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Effects of Environments, *Meloidogyne incognita* Inoculum Levels, and *Glycine max* Genotype on Root-knot Nematode–Soybean Interactions in Field Microplots[1]

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Abstract: Five soybean cultivars (Braxton, Gordon, Jeff, Bragg, and Wright) resistant to *Meloidogyne incognita* (Mi) and three susceptible cultivars (Coker 156, GaSoy 17, and Coker 237) were grown at two locations for four seasons in microplots with increasing initial soil population densities (Pi) of Mi. The resistant cultivars and Coker 156 yielded better than GaSoy 17 and Coker 237 at all Pi. Yield response was dependent on environmental conditions and at one location was stimulated on Braxton, Gordon, Jeff, and Bragg by low Pi. Although Mi reproduced well on all cultivars, the pattern of reproduction differed. Population densities of Mi leveled off after 90 days on GaSoy 17 and Coker 237 but were still increasing after 120 days on the resistant cultivars; population densities were lower on resistant than on the susceptible cultivars. The population density of Mi on Coker 156 after 120 days was intermediate between those on the other susceptible and on the resistant cultivars. Mi population densities followed the same pattern under varying environmental conditions.

Key words: resistant cultivars, nematode reproduction, yield loss, population dynamics, nematode × environment interaction.

The availability of resistance to *Meloidogyne incognita* (Kofoid & White) Chitwood is important in soybean (*Glycine max* (L.) Merr.) cultivars adapted to the southern United States because of the wide distribution of the nematode and its potential for suppressing yields (1,13,15). Currently, planting resistant cultivars is the only economical means of managing root-knot nematodes on soybean (15). Plant breeders have successfully developed many cultivars with resistance to *M. incognita* using one or more approaches to screening genotypes (10,16,19). We use the term "resistant" to describe a genotype on which nematode reproduction is suppressed relative to a "susceptible" (7); however, in practice the designation "resistant" or "susceptible" is dependent on the severity of a plant response, usually galling, and frequently includes an indication of levels of resistance within a continuum of host–parasite interactions.

Variations in levels of resistance expressed by a host genotype can be attributed to variation in nematode genotype or environmental conditions as well as to plant genotype (4). Little information is available on the effects of genotype × environment interaction for the soybean–*M. incognita* relationship, although with the current increase in use and importance of root-knot resistant cultivars, it is essential to deter-

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mine how well available resistance operates in different environments. The objectives in this series of experiments were 1) to evaluate *M. incognita*-resistant cultivars over increasing nematode inoculum levels under different environmental conditions (i.e., years or locations or both) and 2) to determine damage threshold initial nematode population densities for the resistant cultivars.

MATERIALS AND METHODS

Four experiments were conducted during 1981–84 in 80-cm-d fiberglass microplots (3) installed in Appling coarse sandy loam (Typic Hapludult, clayey, kaolinitic, thermic, 73% sand, 15% silt, 12% clay) at the Plant Sciences Farm near Athens, Georgia, and in Dothan loamy sand (Plinthic Paleudult, fine loamy, siliceous, thermic, 88% sand, 10% silt, 2% clay) at the Southeast Branch Experiment Station near Midville, Georgia. Microplots were limed and fertilized according to soil test recommendations by the University of Georgia Agricultural Extension Service. Four weeks before planting microplots were fumigated with methyl bromide at 0.12–0.19 kg/m^2. At planting the top 23 cm of soil was infested with the desired nematode initial population density (Pi) and with spores of mycorrhizal fungi (*Gigaspora margarita* and *Glomus etunicatum*) and commercial inoculum of *Bradyrhizobium japonicum.* Forty-five seeds were planted in a single row through the middle of each microplot. Seedlings were thinned to 20 per microplot after 7–10 days. To simulate production conditions, seeds of the cultivar planted inside the microplot were also planted in the border rows (95.5 cm apart) on either side of the plot and between the microplots within the row. Supplemental irrigation was provided throughout the growing season.

Data were recorded for plant number and height at harvest. Seeds were harvested mechanically, and seed yield and weight (g/100 seed) were adjusted to 13% moisture content. Relative seed yields were calculated on a per replication basis, as the yield of each nematode infested microplot divided by the yield of the noninfested microplot. Maturity date (when 95% of the pods reached maturity) was recorded at the Athens location only.

