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Effects of *Heterodera glycines* and *Meloidogyne incognita* on Early Growth of Soybean[1]

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Abstract: Greenhouse and field microplot studies were conducted to compare soybean shoot and root growth responses to root penetration by *Heterodera glycines* (Hg) and *Meloidogyne incognita* (Mi) individually and in combination. Soybean cultivars Centennial (resistant to Hg and Mi), Braxton (resistant to Mi, susceptible to Hg), and Coker 237 (susceptible to Hg and Mi) were selected for study. In the greenhouse, pot size and number of plants per pot had no effect on Hg or Mi penetration of Coker 237 roots; root weight was higher in the presence of either nematode species compared with the noninoculated controls. In greenhouse studies using a sand or soil medium, and in field microplot studies, each cultivar was grown with increasing initial population densities (Pi) of Hg or Mi. Interactions between Hg and Mi did not affect early plant growth or number of nematodes penetrating roots. Root penetration was the only response related to Pi. Mi penetration was higher in sand than in soil, and higher in the greenhouse than in the field, whereas Hg penetration was similar under all conditions. At 14 days after planting, more second-stage juveniles were present in roots of susceptible than in roots of resistant plants. Roots continued to lengthen in the greenhouse in the presence of either Mi or Hg regardless of host genotype, but only in the presence of Mi in microplots; otherwise, responses in field and greenhouse studies were similar and differed only in magnitude and variability.

Key words: soybean cyst nematode, root-knot nematode, *Glycine max*, root penetration, root length, microplots, *Heterodera glycines*, *Meloidogyne incognita*.

Many studies have related yield losses in soybean (*Glycine max* (L.) Merr.) to initial population densities (Pi) of the soybean cyst nematode, *Heterodera glycines* Ichinohe (Hg), or root-knot nematodes, particularly *Meloidogyne incognita* (Kofoid & White) Chitwood (Mi) (18). The effects of Pi on early growth of soybean, particularly root growth, have not been well characterized despite the potential usefulness of such information in crop growth models (8). Soybean cultivars differ in root morphology (14,17), and differences in resistance to Mi among cultivars have been attributed to this plant characteristic (5,6). Plant age, temperature, soil texture, and Mi Pi were found to influence patterns of early shoot and root growth of a Mi-susceptible soybean cultivar (19). Relationships between root growth patterns and plant responses to cyst nematode infection have also been described. Tolerance of potato cultivars to *Globodera rostochiensis* was attributed to differences in root responses to the nematode (25). Early season damage to wheat roots by *Heterodera avenae*, with subsequent effects on shoot growth, was related to yield suppression (20).

Our objectives were to compare the early growth responses of soybean cultivars differing in resistance to Hg and Mi to infections by each species singly and in combination in field microplots and in a greenhouse.

Materials and Methods

Soybean cultivars used were Centennial (resistant to Hg and Mi, Maturity Group [MG] VI), Braxton (resistant to Mi, susceptible to Hg, MG VII), and Coker 237 (susceptible to Hg and Mi, MG VII). Shoot heights were measured to the shoot apex after excising the shoot at the soil line. Fresh shoot weights included cotyledons. Shoots were dried for 3 days at 60 C for dry weights. Root systems were washed, blotted dry, and weighed for fresh root weights. Nematodes within roots were stained by the method of Byrd et al. (4). Numbers of first order lateral roots and total root length (22,24) were determined for stained roots at 40× at the same time nematodes in roots were counted.

The Hg Race 3 and Mi Race 3 isolates used for inoculum were described previously (16). Inoculum of each nematode

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species was prepared immediately before use by obtaining eggs from greenhouse cultures using a mechanical method for Hg (2) and 0.5% NaOCl for Mi (11). Appropriate numbers of eggs in tap water suspension were mixed into the planting media. Media for greenhouse studies were sterilized river sand or sterilized field soil: sand: attapulgite clay (3:1:1).

Second-stage juveniles (J2) were extracted from soil by elutriation (3) and centrifugal-flotation (13), with an efficiency of ca. 35% for Hg and 20% for Mi. Eggs and J2 were extracted from sand by sieving through nested 75-, 38-, and 25-μm-pore sieves.

Appropriate analyses of variance were conducted on the data from each study, with fixed effects assumed in the models except for replications which were considered random effects. In analyses of data combined for more than one repeat of an experiment, a random effect was assumed for experiments. Significant effects were at $P < 0.05$. Means for qualitative effects were compared by least significant differences where the F-test was significant. Quantitative effects were compared by appropriate single degree of freedom contrasts.

