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Pathogenicity and Reproduction of *Hoplolaimus columbus* and *Meloidogyne incognita* on 'Davis' Soybean[1]

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Abstract: The effects of initial populations of *Hoplolaimus columbus* and *Meloidogyne incognita* on growth and yield of Davis soybean were determined for 1980 and 1981 in microplots and *H. columbus* in field tests in 1981. *M. incognita* suppressed yield in microplots both years and *H. columbus* in 1980. Maximum suppression of dry pod weight by *M. incognita* was 45% and by *H. columbus* 35%. The relationship of yield vs. nematode population at planting time was described by a declining exponential model. Maximum reproductive rates for *M. incognita* and *H. columbus* were 67.0 and 4.7, respectively, and were inversely proportional to initial population level. Nematode reproductive rates, survival ability, and feeding habits suggest species specific life strategies in the ecological community.

Key words: ecology, *Glycine max*, lance nematode, root-knot nematode, reproduction threshold.

Meloidogyne incognita (Kofoid and White) Chitwood, prevalent in soybean (*Glycine max* [L.] Merr.) fields of the Southern Coastal Plain of the United States, can suppress yields by 32–90% in susceptible cultivars (9). However, its severity depends on factors such as climate, initial population level, nematode isolate, and cultivar (1). *Hoplolaimus columbus* Sher also parasitizes soybean and suppresses yields (11), and occurs in several states in the Southern Coastal Plain reproducing on many field crops (10).

Quantitative relationships between nematode populations and crop response affect environmental and economic crop management decisions (6,8,12,13). Growers and advisors often request information about nematode–crop relationships from advisory services to aid in making management decisions. Eventually, quantitative data might be used to determine nematode populations below which expenditure on a control strategy would not be economical. Considerable research is in progress to describe empirical relationships of nematodes with yield before economic analysis of crop production strategies involving nematodes is undertaken.

The objectives of these studies were to (i) determine the effect of the initial population of *H. columbus* or *M. incognita* on yield of 'Davis' soybean, a cultivar susceptible to both nematodes; (ii) describe a nematode population–plant injury relationship for each nematode; and (iii) determine the reproductive potentials of *H. columbus* and *M. incognita* on soybean.

MATERIALS AND METHODS

Microplot studies: Inoculum of *H. columbus* was cultured on 6-week-old cotton (*Gossypium hirsutum* L. 'Coker 310') in water temperature tanks at 30 C, and *M. incognita* was cultured on 4-week-old tomato transplants (*Lycopersicon esculentum* L. 'Rutgers') in water temperature tanks at 27 C in the greenhouse. Microplots (0.8 m^2 surface area × 0.6 m deep) were established at Edisto Experiment Station, Blackville, South

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Carolina, in a Varina sandy loam soil and were fumigated each year with 0.4 kg methyl bromide. Nematodes were added in water suspension to provide populations of 0, 25, 50, 75, 100, 125, 150, 200, 300, and 600/100 cm^3 of soil. Microplots were infested with adults and juveniles of *H. columbus,* or eggs and second-stage juveniles of *M. incognita,* by gently mixing in 11.4 liters of soil removed from each plot and then replaced. *Glomus macrocarpus,* an endomycorrhizal fungus, was added to the soil at the rate of 650 chlamydospores/microplot in Experiment 1 (1980) and 350 in Experiment 2 (1981). Twelve seeds were planted in a single row (30–33 cm) and inoculated with a fresh culture of *Rhizobium japonicum.* After germination, plants were thinned to seven plants per microplot. Plots were limed and fertilized according to soil test recommendations. Treatments were replicated five times in a randomized complete block with a split-plot design; nematode species were whole plots and infestation levels were subplots. Soybeans cv. Davis were planted 3 June 1980 (Experiment 1) and 25 May 1981 (Experiment 2). Growing conditions were poor in 1980, because of high temperatures and severe drought, but excellent in 1981.

Plant growth and nematode populations were measured at physiological maturity (5) in Experiment 1 and at harvest maturity (5) in Experiment 2. Plant heights, weights of shoots, pods, and roots, and numbers of nodules per root system were recorded. Final nematode populations in soil were obtained by elutriation (2) and centrifugal-flotation. *H. columbus* inoculum and final populations were extracted from roots using a mist system (2) with 100 mg/liter zinc sulfate added to facilitate extraction (3). *M. incognita* eggs and juveniles for inoculum and final populations were extracted from roots by the dilute NaOCl method (7) modified by macerating the roots in a blender with NaOCl for 4 minutes.

Data were subjected to analysis of variance. The relationships between plant growth characteristics and initial and final nematode populations were analyzed with linear and nonlinear least-squares models.

Field study: Davis soybeans were sown at 8 seeds/30 cm of row in two Varina sandy loam fields near Blackville, South Carolina, on 29 May 1981. Sixty one-row, 1.5-m-long plots were established 2 days after sowing. The initial population level of *H. columbus* was estimated by assaying a composited soil sample (10 random cores, 25-cm-long × 2.5-cm-d) collected from individual plots. Nematodes were extracted as described previously. Plant growth data and soil and root nematode densities at harvest were determined as in the microplot study. Data were analyzed by correlation analysis. *Meloidogyne* sp. was not present in these fields.

Results

Microplots—plant growth: H. columbus strongly affected ($P \leq 0.05$) mean shoot and pod weight, plant height, and nodules per root system in Experiment 1 but not in Experiment 2. Least-squares analysis described the relationship between soybean growth and initial population level (P_i) as declining curvilinearly (Fig. 1). The largest population of *H. columbus* caused 44% and 13% suppression of dry pod weight in Experiments 1 and 2, respectively. The lower confidence interval ($\alpha = 0.05$) for dry pod weight represented 28% and 17% of the checks for Experiments 1 and 2, respectively.

