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Effects of Interactions among *Heterodera glycines*, *Meloidogyne incognita*, and Host Genotype on Soybean Yield and Nematode Population Densities[1]

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Abstract: The effects of host genotype and initial nematode population densities (Pi) on yield of soybean and soil population densities of *Heterodera glycines* (Hg) race 3 and *Meloidogyne incognita* (Mi) race 3 were studied in a greenhouse and field microplots in 1983 and 1984. Centennial (resistant to Hg and Mi), Braxton (resistant to Mi, susceptible to Hg), and Coker 237 (susceptible to Hg and Mi) were planted in soil infested with 0, 31, or 124 eggs of Hg and Mi, individually and in all combinations, per 100 cm^3 soil. Yield responses of the soybean cultivars to individual and combined infestations of Hg and Mi were primarily dependent on soybean resistance or susceptibility to each species separately. Yield of Centennial was stimulated or unaffected by nematode treatments, yield of Braxton was suppressed by Hg only, and yield suppressions caused by Hg and Mi were additive and dependent on Pi for Coker 237. Other plant responses to nematodes were also dependent on host resistance or susceptibility. Population densities of Mi second-stage juveniles (J2) in soil were related to Mi Pi and remained constant in the presence of Hg for all three cultivars. Population densities of Hg J2 on the two Hg-susceptible cultivars, Braxton and Coker 237, were suppressed in the presence of Mi at low Hg Pi.

Key words: soybean cyst nematode, root-knot nematode, *Glycine max*, interaction, microplot, *Heterodera glycines*, *Meloidogyne incognita*.

The soybean cyst nematode, *Heterodera glycines* Ichinohe (Hg), and the southern root-knot nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood (Mi), are major pathogens of soybean (*Glycine max* (L.) Merr.) (15,16). Concomitant infestations currently represent approximately 10% of the total number of fields infested with either species alone in both Georgia (T. L. Niblack and R. E. Motsinger, unpubl.) and Alabama (23). Soybean genotypes in use or under development in Georgia are routinely screened for resistance to each species (6,19), because planting resistant cultivars is currently the most economical nematode control method available to growers.

Plant resistance is characterized by lower nematode reproduction than on a standard susceptible plant (5) and is a distinct phenomenon for each nematode species and race, although breeders often incorporate resistance to more than one species into a cultivar. Mi reproduction can be considerable on resistant soybean cultivars, and even cultivars considered to be resistant may sustain yield suppression with high initial population densities (Pi) of Mi (15). Reproduction of Hg is generally much lower on resistant than on susceptible soybean cultivars (11).

The expression of resistance to a single nematode species, and consequent effects on plant growth and yield, may be affected by factors other than host genotype, including multiple species of plant pathogenic nematodes (2,7). The potential for economically significant nematode–nematode interactions seems high when two nematodes with similar host–parasite relationships are involved. For example, Eisenback (8) reported a resistance-breaking effect when two *Meloidogyne* species fed concomitantly on tobacco. Most studies with concomitant species of sedentary endoparasites, however, have concentrated on nematode reproduction rather than disease etiology. Ross (21) suggested interactions in microplots between Hg and Mi on Lee soybean, susceptible to both species, with reproduction of both species and plant yields affected. Because concomitant infestations of Hg and Mi are common in soybean fields, and because cultivars resistant to one or both nematodes are frequently planted, studies were undertaken in field microplots and in the greenhouse to de-

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termine how interactions among these two nematode species and soybean genotypes affected plant growth and yield and nematode population dynamics.

Materials and Methods

Soybean cultivars Braxton (Maturity Group [MG] VII; Mi resistant, Hg susceptible), Centennial (late MG VI; Hg and Mi resistant), and Coker 237 (MG VII; Hg and Mi susceptible) were chosen because of their known performance and current wide use in Georgia (6,19).

Cultures of Hg race 3 (10) and Mi race 3 (22) were maintained in the greenhouse. The Hg isolate was cultured on Lee soybean, from which eggs for inoculum were obtained (3). Mi was cultured on tomato (*Lycopersicon esculentum* Mill. cv. Rutgers), and eggs for inoculum were collected using 0.5% NaOCl (12).