Greenhouse studies: All greenhouse studies were conducted under 400-watt Multi-Vapor phosphor-coated GE lamps to provide 16-hour days. Plants were fertilized with Hoagland's solution (10) at planting and on day 8 after planting. A 2 × 2 × 3 factorial treatment design in 10 randomized complete blocks was used to determine the effects of pot size (400 vs. 1,600 cm^3 soil volume), number of plants per pot (one vs. five plants), and nematodes (no nematodes vs. Hg vs. Mi) on root fresh weight and nematode penetration. Nematode inoculum at 125 eggs/100 cm^3 soil or egg-free filtrate (control) was mixed thoroughly into the soil mix, into which either one or five seed of Coker 237 was planted. For five replicates in which all of the one-seed plantings germinated, plants were harvested 10 days after planting, with one plant per pot chosen at random from the five-plant treatments. Roots were weighed fresh and then stained. The experiment was conducted twice.

The effects of Hg and Mi separately on the growth of three soybean cultivars were determined in 400-ml styrofoam cups containing either sterilized sand or soil medium. Nematode Pi were 0, 31, 124, and 248 eggs of either Hg or Mi per 100 cm^3 medium. Three seed were planted into each cup, but only the first seedling to emerge was retained. Plants were harvested 7 and 14 days after planting. Data recorded were shoot height and fresh and dry weights, root fresh weight and total root length, numbers of J2 in roots, and numbers of J2 and eggs in the growing medium. This experiment was conducted twice in sand and twice in the soil medium with five replications per randomized complete block experiment. To determine if nematode interactions occurred, Hg and Mi were inoculated at 0, 31, 124, and 248 eggs of each per 100 cm^3 sand in all combinations. A single experiment was conducted with 10 randomized complete blocks.

Microplot experiments: The methods used in establishment, care, and treatment of the 80-cm-d field microplots were described previously (16). Microplot soil was infested with 0, 31, or 124 eggs/100 cm^3 of either Hg or Mi and then planted with two rows of 20 seed each of the desired soybean cultivar. Inocula of *Bradyrhizobium japonicum* and the endomycorrhizal fungi *Gigaspora margarita* and *Glomus etunicatum* were added to the seed rows. On days 7 and 14 after planting, one row of plants was dug and five seedlings were chosen at random for staining. Juveniles were extracted by elutriation from 250 cm^3 soil and from 100 cm^3 soil placed in a Baermann tray (21) for 1 week to allow hatch of eggs. A single completely randomized design experiment with four replications was conducted, in 1983.

In 1984, the microplot experiment was conducted three times; planting dates were 10 June, 10 July, and 10 August. Microplots were fumigated with methyl bromide (16) 14 days before each planting date. Pi were 0, 31, or 124 eggs of Hg and Mi, in all combinations, per 100 cm^3 soil. Each microplot was planted with three 20-seed rows, one row of each soybean cultivar, and watered on days 4, 8, and 12 after planting. The experimental design was a split plot, with the nematode treatments as main plots and cultivars as subplots. On days 7 and 14 after planting, 250 cm^3 soil was collected

TABLE 1. Effects of pot size, number of soybean Coker 237 plants per pot, and *Heterodera glycines* (Hg) and *Meloidogyne incognita* (Mi) on nematode penetration and root fresh weight 10 days after planting in the greenhouse.

Nematode treatment*	Pot size	1 plant/pot		5 plants/pot†		Mean	
		Juveniles in roots	Root fresh weight (g)	Juveniles in roots	Root fresh weight (g)	Juveniles in roots	Root fresh weight (g)
None	400		0.21		0.19		
	1,600		0.18		0.20		
							0.19
Hg	400	48	0.22	56	0.21		
	1,600	46	0.21	42	0.23		
						48	0.22
Mi	400	36	0.26	36	0.22		
	1,600	33	0.23	41	0.25		
						37	0.24
LSD‡						6	0.02

* Inoculum density for Hg and Mi treatments: 125 eggs/100 cm^3 soil.
† Data taken on one randomly chosen plant per pot.
‡ Least significant differences ($\alpha = 0.05$) for within-column means.

from each microplot for extraction of J2, and plants were dug from half of each row randomly selected. Five plants for study were selected at random from the dug plants. Data recorded were shoot height, shoot fresh and dry weights, root fresh weight, number of lateral roots, total root length, and numbers of nematodes in roots.