Meloidogyne incognita was propagated in a greenhouse on *Lycopersicon esculentum* Mill. cv. Rutgers. The culture had been established from a mixture of three collections selected for their aggressiveness to soybean (10). Eggs were collected for inoculum by 0.5% NaOCl extraction of galled tomato roots (9) and were added to each microplot in 1,600 ml of water suspension at planting. The Pi were 0, 62, 250, and 1,000 eggs/100 cm^3 soil in 1981 and 0, 31, 125, and 500 eggs/100 cm^3 soil in 1982–84. At 60, 90, and 120 days after infestation, six 2.5-cm-d soil cores were taken 15–20 cm deep from each microplot and bulked. Second-stage juveniles (J2) were extracted from 250 cm^3 of the sample by combined elutriation (6) and centrifugal-flotation (11), for which the efficiency was ca. 20% for *M. incognita* J2. Nematode data were not adjusted for extraction efficiency but were transformed to $\log_{10}(X + 1)$ values to remove the correlation between treatment means and variances. Nematode population densities reported are antilogs of the data analyzed. The rates of increase between sampling dates were calculated on nontransformed data as simple ratios per 100 cm^3 soil: the reproductive factor (RF1) refers to the number of J2 extracted at 90 days per J2 extracted at 60 days; RF2 refers to the same relationship between 120 and 90 days. RF_f is the number of J2 extracted at 120 days per egg of Pi.

The soybean cultivars used were designated as either susceptible or resistant to *M. incognita* based on their root galling responses in greenhouse tests (8,18). Cultivars Bragg, Braxton, Jeff, Gordon, and Wright were resistant, whereas GaSoy 17, Coker 156, and Coker 237 were susceptible. All cultivars were from Maturity Group VII except Coker 156, a Group VI cultivar. In Experiment 1, conducted at the Athens location, Braxton and GaSoy 17 were used to determine appropriate Pi. Experiment 2, conducted in 1982 at Athens and Midville, included Bragg, Braxton, Wright, and GaSoy 17. Experiments 3 (1983 at Midville) and 4 (1984 at Athens) each included Gordon, Jeff, and Coker 156; GaSoy 17 was used in 1983 and Coker 237 in 1984. Data from each experiment were subjected to a separate analysis of variance. For estimation of the effect of environment, only data for Gordon, Jeff, and Coker 156 were

TABLE 1. Effect of initial population densities (Pi) of *Meloidogyne incognita* on yield and plant height of resistant (Braxton) and susceptible (GaSoy 17) soybean cultivars in field microplots near Athens, Georgia, in 1981.

	Yield (g/plot)†		Plant height (cm)‡	
Pi*	Braxton	GaSoy 17	Braxton	GaSoy 17
0	100.3	101.2	31.5	31.8
62	120.3	50.8	33.3	31.2
250	72.3	18.3	28.7	24.7
1,000	73.4	10.7	30.0	18.2
Cultivar mean§	92.4	45.3	31.0	26.3

* *M. incognita* eggs/100 cm^3 soil.

† Regression equations ($P < 0.01$) for relative yield (Y) on $\log_{10}$Pi (X): Braxton, $Y = 1.0 + 0.292X - 0.147X^2$, $r^2 = 0.485$; GaSoy 17, $Y = 1.0 + 0.331X$, $r^2 = 0.937$.

‡ Regression equations ($P < 0.01$) for plant height (Y) on $\log_{10}$Pi (X): Braxton, NS; GaSoy 17, $Y = 33.41 - 3.723X$, $r^2 = 0.438$.

§ Cultivar main effect significant at $P < 0.01$ for both variables.

included in the analysis. All experiments were conducted in randomized complete blocks with four replications except for Experiment 1, which was replicated six times.

Analyses of variance were conducted for all response variables assuming a mixed model cultivar, Pi, and environment (years or locations) as fixed effects and replication as a random effect nested within environments, where appropriate. Qualitative effects (cultivars and environments) were compared by least significant differences (LSD) where the F-test was significant ($P = 0.05$). Quantitative effects and interactions were investigated using orthogonal sets of single degree of freedom comparisons. Regression models were constructed based on the results of orthogonal partitioning of the linear and quadratic effects of Pi converted to $\log_{10}(X + 1)$ values to approximate equally spaced levels.

RESULTS

Experiment 1: Plant height and seed yield were significantly influenced by both cultivar and Pi main effects and their interaction (Table 1). There was no difference in seed yield between cultivars in the absence of *M. incognita*, but the negative yield responses to increasing Pi were best described as quadratic for Braxton and linear for GaSoy 17. Plant height was not significantly affected by Pi for Braxton but was suppressed linearly over increasing Pi for GaSoy 17. Maturity was not affected by Pi or cultivar, and seed weight differed only between cultivars (14.8 and 12.8 g/100 seed for Braxton and GaSoy 17, respectively).