Second-stage juveniles (J2) were extracted from soil by a combination of elutriation (4) and centrifugal-flotation (14), for which our efficiency is ca. 20% for Mi and 35% for Hg for both field and greenhouse soils. Nematode data were adjusted for extraction efficiency, then transformed to $\log_{10}(X + 1)$ values to remove a correlation between treatment means and variances. Nematode population densities reported are antilogs of the analyzed data.

Microplot experiments: In 1983 and 1984, experiments were conducted in 80-cm-d fiberglass microplots (1) at the University of Georgia Plant Sciences Farm near Athens. The microplots were established in Appling coarse sandy loam (Typic Hapludult, clayey, kaolinitic, thermic, 73% sand, 12% clay, 15% silt). Microplots and immediately adjacent plot land were limed and fertilized according to University of Georgia Extension Services soil test recommendations. Microplots were fumigated with methyl bromide at 0.12–0.19 kg/m^2 4 weeks before planting. Plot land surrounding the microplots was treated with ethylene dibromide (EDB) for nematode control and trifluralin ($\alpha\alpha\alpha$-trifluoro-2,6-dinitro-N,N-dipropyl-p-toluidine, Treflan, 0.56 kg a.i./ha) for weed control before planting in 1983 but not in 1984.

Planting dates were 27 May 1983 and 7 June 1984. The day before planting, appropriate nematode Pi were provided by adding eggs or egg-free filtrate, diluted in 1,600 ml tap water, to the top 23 cm of soil in each microplot. Pi were 0, 31, and 125 eggs/100 cm^3 soil in 1983 and 0, 31, 125, and 250 eggs/100 cm^3 soil in 1984. At planting, spores of mycorrhizal fungi (*Gigaspora margarita* and *Glomus etunicatum*) and commercial inoculum of *Bradyrhizobium japonicum* were added to each microplot within the row. Forty-five seed were planted in a row in the center of each microplot, and the seedlings were thinned to 20 per plot after 7–10 days. To simulate field row conditions, seed of the cultivar planted inside the microplot were also planted in the border rows (96.5 cm apart) on either side of the microplot and between microplots within the row. Irrigation was provided as needed.

Soil samples were taken from each microplot at 60, 90, and 120 days after planting for extraction of J2. Samples analyzed were 250 cm^3 from a composite of six 2.5-cm-d cores taken to 20–30 cm deep. Plant height was measured on three randomly selected plants per plot at each soil sampling date. Stage of development (9) was determined for three plants per microplot at 30, 60, and 90 days after planting. Plant maturity was recorded as the date on which 95% of the pods had mature color. Seed were harvested mechanically, and seed yield (g/microplot) and weight (g/100 seed) were measured after adjustment to 13% moisture. Seed oil and protein content (%) determinations were provided in 1984 by the Northern Regional Research Center, USDA SEA, Peoria, Ill.

Factorial treatment combinations (cultivar × Hg Pi × Mi Pi) comprised each block of the randomized complete block experimental design used in both experiments, replicated four times in 1983 and five times in 1984. In 1983 the treatment design was a complete factorial. In 1984 an incomplete factorial was used, with the high Hg and Mi Pi (250 eggs/100 cm^3 soil) included to compare effects of total nematode numbers; i.e., 250 of a single species compared with 125 each of the two species. The high Pi (monospecific treatment) was not included in analyses of data combined for the 2 years. Analyses of variance were conducted for all response variables in each year, assuming a mixed model with fixed

TABLE 1. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination on plant height relative to noninoculated controls of three soybean cultivars grown in field microplots near Athens, Georgia, during 1983 and 1984.

	Hg PI*								
	Braxton†			Centennial‡			Coker 237†		
Mi Pi*	0	31	124	0	31	124	0	31	124
0	1.00	1.00	0.92	1.00	1.02	1.00	1.00	0.88	0.82
31	1.12	0.99	0.94	1.09	1.00	1.10	0.92	0.86	0.89
124	1.22	1.09	0.93	1.03	1.07	1.08	1.00	0.92	0.82

* Pi = initial population density of eggs/100 cm^3 soil.

† For Braxton and Coker 237: Significant Hg main effect due to average effect (presence vs. absence) of Hg; no Mi main effect or Hg × Mi interaction.