RESULTS

Greenhouse studies: Neither the number of plants per pot nor pot size affected root fresh weight or numbers of J2 penetrating roots of Coker 237 plants (Table 1). Root fresh weights were higher in the presence of both Hg and Mi compared with non-infected plants. More Hg than Mi J2 penetrated roots. Penetration rates (number of J2 in roots/Pi eggs inoculated × 100) were 9.6% for Hg and 7.4% for Mi.

In the second greenhouse study, Pi of Hg or Mi had no effect on any plant growth parameter (data not presented). Differences among measurements depended on

TABLE 2. Effects of *Heterodera glycines* (Hg) and *Meloidogyne incognita* (Mi) on shoot growth of three soybean cultivars at 7 and 14 days after planting in a greenhouse.

Cultivar	Nematode	Shoot height (mm)		Shoot dry weight (g)	
		7 days	14 days	7 days	14 days
Braxton	None	38.3	108.0	0.13	0.30
	Hg	54.8	112.8	0.12	0.34
	Mi	57.6	127.7	0.13	0.34
Centennial	None	38.3	131.0	0.08	0.37
	Hg	49.6	137.2	0.09	0.32
	Mi	62.3	131.8	0.11	0.32
Coker 237	None	28.7	100.5	0.11	0.33
	Hg	47.3	97.4	0.11	0.32
	Mi	45.6	116.6	0.11	0.21
LSD*		11.2	14.4	NS	0.09

* Least significant differences ($\alpha = 0.05$) for comparison of means within columns.

TABLE 3. Effects of *Heterodera glycines* (Hg) and *Meloidogyne incognita* (Mi) on shoot growth of three soybean cultivars at 7 and 14 days after planting in greenhouse studies.

Cultivar	Nematode	Root fresh weight (g)		Root length (cm)	
		7 days	14 days	7 days	14 days
Braxton	None	0.30	2.03	342	1,176
	Hg	0.56	2.57	638	1,333
	Mi	0.48	1.99	513	1,842
Centennial	None	0.26	1.95	442	1,484
	Hg	0.28	1.78	496	1,929
	Mi	0.39	1.84	574	2,572
Coker 237	None	0.21	1.97	362	1,376
	Hg	0.37	1.84	410	2,614
	Mi	0.38	2.04	422	3,073
LSD*		0.11	0.72	176	597

* Least significant differences ($\alpha = 0.05$) for comparison of means within columns.

TABLE 4. Numbers of *Meloidogyne incognita* (Mi) in roots of three soybean cultivars at 7 and 14 days after planting in sand or soil medium infested with three inoculum levels of Mi eggs/100 cm³ medium.

Cultivar	Inoculum level	Numbers of juveniles in roots† 7 days Sand	14 days Sand	14 days Soil
Braxton	31	8	16	8
	124	31	128	93
	248	128	311	142
Mean		56	152	81
Centennial	31	11	10	5
	124	28	76	60
	248	101	327	175
Mean		47	138	80
Coker 237	31	25	37	22
	124	67	209	99
	248	45	329	199
Mean		46	192	107
LSD*		10	18	23

* Least significant differences ($\alpha = 0.05$) for comparison of cultivar means within columns.
† Total soil volume of 400 cm³.

TABLE 5. Numbers of *Heterodera glycines* (Hg) and *Meloidogyne incognita* (Mi) juveniles (J2) per Coker 237 root system at 14 days after planting in pots infested with 0, 31, 124, or 248 eggs of Hg and Mi/100 cm³ soil in all combinations.

Mi inoculum level	Hg inoculum level 0	31	124	248	Mi mean
0		12/0	47/0	136/0	
31	0/42	9/36	60/57	91/29	41
124	0/178	5/124	67/143	117/161	151
248	0/416	22/628	44/514	103/472	508
Hg mean		12	55	112	

Data expressed as the number of Hg J2/number of Mi J2.

soybean cultivar or nematode species. No cultivar × nematode interactions were detected. Shoot heights of all three cultivars on day 7 after planting were higher in the presence of Hg or Mi than without nematodes (Table 2). At 14 days, shoot height of Centennial plants was not affected by either nematode, whereas heights of Braxton and Coker 237 plants were increased by Mi but not by Hg. Shoot fresh weights followed a similar pattern. Shoot dry weight of only Coker 237 plants was decreased by nematode infection; that decrease was by Mi at 14 days.