For both cultivars, J2 population densities were directly related to Pi at 60 days; however, J2 population densities were inversely related to Pi on GaSoy 17 at 120 days while still directly related on Braxton (Table 2). RF1 was greater than RF2 for both cultivars at each Pi, but regression of J2 population density on days after planting yielded linear relationships for all but GaSoy 17 at the high Pi, in which densities did not significantly change between 60 and 120 days. The best fits of the linear relationship were obtained at the low Pi for both cultivars. RF_f was inversely related to Pi on both cultivars.

Experiment 2: Except for plant height

TABLE 2. Effect of initial population densities (Pi) of *Meloidogyne incognita* and resistant (Braxton) and susceptible (GaSoy 17) soybean cultivars on nematode population development in field microplots near Athens, Georgia, in 1981.

		Juveniles/100 cm^3 soil						
Cultivar	Pi*	60†	RF1‡	90†	RF2‡	120†	R^2§	RF_f‖
Braxton	62	26	14.9	293	2.9	635	0.79	11.8
	250	86	12.6	671	10.5	1,170	0.38	9.7
	1,000	451	2.7	949	1.7	1,360	0.46	1.5
GaSoy 17	62	60	26.1	954	3.0	1,940	0.78	36.6
	250	234	7.6	1,120	1.7	1,792	0.55	9.6
	1,000	425	2.0	587	1.2	623	NS	0.7

* *M. incognita* eggs/100 cm^3 soil.

† Days after planting.

‡ Reproductive factor between sampling dates (juvenile per juvenile). These factors were means calculated from raw data, not the antilogs presented in the table.

§ R^2 values for fit ($P < 0.01$) of linear regressions of juvenile densities (Y) on days after planting (X) at each Pi.

‖ Reproductive factor (number of juveniles produced per egg of inoculum): population density at 120 days/Pi.

TABLE 3. Effect of initial population densities (Pi) of *Meloidogyne incognita* on yield, plant height, and seed weight of resistant (Bragg, Braxton, and Wright) and susceptible (GaSoy 17) soybean cultivars in field microplots in 1982 at two locations in Georgia.

		Seed yield (g/plot)		Plant height (cm)		Seed weight (g/100 seed)	
Cultivar	Pi*	Athens	Midville	Athens	Midville	Athens	Midville
Bragg	0	70.0	314.5	36.3	44.5	12.7	11.9
	31	86.3	325.8	40.8	43.5	11.7	11.9
	125	86.8	293.8	35.8	42.8	12.7	11.9
	500	46.8	250.5	40.0	43.5	11.6	12.1
Mean†		72.6	296.1	38.2	43.4	12.1	11.9
Braxton	0	100.8	333.5	36.5	41.3	13.6	14.4
	31	117.3	332.8	40.0	41.0	13.4	14.3
	125	107.8	290.8	39.8	43.0	13.1	14.1
	500	84.8	256.8	36.3	43.3	13.2	14.4
Mean†		102.6	303.4	38.1	42.1	13.6	14.0
Wright	0	113.3	346.5	37.0	43.8	11.5	11.9
	31	114.3	246.0	37.0	41.2	11.6	10.9
	125	60.8	313.0	38.5	43.5	11.1	11.6
	500	42.8	241.0	37.3	42.0	10.5	11.5
Mean†		80.6	286.6	37.4	45.2	11.2	11.4
GaSoy 17	0	150.3	343.8	42.3	47.3	11.2	11.6
	31	25.3	161.0	38.5	44.5	10.9	10.4
	125	20.8	64.8	38.0	46.5	10.8	9.9
	500	1.5	60.3	32.5	42.5	10.5	9.9
Mean†		42.7	157.4	37.8	42.8	10.9	10.5
LSD‡	$P = 0.05$	44.5		NS		1.0	

* *M. incognita* eggs/100 cm^3 soil.

† Means for cultivars over Pi. Environment main effect significant ($P < 0.01$) for seed yield and plant height, not significant for seed weight.

‡ Protected LSD for comparison of cultivar means only.

(Table 3), all plant and nematode responses measured were significantly affected by cultivar and Pi ($P = 0.05$). Plant height variation was dependent on an environment main effect and Pi × cultivar interaction, although there was no cultivar or Pi main effect. There was a significant interaction between environment and another effect (environment × cultivar, $P < 0.01$, Table 3) only for seed yield. In the absence of *M. incognita,* yields were 2–5-fold different within cultivars between the two environments and became greater in nematode-infested plots except for Braxton. Conversion of yield values to relative yield did not remove the environment main effect. In each environment, the average effect of the treatments including *M. incognita* vs. noninoculated controls was significant for Wright and GaSoy 17 but not for Bragg or Braxton; neither linear nor quadratic regressions of yield on Pi fit the observed data for Bragg and Braxton in either environment (Figs. 1, 2), although there was a significant yield stimulation in one environment (Fig. 1). Wright's response to *M. incognita* was a linear decrease over Pi in one environment with a yield loss of 63% at the highest Pi (Fig. 1), but a response similar to that for Bragg and Braxton occurred in the other environment (Fig. 2). Relative yield of GaSoy 17 was suppressed 53–82% at the lowest Pi and decreased as Pi increased in both environments.