‡ For Centennial: Significant Mi main effect due to average effect (presence vs. absence) of Mi; no Hg main effect or Hg × Mi interaction.

Hg, Mi, and cultivar effects, fixed interaction terms for each factor, and random replication effects. A random year effect was included for analyses of combined data. Qualitative effects (average effect of nematode species presence vs. absence), quantitative effects (over Pi), and interactions were investigated using planned orthogonal sets of single degree of freedom comparisons.

Greenhouse experiments: Three greenhouse experiments were conducted, one identical in design to the 1983 microplot experiment and the other two identical to the 1984 microplot experiment. In each greenhouse experiment, 1,600 cm^3 sterilized soil in 15-cm-d plastic pots was infested with eggs to obtain an appropriate nematode species × Pi treatment combination. Three seed of the desired cultivar were planted per pot and thinned to one plant per pot after 7 days. Plants were fertilized at 14-day intervals with a soluble trace element mix and 20-20-20 (N = 20%, P = 8.7%, K = 16.6%). Each experiment was terminated at 65 days after planting, at which time 500 cm^3 soil was processed for J2, and shoot height, shoot fresh and dry weight, and root fresh weight were recorded. Data analysis was similar to that described for microplots.

RESULTS

Error variances among cultivars were heterogeneous ($P < 0.01$) for all plant responses measured. None of the commonly used data transformations (log, square root, arc-sine) provided homogeneous variances. The problem was overcome by completing separate analyses for each cultivar; therefore, no direct statistical comparisons of cultivar effects were possible without violating the assumptions required for such comparisons.

Microplot experiments: In analyses of relative plant heights (height of treated plant/height of noninoculated control), no year main effects of interactions were detected; at 120 days, the average effect of Hg was reduction in plant height of Braxton and Coker 237, and the average effect of Mi on Centennial was increase in plant height (Table 1). The analyses for 60 and 90 days were consistent with those for 120 days. Regardless of treatment combination or time of measurement, actual plant heights averaged 19% lower in 1983 than in 1984. Overall plant heights at 120 days in 1983 and 1984 were, respectively, 64.7 and 76.8 cm for Braxton, 65.8 and 83.4 cm for Centennial, and 50.3 and 62.6 cm for Coker 237. In 1983 plant heights increased an average of 20% between 60 and 120 days, whereas in 1984 the increase was 11% during the same period. In each year and in

TABLE 2. Correlations (r) among relative plant heights on three sampling dates and relative seed yield for three soybean cultivars in field microplots near Athens, Georgia, during 1983 and 1984.

	Braxton		Centennial		Coker 237	
	120 days	Yield	120 days	Yield	120 days	Yield
60 days	0.93	0.65	0.96	0.51	0.95	0.52
90 days	0.98	0.63	0.99	0.51	0.97	0.53
120 days		0.62		0.50		0.54

TABLE 3. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination on seed yield relative to noninoculated controls of three soybean cultivars grown in field microplots near Athens, Georgia, in 1983 and 1984.

	Hg Pi*								
	Braxton†			Centennial‡			Coker 237§		
Mi Pi*	0	31	124	0	31	124	0	31	124
0	1.00	0.46	0.34	1.00	0.93	1.07	1.00	0.57	0.43
31	1.01	0.49	0.37	1.09	1.27	1.18	0.91	0.49	0.27
124	0.99	0.52	0.34	1.07	1.19	1.23	0.70	0.32	0.14

* Pi = initial population density of eggs/100 cm^3 soil.
† Significant Hg main effect due to average effect (presence vs. absence) of Hg; no Mi main effect or Hg × Mi interaction.
‡ Significant Hg × Mi interaction.
§ Significant linear Hg main effect; significant linear Mi effect; no Hg × Mi interaction.

combined analysis, however, relative plant heights at 60 and 90 days were highly correlated ($P < 0.01$) with heights at 120 days, and the correlations between relative heights at each sampling date and relative yields were very similar within cultivars and did not increase as the season progressed (Table 2).

Stages of plant development and maturity dates were unaffected by nematode treatment combinations for all three cultivars in 1983, but in 1984 Hg delayed the Braxton maturity date by 4 days. All three cultivars matured later in 1983 than in 1984. Irrespective of nematode treatments, plant maturity dates for October 1983 and 1984, respectively, were 22 and 17 for Braxton, 19 and 14 for Centennial, and 19 and 13 for Coker 237.

