars only in 1999 at the Currituck County site. Nevertheless, MG V cultivars with resistance derived from PI 437654 (Delsoy 5710, Hartwig, Anand, and Fowler) all had relative yields of 1.00 or greater. Cultivars with resistance derived from PI 90763 (Cordell, TN5-92, and S61-89) had relative yields less than 1 except that the relative yield of TN5-92 was equal to 1.

There was considerable variation in the ability of SCN populations to parasitize cultivars with resistance derived from Peking and PI 88788. At several sites where the population was categorized as race 2, 4, or 5, some cultivars purportedly resistant to races 3, 9, or 14 were moderately to highly resistant, whereas other cultivars with the same putative resistance were susceptible. These data indicate that different genes for resistance may be present in various cultivars derived from PI 88788 and Peking. Some discrepancies in cultivar resistance probably are related to differences in populations used in screening resistant cultivars. As a result of founder effects and genetic drift in greenhouse-maintained populations, considerable variation in the virulence of greenhouse populations may occur. A new system for classification of *H. glycines* populations has been proposed, and may rectify this situation (20). The proposed system, however, still relies on the use of a series of plant introductions to delineate "*Hetero-*

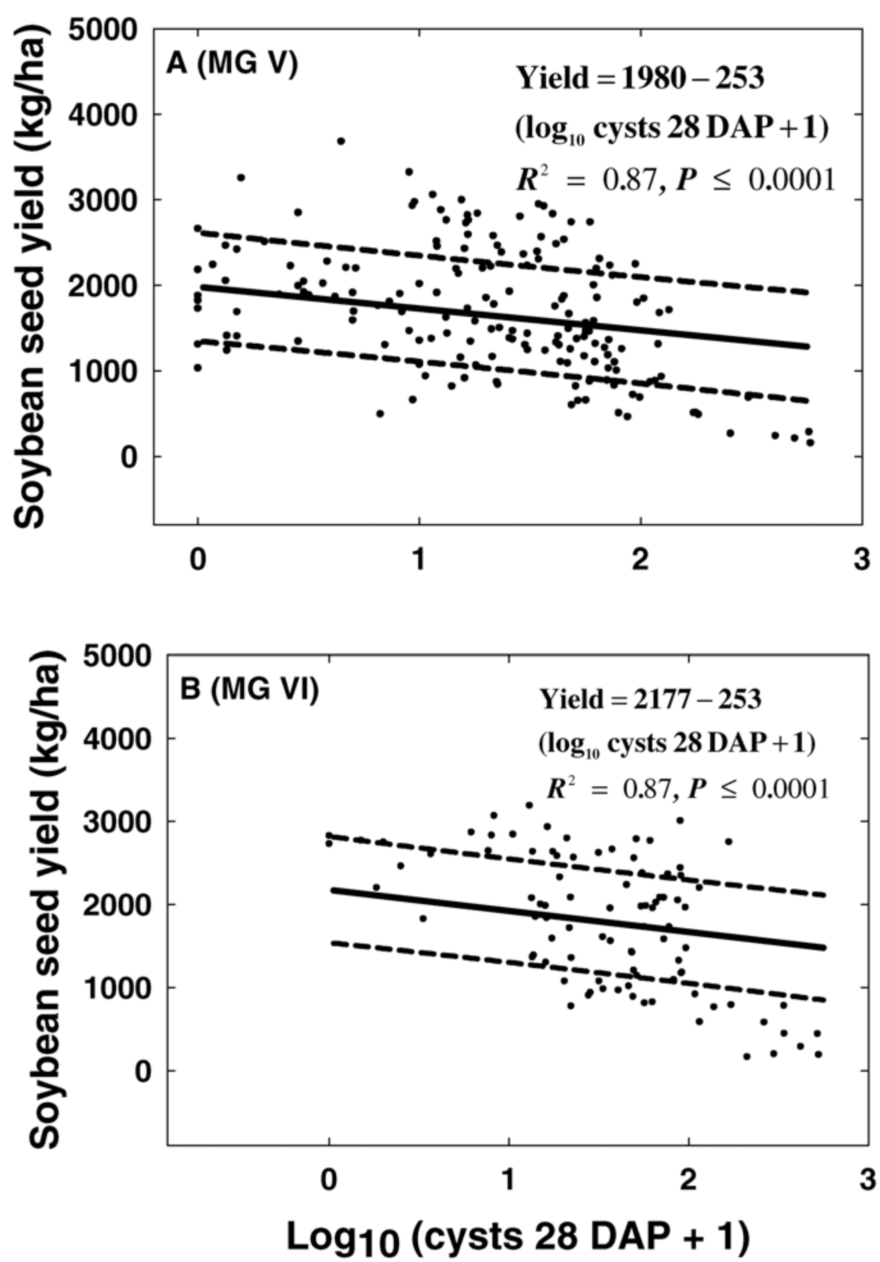

Fig. 3. Influence *Heterodera glycines* cysts per three plants (transformed $\log_{10}$ [mean preplant population density for the field (Pi) + 1]) at 28 days after planting (DAP) on soybean seed yield. Each data point is the mean of four to six observations per cultivar at each location from 1992 to 1999. Solid line is predicted response and dotted lines are the 99% confidence level. Responses differed ($P \leq 0.0001$) by maturity group (MG); thus, data are reported separately for **A,** MG V and **B,** MG VI. R^2 value is for regression analysis, including both MGs as qualitative variables.

dera glycines (HG) type". The HG type may not adequately discriminate between the ability of diverse SCN populations to reproduce on resistant cultivars derived from several resistant sources or that may not contain all genes for resistance contained in the parent PI.

The research in this article contrasts greatly from research conducted in Minnesota (8), where the majority of the cultivars were resistant to SCN field populations. There was an obvious advantage to using resistant cultivars in Minnesota, whereas the diversity of SCN populations in North Carolina indicates that the use of resistant cultivars is of minimal value except where the race has been identified and highly resistant cultivars with resistance derived from sources other than PI 88788 and Peking are available. A recent study conducted in Missouri concluded that most populations of SCN in that state were able to reproduce on PI 88788 and Peking (21). There is a continuing need to introgress host-plant resistance genes from diverse sources into productive soybean cultivars.

Schmitt and Ferris (26) proposed that field-specific probes or bioassays of soil be conducted to calibrate damage functions. Potentially, this proposal could be expanded to include the use of different resistant cultivars. The current research shows that the number of cysts at 28 DAP is a good field-specific predictor of soybean yield and subsequent SCN reproduction. The number of cysts at 28 DAP was a better indicator of yield and SCN Pf than Pi, which is consistent with the fact that cultivars varied in their relative level of resistance to different populations of *H. glycines*. Thus, a quantitative model incorporating the relative amount of resistance to a given population could be combined with the initial population density for improved accuracy in predicting yield losses to SCN. Possibly, the results of greenhouse bioassays would be a better predictor of soybean yield potential in the presence of this pathogen, since they would integrate genetic, edaphic, other biologic (i.e., soil suppressiveness), and population density as factors affecting productivity. This information could be used to better deploy additional management tactics as required.

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