M. incognita J2 population densities at 60 days after planting were directly related to Pi on all cultivars. Rates of increase in J2 population densities between 60 and 90 days were inversely related to Pi, except on Braxton, and higher than rates of increase between 90 and 120 days (Table 4). There was no environment effect on J2 population densities at 60, 90, or 120 days. At the low and intermediate Pi, regressions of J2 population densities on sampling dates (days after planting) were linear and homogeneous among Bragg, Braxton, and

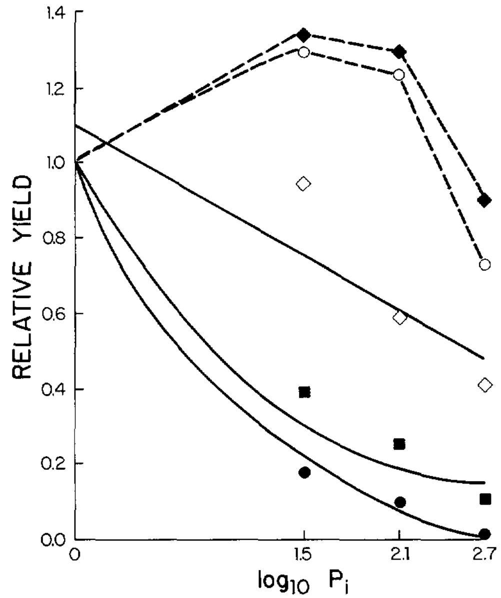

FIG. 1. Relative yield responses of soybean cultivars to *Meloidogyne incognita* at increasing initial population densities (Pi) in field microplots at Athens, Georgia. Dashed lines (– – –) connect means for cultivars among which there were no differences and for which there was no significant linear or quadratic regression of relative yield ($\hat{Y}$) on $\log_{10}$Pi (X): Coker 156, Gordon, and Jeff in 1984 (◆); Bragg and Braxton in 1982 (○). Solid lines describe regressions for: Wright in 1982 (◇), where $\hat{Y} = 1.1 - 0.228X$, $r^2 = 0.50$; GaSoy 17 in 1982 (●), where $Y = 1.0 - 0.716X + 0.132X^2$, $r^2 = 0.95$; and Coker 237 in 1984 (●), where $\hat{Y} = 1.0 - 0.671X + 0.135X^2$, $r^2 = 0.40$.

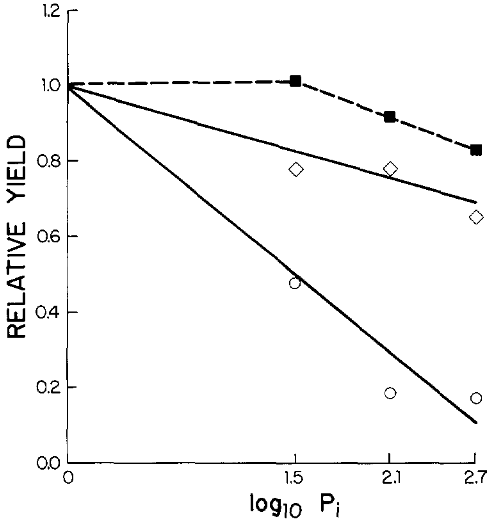

FIG. 2. Relative yield responses of soybean cultivars to *Meloidogyne incognita* at increasing initial population densities (Pi) in field microplots at Midville, Georgia. Dashed lines (– – –) connect means for cultivars Bragg, Braxton, and Wright in 1982, which did not differ and for which there was no significant linear or quadratic regression of relative yield ($\hat{Y}$) on $\log_{10}$Pi (X). Solid lines describe regressions for: GaSoy 17 in 1982 and 1983 combined (○), where $\hat{Y} = 1.0 - 0.315X$, $r^2 = 0.64$; and Coker 156, Gordon, and Jeff, combined, in 1983 (◇), where $\hat{Y} = 1.0 - 0.117X$, $r^2 = 0.45$.

Wright (slopes and elevations not significantly different at $P < 0.01$, Fig. 3). At the high Pi, J2 population densities and sampling dates were unrelated on Bragg and Braxton but were linear for Wright (Table 4). At the intermediate and high Pi, J2 regressions on sampling dates were quadratic on GaSoy 17 (Fig. 4). RF_f was inversely related to Pi on all cultivars (Table 4).