Expression of seed yields as values relative to the check treatments removed a year main effect (Table 3). Analyses of relative yields revealed that Hg suppressed Braxton yield irrespective of Mi Pi, yield reduction was additive for Hg and Mi on Coker 237, and yield increased up to 27% with a significant Hg × Mi interaction on Centennial. All actual seed yields were higher in 1983 than in 1984.

Seed weight (g/100 seed) was greater in 1984 than in 1983 for Braxton and Centennial but not for Coker 237; data from 1984 are presented (Table 4). Nematode treatment did not affect Centennial seed weight either year, Braxton seed weight increased with Mi in both years, and Coker 237 seed weight was suppressed by both Hg and Mi in both years. No Hg × Mi seed weight interactions were detected.

Seed protein content increased with Hg for Braxton and Coker 237 (Table 5). No other nematode–cultivar combination affected seed protein content. Seed oil content was 19.4% for Braxton, 20.3% for Centennial, and 18.9% for Coker 237, with no nematode effects.

There was no significant year effect on Hg and Mi soil population densities at 60

TABLE 4. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination on seed weight (g/100 seed) of three soybean cultivars grown in field microplots near Athens, Georgia, in 1984.

	Hg Pi*											
	Braxton†				Centennial‡				Coker 237§			
Mi Pi*	0	31	124	250	0	31	124	250	0	31	124	250
0	14.8	15.6	15.7	15.4	12.9	12.7	12.8	12.9	11.7	11.8	11.3	10.7
31	15.9	16.4	16.1		12.0	12.5	13.4		11.8	13.5	11.4	
124	15.6	15.3	14.6		12.2	13.8	13.0		9.8	10.8	9.5	
250	14.9				12.4				9.4			

* Pi = initial population density of eggs/100 cm^3 soil.
† Significant Mi main effect due to average effect (presence vs. absence) of Mi; no Hg main effect or Hg × Mi interaction.
‡ No significant Hg or Mi main effects or Hg × Mi interaction.
§ Significant Hg main effect due to average effect (presence vs. absence) of Hg; significant Mi main effect due to average effect (presence vs. absence) of Mi; no Hg × Mi interaction.

TABLE 5. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination on seed protein content (%) of three soybean cultivars grown in field microplots near Athens, Georgia, 1984.

	Hg Pi*											
	Braxton†				Centennial‡				Coker 237†			
Mi Pi*	0	31	124	250	0	31	124	250	0	31	124	250
0	37.5	41.1	42.3	41.8	39.0	38.7	38.8	38.6	39.5	42.9	42.4	41.4
31	39.7	42.0	41.8		40.1	38.8	39.2		39.9	44.0	42.3	
124	37.5	42.1	42.2		38.3	39.2	38.4		41.9	42.2	43.1	
250	38.3				38.0				40.8			

* Pi = initial population density of eggs/100 cm³ soil.
† For Braxton and Coker 237: significant Hg main effect due to average effect (presence vs. absence) of Hg; no Mi main effect or Hg × Mi interaction.
‡ No significant Hg or Mi main effects or Hg × Mi interaction.

and 90 days after planting for any cultivar, and densities for each nematode species were independent of the Pi of the other species. At 120 days after planting in 1984, however, soils were extremely dry despite irrigation, and recovery of live J2 of both species was erratic. Coefficients of variation exceeded 200% for log-transformed data, and data transformations failed to remove the correlation between means and variance; hence, the data reported herein for 120 days after planting are from 1983 only.

Soil population densities of Hg on Braxton at 120 days were influenced by an Hg × Mi interaction (Table 6). Hg densities at the low Hg Pi were significantly higher in the absence than in the presence of Mi at either Mi Pi. Conversely, at the high Hg Pi, Hg densities increased linearly over Mi Pi. Hg densities on Centennial were unaffected by nematode treatment combination, but on Coker 237 Hg densities were influenced by both Hg and Mi Pi. At the low Hg Pi, Hg densities on Coker 237 were significantly higher in the absence of Mi, similar to the response for Braxton. At the high Hg Pi, however, densities were lower than at the low Hg Pi at all Mi Pi and did not differ among Mi Pi.