Except for Hg on Centennial plants, root fresh weights were increased in the presence of either nematode species at 7 days but not at 14 days (Table 3). At 7 days, root lengths of only Braxton plants with Hg were greater than those of noninoculated plants, whereas at 14 days roots of all cultivars with Mi and roots of Coker 237 plants with Hg were longer than those without nematodes. Root length increases with nematodes were greater for Coker 237 than for Centennial or Braxton; length increases were higher with Mi than with Hg, but differences were significant only on Centennial plants. Root fresh weights and root lengths were correlated at 7 days ($r =$ 0.26 irrespective of cultivar) but not at 14 days. Plant growth was similar in sand vs. soil media for all responses measured, but coefficients of variation (CV) were higher for responses in soil than in sand.

More Mi J2 were observed in roots of plants growing in sand than in soil (Table 4). Cultivars did not differ in numbers of J2 penetrating roots at 7 days, but at 14 days Coker 237 roots contained more Mi J2 than roots of either Braxton or Centennial plants. In both sand and soil, numbers of Hg and Mi J2 in roots increased with increasing Pi. Numbers of Hg J2 penetrating roots was not affected by the growing medium, and numbers in roots were similar to Mi at 7 days but fewer than Mi at 14 days. Hg population densities in roots ranged from 4 at the low Pi to 50 at the high Pi and were not affected by cultivar (data not shown).

No interactions between Hg and Mi were detected among the parameters measured. For example, on Coker 237 plants numbers of Hg and Mi J2 penetrating roots increased linearly with Pi and numbers penetrating were independent of the Pi of the other species (Table 5).

Microplot studies: In the 1983 study, numbers of J2 recovered from microplot soil samples collected at 7 and 14 days, either directly from soil or from Baermann trays, were very low and unrelated to nematode Pi or soybean cultivar (Table 6). Numbers of Mi J2 in roots were not different among cultivars at 7 days after planting but were highest in Coker 237 roots at 14 days. Numbers of Hg J2 in roots were greater than Mi at both 7 and 14 days and highest in Coker 237 roots at both

sampling times. CV of means were high (> 38%) for each variable.

In the 1984 study, numbers of J2 recovered from soil were again low and unrelated to nematode Pi, soybean cultivar, sampling time, or month in which the study was conducted. Numbers of J2 in roots at 7 days in all 1984 studies were similar to those obtained in the 1983 study of single species infestations. Presence of one species did not affect root penetration by the other species.

Numbers of Hg and Mi in roots at 14 days were higher in August than in June (Table 7). Numbers recorded in June and July were not different. A larger percentage of Mi juveniles in roots were swollen in August than in June regardless of cultivar. A larger percentage of Hg juveniles, however, were swollen in roots of Braxton and Coker 237 than in Centennial regardless of month.

Cultivar differences in numbers of lateral roots in microplot and greenhouse studies were similar: by 14 days, Braxton plants developed 60, Coker 237 61, and Centennial 68 lateral roots. Only cultivar main effects were detected for root fresh weights, and root fresh weights were not correlated with either numbers of lateral roots or root lengths. Root lengths were extremely variable (CV = 165%) and did not differ among cultivars, but in general they were higher with Mi than with Hg or no nematodes (Table 8). Shoot heights and shoot fresh and dry weights were also highly variable (CV = 77–135%) and were not affected by treatments. Various transformations of data did not improve R^2 values for the model.

TABLE 6. Effects of soybean cultivar and nematode inoculum level (Pi) (eggs/100 cm³) on numbers of *Heterodera glycines* and *Meloidogyne incognita* recovered from soil and in roots at 7 and 14 days after planting in field microplots near Athens, Georgia, in 1983.

Nematode and cultivar	Pi	7 days			14 days		
		Soil*	Soil†	Root	Soil*	Soil†	Root
M. incognita							
Braxton	31	6	8	1	2	3	18
	124	2	5	2	2	10	28
Mean		4	7	2	2	7	23
Centennial	31	6	1	2	4	4	12
	124	4	4	5	10	5	24
Mean		5	3	4	7	5	18
Coker 237	31	4	6	5	14	7	34
	124	2	4	13	14	12	45
Mean		3	5	9	14	10	40
LSD‡		ns	ns	ns	7	ns	12
H. glycines							
Braxton	31	8	4	12	10	10	32
	124	4	5	18	8	6	66
Mean		6	5	15	9	8	49
Centennial	31	12	2	17	6	3	22
	124	4	5	18	8	6	56
Mean		8	4	18	7	5	36
Coker 237	31	8	7	25	10	7	81
	124	8	6	78	8	14	76
Mean		8	7	52	9	11	79
LSD‡		ns	ns	23	ns	ns	27

* Recovered from 250 cm³ soil by elutriation and centrifugal flotation.