Experiments 3 and 4: The analyses of variance for plant responses in each experiment were similar: cultivar main effects were significant ($P < 0.05$) for seed yield, plant height, and seed weight; the Pi main effect was significant for all traits; and there were no cultivar × Pi interactions. For seed yield responses in each experiment, comparisons of cultivar main effects separated GaSoy 17 or Coker 237 in their respective environments from the other three cultivars and did not differentiate among Gordon, Jeff, and Coker 156. In analysis over environments for the latter three cultivars (Table 5), the environment main effect on seed yield was highly significant ($P < 0.01$). Seed weight was affected by environment and environment × cultivar interaction, whereas plant height was influenced by environment × cultivar as well as environment × Pi interaction. There was no cultivar main effect for yield, but yield, plant height, and seed weight were all influenced by Pi ($P < 0.05$).

Final population densities of *M. incognita* J2 were significantly higher on Coker 156 than on Gordon or Jeff, which did not differ from one another or between environments, at all Pi (Table 6). Within all three cultivars, population densities in plots at Pi = 31 and Pi = 125 were not different and increased linearly over sampling dates (Fig. 3). Final populations and slopes of population increase over sampling dates for Coker 237 in one environment were similar to those for GaSoy 17 in the other (data not presented). These responses for GaSoy 17 were not affected by an environment

TABLE 4. Effect of initial population densities (Pi) of *Meloidogyne incognita* and resistant (Bragg, Braxton, and Wright) and susceptible (GaSoy 17) soybean cultivars on nematode population development in field microplots in 1982 at two locations in Georgia.

		Juveniles/100 cm^3 soil						
Cultivar	Pi*	60†	RF1‡	90†	RF2‡	120†	R^2§	RF_f‖
Bragg	31	26	31.6	376	9.4	1,423	0.80	51.9¶
	125	77	15.6	809	3.5	1,704	0.66	14.8
	500	186	4.6	266	1.9	497	NS	1.3
Braxton	31	25	15.6	351	2.4	507	0.54	18.8
	125	134	21.1	543	2.3	1,106	0.45	10.0
	500	226	2.9	485	1.6	405	NS	1.3
Wright	31	26	53.4	155	17.1	942	0.46	38.7
	125	130	13.9	664	2.4	1,264	0.49	12.3
	500	304	2.9	731	2.2	1,293	0.36	3.0
GaSoy 17	31	40	36.2	748	6.5	3,570	0.68	126.6
	125	170	14.9	2,089	1.8	2,998	—#	26.2
	500	170	7.2	989	1.8	1,390	—#	5.8

* *M. incognita* eggs/100 cm^3 soil.

† Days after planting.

‡ Reproductive factor between sampling dates (juvenile per juvenile). These factors were means calculated from raw data, not the antilogs presented in the table.

§ R^2 values for fit ($P < 0.01$) of linear regressions of juvenile densities (Y) on days after planting (X) at each Pi.

‖ Reproductive factor (number of juveniles produced per egg of inoculum): population density at 120 days/Pi.

¶ Cultivar means for RF_f were Bragg = 22.3, Braxton = 10.4, Wright = 18.0, GaSoy 17 = 54.0. Protected LSD for comparison of cultivar means = 7.7 juveniles/egg ($P < 0.05$). Linear component of Pi main effect was significant for all cultivars ($P < 0.01$).

Response quadratic rather than linear (see Fig. 4).

main effect when combined with the data from Experiment 2 (Fig. 4).

DISCUSSION

Overall, *M. incognita* reproduction, as assessed by J2 population densities in soil, corresponded well with reproduction inferred from gall indices obtained in greenhouse screening for root-knot nematode resistance (8,10,18). On cultivars classified as resistant according to their gall indices (Bragg, Braxton, Gordon, Jeff, and Wright), nematode reproduction was generally lower over time and Pi than it was on the susceptible genotypes GaSoy 17 or Coker 237. There was one exception, Coker 156, for which greenhouse gall indices were high (8,18) but reproduction in microplots was intermediate between that on other susceptible and on resistant cultivars. Possibly on Coker 156 the plant galling response and nematode reproduction are independent, as Shepherd (21) found with