Mi densities on all three cultivars were influenced by highly significant Mi main effects but were not affected by Hg (Table 7).

Greenhouse experiments: Increasing Hg Pi resulted in a linear suppression of shoot weight for Braxton and Coker 237 (Table 8). Mi suppressed shoot weight only on Braxton, and no Hg × Mi interaction was detected for any cultivar. A pattern of responses identical to that for shoot weight was observed for plant height, except that Mi did not decrease height of Braxton plants. Root fresh weights were unaffected

TABLE 6. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination, and soybean genotype on soil population densities (number of second-stage juveniles/100 cm³ soil) of *H. glycines* 120 days after infestation of field microplots near Athens, Georgia, in 1983.

	Hg Pi*					
	Braxton†		Centennial‡		Coker 237§	
Mi Pi*	31	124	31	124	31	124
0	3,034	682	4	10	5,527	273
31	2,156	1,341	18	14	470	60
124	1,384	4,659	12	12	1,218	399

* Pi = initial population density of eggs/100 cm³ soil.
† Significant Hg × Mi interaction.
‡ No Hg or Mi main effect, no Hg × Mi interaction.
§ Significant Hg main effect; significant Mi main effect due to average effect (presence vs. absence) of Mi; no Hg × Mi interaction.

TABLE 7. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination, and soybean genotype on soil population densities (number of second-stage juveniles/100 cm³ soil) of *M. incognita* 120 days after infestation of field microplots near Athens, Georgia, 1983.

	Mi Pi*					
	Braxton†		Centennial†		Coker 237†	
Hg Pi*	31	124	31	124	31	124
0	224	683	72	300	74	938
31	169	861	78	166	503	958
124	328	1,772	48	358	831	1,030

* Pi = initial population density of eggs/100 cm³ soil.
† For all three cultivars: Significant Mi main effect; no Hg main effect or Hg × Mi interaction.

TABLE 8. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination on shoot dry weight (g) of three soybean cultivars at 65 days after planting in the greenhouse.

	Hg Pi*											
	Braxton†				Centennial‡				Coker 237§			
Mi Pi*	0	31	124	250	0	31	124	250	0	31	124	250
0	16.3	15.1	14.4	14.0	15.0	15.7	16.2	15.4	14.8	14.1	13.4	12.2
31	15.3	14.8	14.3		15.9	15.8	15.6		14.7	14.7	13.8	
124	15.4	14.2	13.0		16.3	15.9	15.1		14.1	12.8	12.9	
250	14.2				15.7				14.2			

* Pi = initial population density of eggs/100 cm^3 soil.
† Significant linear Hg main effect; significant Mi main effect due to average effect (presence vs. absence) of Mi; no Hg × Mi interaction.
‡ No significant Hg or Mi main effects, or Hg × Mi interaction.
§ Significant linear Hg main effect; no significant Mi main effect or Hg × Mi interaction.

by Hg for any cultivar and unaffected by Mi on Centennial and Braxton, but they were significantly increased on Coker 237 by Mi.

Nematode soil population density data were highly variable. Coefficients of variation for J2 densities of both species ranged upward from 60%. Despite variability, some general trends were discernible. Mi J2 densities were dependent on Mi Pi for all three cultivars (Table 9) and were unaffected by Hg. Hg J2 densities on Braxton were dependent on Pi and were extremely low for all Centennial treatment combinations (Table 10). On Coker 237, Hg J2 densities were nearly 90% lower in the presence than in the absence of Mi.

DISCUSSION

The response of a soybean cultivar to single and combined infestations of Hg and Mi was primarily dependent on plant resistance or susceptibility to each nematode species. Although direct statistical comparison of cultivar responses was not possible, we observed consistent plant genotype-dependent responses. Furthermore, we observed within-cultivar similarity of various plant responses in both field microplots and greenhouse in which statistical interactions between Hg and Mi were infrequently detected. Hg caused yield suppressions on the two Hg-susceptible cultivars, Braxton and Coker 237, without detectable interaction with Mi. Braxton and Centennial, resistant to Mi, expressed this resistance regardless of concomitant Hg. Yield increases associated with the presence of Mi on the resistant cultivars Braxton and Centennial were similar to those reported by Niblack et al. (17) for soybean–Mi relationships. Both Hg and Mi caused significant yield suppression on sus-

TABLE 9. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination, and soybean genotype on soil populations densities (number of second-stage juveniles/100 cm^3 soil) of *M. incognita* 65 days after planting in the greenhouse.