† Recovered from 100 cm³ soil on Baermann tray.

‡ Least significant differences ($\alpha = 0.05$) for comparison of means within columns. ns = not significant.

DISCUSSION

Regardless of differences in resistance to Hg and Mi, the three soybean cultivars tested responded similarly to early infection with either or both nematode species. Infection by Mi consistently resulted in greater root length increases than in noninfected roots irrespective of host genotype and nematode inoculum levels in both field microplot and greenhouse studies, and with Hg in the greenhouse. Low Pi of cyst and root-knot nematodes have stimulated plant growth in certain cases (1,15); however, the Pi used in our studies were sufficient to cause significant yield losses to susceptible cultivars in concurrent studies under similar conditions (16). Root proliferation was observed on a Mi-susceptible soybean cultivar, but only with low Mi Pi at a single plant age–temperature combination (19). The nematode-induced stimulation of root growth that we observed was, at most, weakly correlated with increased fresh weight, suggesting that stimulated root growth was from proliferation of fine roots which contribute little to root weight. A similar response occurred in cereals inoculated with *H. avenae* (23). Cultivar differences in numbers of first-order lateral roots were unaffected by nematodes in our studies, and appeared unrelated to nematode resistance, contrary to other findings (5,6,12).

TABLE 7. Numbers of *Heterodera glycines* (Hg) and *Meloidogyne incognita* (Mi) in roots of three soybean cultivars 14 days after planting in field microplots in June and August in 1984. Data are means of treatments containing Hg or Mi, including concomitant treatments. Percentages of swollen juveniles are in parentheses.

Cultivar	Hg juveniles		Mi juveniles	
	June	August	June	August
Braxton	58 (38%)	115 (53%)	28 (21%)	176 (64%)
Centennial	20 (6%)	49 (4%)	25 (16%)	133 (56%)
Coker 237	79 (46%)	149 (62%)	48 (26%)	274 (67%)
LSD*	26 (14%)	33 (16%)	23 (12%)	41 (12%)

* Least significant differences ($\alpha = 0.05$) for comparison of cultivar means within columns.

We observed considerably more variation in data from microplot studies than from greenhouse studies. Variation was particularly evident in the root growth responses to Mi comparing greenhouse and field experiments; this was attributed in part to the inability to recover whole root systems from microplots but was also related to soil type. In our study, root growth in the presence of Mi was greatest in sand; this agrees with the findings of Shane and Barker (19) who used a low clay soil. Others have found that soybean root growth decreased as soil bulk density increased (9), as we observed in the absence of nematodes.

The early increases in root growth and lack of obvious effects on shoot top growth associated with infection by either nematode species suggests that it is later generations of the nematode that directly relate to yield suppression of susceptible cultivars. The negative correlation between yield and Pi would still be apparent if this were the case, because numbers of nematodes of both species penetrating roots was closely related to Pi. Increases in root growth would provide more sites for nematode invasion; however, we found no evidence of interactions between Hg and Mi during early seedling growth.

Numbers of both nematode species penetrating roots was closely related to Pi in all experiments, but Mi was more responsive to changes in environmental conditions than was Hg. For example, Mi, but not Hg, penetrated roots more quickly in sand than in soil both in the greenhouse and field. Similarly, Mi developed more rapidly in August than in June in microplots, whereas Hg developed at the same rate in both August and June. Our studies confirmed observations that both Hg and Mi J2 readily penetrate roots of both resistant and susceptible soybean cultivars (7,26).

In conclusion, we found in both greenhouse and microplot studies that plant and nematode responses occurring early in the establishment of soybean–Hg and soybean–Mi relationships are generally similar. Soybean cultivars responded similarly to most treatments irrespective of genotypic differences in nematode resistance. No evidence of interaction between Hg and Mi affecting plant or nematode responses was found, but increases in root length in the presence of either nematode species might provide a mechanism for later interaction by increasing the number of potential invasion sites. This stimulatory response to infection also suggests that later generations of nematodes are responsible for yield loss.

TABLE 8. Effects of *Heterodera glycines* (Hg) and *Meloidogyne incognita* (Mi) alone and in combination on root lengths (cm) of three soybean cultivars 14 days after planting in infested field microplots near Athens, Georgia.