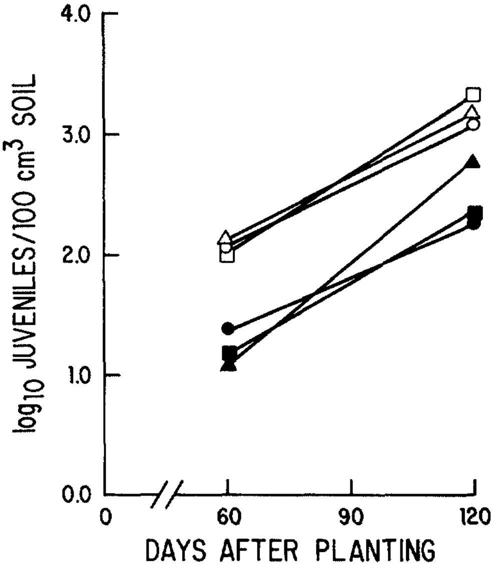

FIG. 3. Change in soil population densities of *Meloidogyne incognita* in field microplots at 60, 90, and 120 days after planting. Linear regressions of $\log_{10}$(juveniles/100 cm^3 soil = $\hat{Y}$) on days after planting (X) are illustrated for combined data from two locations in 1982 (open symbols) and 1983, 1984 (filled symbols). Slopes were homogeneous among Braxton, Bragg, and Wright: Braxton (○) $\hat{Y} = 1.266 + 0.0152X$, $r^2 = 0.45$; Bragg (□) $\hat{Y} = 0.708 + 0.0218X$, $r^2 = 0.68$; Wright (△) $\hat{Y} = 1.201 + 0.0164X$, $r^2 = 0.49$. Slopes were homogeneous between Jeff and Gordon, and heterogeneous between Coker 156 and either Jeff or Gordon: Jeff (●) $\hat{Y} = 0.685 + 0.0116X$, $r^2 = 0.59$; Gordon (■) $\hat{Y} = 0.289 + 0.0156X$, $r^2 = 0.32$; Coker 156 (▲) $\hat{Y} = -0.368 + 0.026X$, $r^2 = 0.54$.

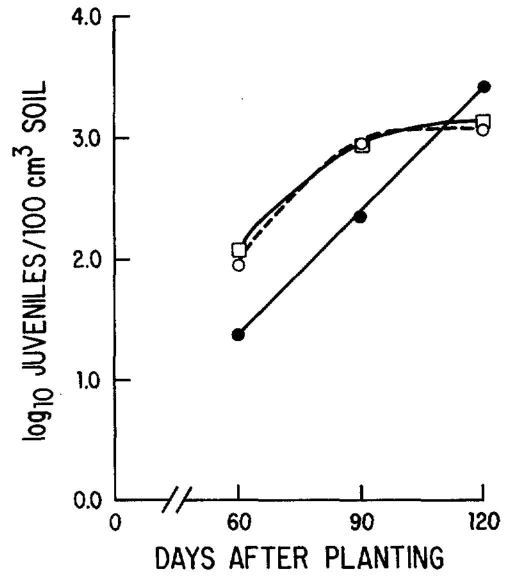

FIG. 4. Regressions of soil population densities (Pi) of *Meloidogyne incognita* ($\log_{10}$ juveniles/100 cm^3 soil = $\hat{Y}$) on days after planting (X) for GaSoy 17 in field microplots in three environments at three Pi of eggs/100 cm^3 soil. Slopes were homogeneous for Pi = 125 and Pi = 500: for Pi = 125 (○), $\hat{Y} = -2.029 + 0.091X - 0.004X^2$, $r^2 = 0.71$; for Pi = 500 (□), $\hat{Y} = -1.39 + 0.077X - 0.0003X^2$, $r^2 = 0.37$. For Pi = 31 (●), $\hat{Y} = 0.748 + 0.035X$, $r^2 = 0.69$.

certain cotton accessions challenged with *M. incognita.* Barker (2) referred to Coker 156 as "moderately field tolerant," and Boerma and Hussey (5) found it to be moderately tolerant to *Heterodera glycines* in the field, although no genes for nematode resistance are known in this cultivar's pedigree. Further investigation of the Coker 156–*M. incognita* relationship is in progress.

M. incognita reproduced well on all soybean cultivars tested but differed in the pattern of reproduction. On susceptible GaSoy 17 and Coker 237, J2 soil population densities leveled off after 90 days at the intermediate and high Pi as indicated by the quadratic relationship between J2 population densities and sampling date. Nematode population densities were still increasing at 120 days after planting on the resistant cultivars and Coker 156, and although lower in general at 120 days than on the susceptible cultivars, this increase may result in post-harvest soil population densities as high as on susceptible cultivars. Minton et al. (17) and Kinloch (15) reached similar conclusions in field studies with natural root-knot nematode infestations. It is interesting that the measurements of pa-

TABLE 5. Effect of initial population densities (Pi) of *Meloidogyne incognita* on yield, plant height, and seed weight of selected soybean cultivars in field microplots near Athens and Midville, Georgia, during 1983 and 1984.