	Mi Pi*					
	Braxton†		Centennial†		Coker 237†	
Hg Pi*	31	124	31	124	31	124
0	52	116	38	130	128	176
31	39	89	26	68	116	158
124	48	118	42	86	122	174

* Pi = initial population density of eggs/100 cm^3 soil.
† For all three cultivars: Significant Mi main effect; no Hg main effect or Hg × Mi interaction.

TABLE 10. Effects of *Meloidogyne incognita* (Mi) and *Heterodera glycines* (Hg) alone and in combination, and soybean genotype on soil population densities (number of second-stage juveniles/100 cm^3 soil) of *H. glycines* 65 days after planting in the greenhouse.

	Hg Pi*					
	Braxton†		Centennial†		Coker 237‡	
Mi Pi*	31	124	31	124	31	124
0	84	113	2	3	1,237	1,313
31	52	85	1	3	162	158
124	22	73	2	3	139	136

* Pi = initial population density of eggs/100 cm^3 soil.
† For Braxton and Centennial: Significant Hg main effect; no Mi main effect or Hg × Mi interaction.
‡ For Coker 237: Significant Hg main effect; significant Mi main effect due to average effect (presence vs. absence) of Mi; no Hg × Mi interaction.

ceptible Coker 237, and yield suppression was additive in combined infestations. Our results for this cultivar are consistent with results for Lee soybean, also susceptible to both species, regarding yield suppression (21). In our study, in contrast to other findings (20,21), the protein content of seed increased with Hg on both Hg-susceptible cultivars and was unaffected in any cultivar by Mi. Nematode treatments had no effect on seed protein content of the Hg-resistant Centennial or on seed oil content of any cultivar. Protein content of soybeans can also be affected by cultural conditions (18). Significant year effects for plant height, seed yield, maturity date, and seed weight for each cultivar were generally unrelated to nematode treatment and disappeared in analyses of relative values; therefore, the relative nematode effects were not environment dependent.

Our results provide evidence that Mi and Hg do not mutually affect resistance as expressed in plant responses within the boundaries of a single growing season and at moderate Pi. Another potentially important effect of species interactions may be on final (postharvest) population densities and, thus, Pi the following season. Mi population densities were related only to Mi Pi on all three cultivars in both greenhouse and microplots; on Centennial, Hg densities were dependent on Hg Pi only. On Braxton, the Hg × Mi interaction effect on Hg densities observed in the microplots was not detected in the greenhouse. On Coker 237, Hg densities were 10 times higher in the absence than in the presence of Mi regardless of Hg Pi in the greenhouse; in microplots a similar but less pronounced relationship occurred at the low Hg Pi. Hg densities at the high Hg Pi in microplots were considerably lower than at the low Hg Pi and unrelated to Mi Pi; this reflected a suppressive effect of Hg, perhaps through restriction of root growth. A comparable relationship was also observed by Ross (21) in 2 of 3 years, but his reported suppression of Mi by Hg did not occur in our study. That Mi did not suppress Hg may be explained by our use of relatively low Pi and a highly virulent Mi isolate (13,24); thus, we suggest that interactions may be both soybean genotype and nematode genotype dependent. Our data suggest, however, that the presence of an Mi infestation in a field may retard buildup of an Hg infestation on a susceptible cultivar, perhaps masking a potential problem to the grower.

Our experimental approach limited the number of Pi that could be included and therefore limited the range of Pi over which our conclusions could apply. Data from microplots and the greenhouse corresponded fairly well; thus, future investigation of interactions could be conducted in less labor-intensive studies in the greenhouse and could yield useful applied information. We demonstrated that at nematode Pi sufficient to cause severe damage to susceptible cultivars in the field, interaction between Hg and Mi does not affect plant yield responses within a growing season. The effects of the two nematodes were additive and Pi dependent on a cultivar lacking resistance. Mi population densities were unaffected by Hg irrespective of Pi, but Hg densities were higher in the absence of Mi if the cultivar were Hg susceptible.

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