Cultivar	Root lengths (cm)			
	None	Hg alone	Mi alone	Hg + Mi
Braxton	341	292	534	578
Centennial	329	441	782	538
Coker 237	300	393	980	752

* Least significant difference for comparison of cultivar means ($\alpha = 0.05$) = 163.

LITERATURE CITED

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

2. Boerma, H. R., and R. S. Hussey. 1984. Tol-

erance to *Heterodera glycines* in soybean. Journal of Nematology 16:289–296.

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

4. Byrd, D. W., Jr., T. Kirkpatrick, and K. R. Barker. 1983. An improved technique for clearing and staining plant tissues for detection of nematodes. Journal of Nematology 15:142–143.

5. Crittenden, H. W. 1959. Production of lateral roots in soybean varieties resistant and susceptible to *Meloidogyne incognita acrita.* Phytopathology 49:523 (Abstr.).

6. Crittenden, H. W. 1954. Factors associated with root-knot nematode resistance in soybean. Phytopathology 44:388 (Abstr.).

7. Endo, B. Y. 1965. Histological responses of resistant and susceptible varieties, and backcross progeny to entry and development of *Heterodera glycines.* Phytopathology 55:375–381.

8. Ferris, H. 1976. Development of a computer-simulation model for a plant-nematode system. Journal of Nematology 8:255–263.

9. Hallmark, W. B., and S. A. Barber. 1981. Root growth and morphology, nutrient uptake, and nutrient status of soybeans as affected by soil K and bulk density. Agronomy Journal 73:779–782.

10. Hoagland, D. R., and W. C. Snyder. 1933. Nutrition of strawberry plants under controlled conditions. (a) Effects of deficiencies of boron and certain other elements. (b) Susceptibility to injury from sodium salts. Proceedings of the American Society for Horticultural Science 30:288.

11. 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.

12. Ibrahim, I. K. A., I. A. Ibrahim, and S. I. Massoud. 1972. Induction of galling and lateral roots on five varieties of soybeans by *Meloidogyne javanica* and *M. incognita.* Plant Disease Reporter 56:882–884.

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

14. Mitchell, R. L., and W. J. Russell. 1971. Root development and rooting patterns of soybean (*Glycine max* (L.) Merrill) evaluated under field conditions. Agronomy Journal 63:313–316.

15. Niblack, T. L., R. S. Hussey, and H. R. Boerma. 1986. Effects of environments, *Meloidogyne incognita* inoculum levels, and *Glycine max* genotype on root-knot nematode-soybean interactions in field microplots. Journal of Nematology 18:338–346.

16. Niblack, T. L., R. S. Hussey, and H. R. Boerma. 1986. Effects of interactions among *Heterodera glycines, Meloidogyne incognita,* and host genotype on soybean yield and nematode population densities. Journal of Nematology 18:436–443.

17. Raper, C. D., Jr., and S. A. Barber. 1970. Rooting systems of soybeans. I. Differences in root morphology among varieties. Agronomy Journal 62: 581–584.

18. Schmitt, D. P., and G. R. Noel. 1984. Nematode parasites of soybeans. Pp. 13–59 *in* W. R. Nickle, ed. Plant and insect nematodes. New York: Marcel Dekker.

19. Shane, W. W., and K. R. Barker. 1986. Effects of temperature, plant age, soil texture, and *Meloidogyne incognita* on early growth of soybean. Journal of Nematology 18:320–327.

20. Simon, A., and A. D. Rovira. 1982. The relation between wheat yield and early damage of roots by the cereal cyst nematode. Australian Journal of Experimental Agriculture and Animal Husbandry 22: 201–208.

21. Southey, J. F. 1970. Laboratory methods for work with plant and soil nematodes. Technical Bulletin 2. London: Ministry of Agriculture, Fisheries, and Food.

22. Spaull, A. M. 1981. A simple and reliable method of estimating root length. Nematologica 27: 119.

23. Spaull, A. M. 1979. Effect of the cereal cyst nematode, *Heterodera avenae,* on the early growth of oats, wheat, and barley. Plant Pathology 28:138–142.

24. Tennant, D. 1975. A test of a modified line intersect method of estimating root length. Journal of Ecology 63:995–1001.

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

26. Veech, J. A., and B. Y. Endo. 1970. Comparative morphology and enzyme histochemistry of root-knot resistant and susceptible soybean. Phytopathology 60:896–902.