		Seed yield (g/plot)		Plant height (cm)		Seed weight (g/100 seed)	
Cultivar	Pi*	Athens	Midville	Athens	Midville	Athens	Midville
Coker 156	0	75.8	266.5	27.8	27.8	9.7	12.1
	31	109.8	213.0	30.3	29.0	9.7	11.9
	125	77.3	197.0	28.3	26.8	9.8	11.9
	500	53.3	191.0	25.0	27.3	9.3	11.3
Mean†		79.1	216.9	27.8	27.7	9.6	11.8
Gordon	0	76.6	260.3	31.0	31.3	10.3	11.6
	31	88.3	219.8	36.0	31.3	10.0	11.4
	125	99.5	227.8	34.8	31.3	9.9	11.0
	500	82.2	132.5	34.8	28.5	10.0	10.5
Mean†		86.7	221.1	34.1	30.8	10.0	11.2
Jeff	0	80.9	254.3	29.5	33.8	11.4	13.8
	31	87.2	180.0	31.3	33.8	11.6	12.9
	125	115.8	190.3	35.5	31.8	11.7	13.3
	500	65.6	160.3	29.3	32.5	11.0	12.9
Mean†		87.4	196.2	31.3	32.9	11.4	13.2
LSD‡	$P = 0.05$	NS		2.7		1.1	

* *M. incognita* eggs/100 cm^3 soil.

† Means for cultivars over Pi. Environment main effect significant ($P < 0.01$) for yield and seed weight, not significant for plant height.

‡ Protected LSD for comparison of cultivar means only.

TABLE 6. Effect of soybean cultivars and initial population densities (Pi) of *Meloidogyne incognita* on nematode population development in field microplots at two locations in Georgia in 1983 and 1984.

		Juveniles/100 cm^3 soil						
Cultivar	Pi*	60†	RF1‡	90†	RF2‡	120†	R^2§	RF$_f$‖
Coker 156	31	12	3.4	28	21.4	270	0.56	12.9
	125	18	10.0	64	23.8	677	0.54	8.7
	500	38	14.5	263	12.9	1,548	0.71	3.8
Gordon	31	6	6.0	26	5.0	112	0.41	8.9
	125	18	4.3	38	5.0	161	0.32	1.6
	500	86	4.6	198	3.2	336	0.32	0.8
Jeff	31	2	14.9	57	3.0	124	0.59	7.2
	125	20	8.1	72	2.2	103	NS	4.4
	500	58	10.2	229	5.4	694	0.51	2.1

* *M. incognita* eggs/100 cm^3 soil.

† Days after planting.

‡ Reproductive factor between sampling dates (juvenile per juvenile). These factors were means calculated from raw data, not the antilogs presented in the table.

§ R^2 values for fit ($P < 0.01$) of linear regression of juvenile population densities (Y) on days after planting (X) at each Pi.

‖ Reproductive factor (number of juveniles produced per egg of inoculum): population density at 120 days/Pi. Cultivar main effect was not significant for RF$_f$. Linear component of Pi main effect was significant for all cultivars ($P < 0.05$).

rameters used for determining nematode responses were not affected by environment. Reproduction on GaSoy 17 followed the same pattern in all three environments in which the cultivar was grown, and no consistent environment effects were detected for nematode responses on the other cultivars. The stability of nematode reproduction over varying environments was unexpected.

All cultivars classified as resistant to *M. incognita* and Coker 156 produced higher yields than GaSoy 17 or Coker 237 in the presence of the nematode. In contrast to nematode reproduction, yield response was highly dependent on environmental effects. Schmitt and Barker (20) reported similar observations in microplot studies with *Pratylenchus* spp. on soybean. The large differences in seed yields we found between the two Georgia locations, even in the absence of *M. incognita,* could not be accounted for. Microplots at both locations were irrigated, and soil texture differences were not great. Also, similar yield differences were obtained with different sets of cultivars. Even the relative yields over Pi were different between locations. Plants grown in 1982 were subject to less moisture stress than those grown in 1983 and 1984. Drought conditions may account for the significant yield suppression at Midville in 1983 for Gordon, Jeff, and Coker 156 as Pi increased, even though the plots were irrigated. The lower yield for Bragg and Braxton at one location was not different statistically from the other location, although mean yields decreased as Pi increased. In the 1981 experiment, Braxton yields were significantly suppressed at high Pi, indicating nematicides may be beneficial on resistant cultivars at certain high Pi. In fact, Kinloch (12) reported yield increases of Bragg in *M. incognita*-infested field plots treated with nematicides. Stimulation of seed yield at low Pi, such as that observed for the resistant cultivars Bragg, Braxton, Gordon, and Jeff at one location in separate experiments, has been reported in other plant–nematode relationships (4) and probably reflects a real environmental effect.

There were too few Pi included in our studies to determine tolerance limits with any degree of precision, yet it is clear that 31 eggs/100 cm^3 soil (of an aggressive *M. incognita* population) is above the tolerance limit for susceptible intolerant cultivars. Assuming 20% egg hatch in microplots (T. L. Niblack, unpubl.) and 20% extraction efficiency, this population density is below consistently detectable levels if the soil is extracted for J2 unless extraction efficiency is very high. Barker and Olthof (4) reported a threshold population density of 20 J2/100 g soil which is considerably higher than ours based on the above assumptions of hatch and extraction efficiency. The population we used in the microplots, however, was highly aggressive compared with a North Carolina isolate (22). Furthermore, how responses obtained in fumigated microplots correspond to field responses with naturally occurring nematode populations remains to be determined.

Although the yield response over Pi was dependent on environment, tolerant and intolerant genotypes, corresponding respectively to the resistant and susceptible genotypes identified by greenhouse screening, were clearly differentiated at each location. It would be of little value to qualify a resistant or susceptible designation further because of the dependence on location. The important findings are that resistance (based on nematode reproductive rate) operates in different environments, that significant yield suppression can occur on resistant cultivars under large nematode Pi, and that greenhouse screening is an adequate indicator of plant resistance for practical purposes.

LITERATURE CITED

1. Appel, J. A., and S. A. Lewis. 1984. Pathogenicity and reproduction of *Hoplolaimus columbus* and *Meloidogyne incognita* on 'Davis' soybean. Journal of Nematology 16:349–355.

2. Barker, K. R. 1982. Influence of soil moisture, cultivar, and population density of *Meloidogyne incognita* on soybean yield in microplots. Journal of Nematology 14:429 (Abstr.).

3. Barker, K. R., B. I. Daughtry, and D. W. Corbett. 1979. Equipment and techniques for establishing field microplots for the study of soilborne plant pathogens. Journal of Nematology 11:106–108.

4. Barker, K. R., and T. H. A. Olthof. 1976. Relationships between nematode population densities and crop response. Annual Review of Phytopathology 14: 327–353.

5. Boerma, H. R., and R. S. Hussey. 1984. Tolerance to *Heterodera glycines* in soybean. Journal of Nematology 16:289–296.

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

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

8. Day, J. L., C. D. Fisher, and W. T. Pettigrew. 1984. 1983 field crops performance tests: Soybeans, peanuts, sorghum, cotton, tobacco, sunflowers, and summer annual forages. Research Report 447, University of Georgia College of Agriculture Experiment Stations, Athens.

9. 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.

10. Hussey, R. S., and H. R. Boerma. 1981. A greenhouse screening procedure for root-knot nematode resistance in soybeans. Crop Science 21:794–796.

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

12. Kinloch, R. A. 1974. Response of soybean cultivars to nematicidal treatments of soil infested with *Meloidogyne incognita*. Journal of Nematology 6:7–11.

13. Kinloch, R. A. 1980. The control of nematodes injurious to soybean. Nematropica 10:141–153.

14. Kinloch, R. A. 1982. The relationship between soil populations of *Meloidogyne incognita* and yield reduction of soybean in the Coastal Plain. Journal of Nematology 14:162–167.

15. Kinloch, R. A. 1985. Comparative root-knot galling and yield responses of soybean cultivars to *Meloidogyne incognita*. Plant Disease 69:334–336.

16. Kinloch, R. A., and K. Hinson. 1972. The Florida program for evaluating soybean (*Glycine max* L. Merr.) genotypes for susceptibility to root-knot nematode disease. Proceedings of the Soil and Crop Science Society of Florida 32:173–176.

17. Minton, N. A., M. B. Parker, and B. G. Mullinix. 1978. Effects of cultivars, subsoiling, and fumigation on soybean yields and *Meloidogyne incognita* populations. Journal of Nematology 10:43–47.

18. Raymer, P. L., J. L. Day, C. D. Fisher, and W. T. Pettigrew. 1985. 1984 field crops performance tests: Soybeans, peanuts, cotton, tobacco, sorghum, summer annual forages, and sunflowers. Research Report 472, University of Georgia College of Agriculture Experiment Stations, Athens.

19. Saichuk, J. K., C. Williams, and W. Birchfield. 1976. A technique for screening soybeans for resistance to root-knot nematodes. Plant Disease Reporter 60:868–870.

20. Schmitt, D. P., and K. R. Barker. 1981. Damage and reproductive potentials of *Pratylenchus brachyurus* and *P. penetrans* on soybean. Journal of Nematology 13:327–332.

21. Shepherd, R. L. 1979. A quantitative technique for evaluating cotton for root-knot nematode resistance. Phytopathology 69:427–430.

22. Windham, G. L. and K. R. Barker. 1986. Effects of soil type on the damage potential of *Meloidogyne incognita* on soybean. Journal of Nematology 18:331–338.