M. incognita affected Davis soybean in both experiments. Numbers of nodules, plant heights, and weights of shoots and pods were suppressed with increasing levels of *M. incognita* ($P \leq 0.05$) in Experiment 1. The relationships were curvilinear except for plant height, which was linear (Fig. 2). In the second experiment, shoot and pod weights were suppressed ($P = 0.01$) with increasing population densities of *M. incognita,* but not height ($P = 0.09$). *M. incognita* suppressed dry pod weight by a maximum of 45% and 31% in Experiments 1 and 2, respectively. The lower confidence interval ($\alpha = 0.05$) for pod weight represented 24% and 19% of the checks, for Experiments 1 and 2, respectively. Fresh root weights increased ($P = 0.01$) with increasing P_i in both experiments (Fig. 3).

H. columbus and *M. incognita* may have also affected plant nodulation. When plants were harvested at physiological maturity in Experiment 1, nodules per root system declined with increasing nematode density. In Experiment 2, when plants were harvested after onset of leaf abscission, no re-

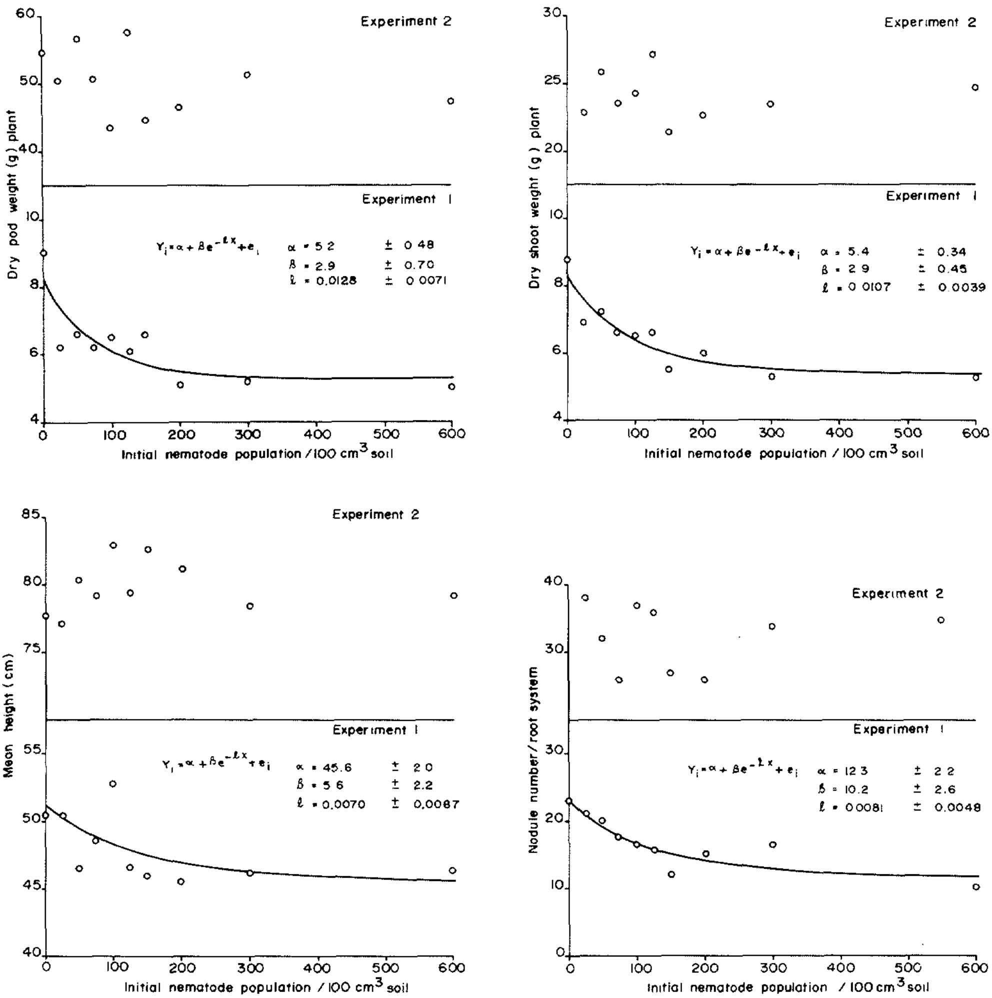

FIG. 1. Relationships of height, nodules per root system, and shoot and pod weights of 'Davis' soybean to initial populations of *Hoplolaimus columbus* in microplots.

lation was found between initial nematode numbers and nodule number. Chlorosis was not observed in either experiment.

Microplots—nematode reproduction: Final populations (P_f) of *H. columbus* were larger ($P = 0.01$) than P_is (Table 1) and increased curvilinearly ($P = 0.01$). Final root and soil populations of *M. incognita* (Table 2) also increased curvilinearly ($P = 0.01$) as a function of increasing P_i in Experiment 2, but the relationship was linear ($P = 0.01$) in Experiment 1. Davis soybean was considered a good host because the maximum rate of reproduction was high and the equilibrium density, if achieved, would have been large. Nematode populations of either species in the soil represented 7–16% of the total P_f. The maximum rate of reproduction of *M. incognita* was 14 times greater than that of *H. columbus* in 1981. P_f of *H. columbus* in roots was not determined in 1980.

Field study: Negative correlations between *H. columbus* and dry pod, shoot, and seed weights and height of Davis soybean were significant ($P = 0.05$), indicating suppressed soybean growth was associated, though weakly ($r = -0.29$ to -0.48), with increasing P_i in field one (Table 3). No correlations between *H. columbus* and soybean

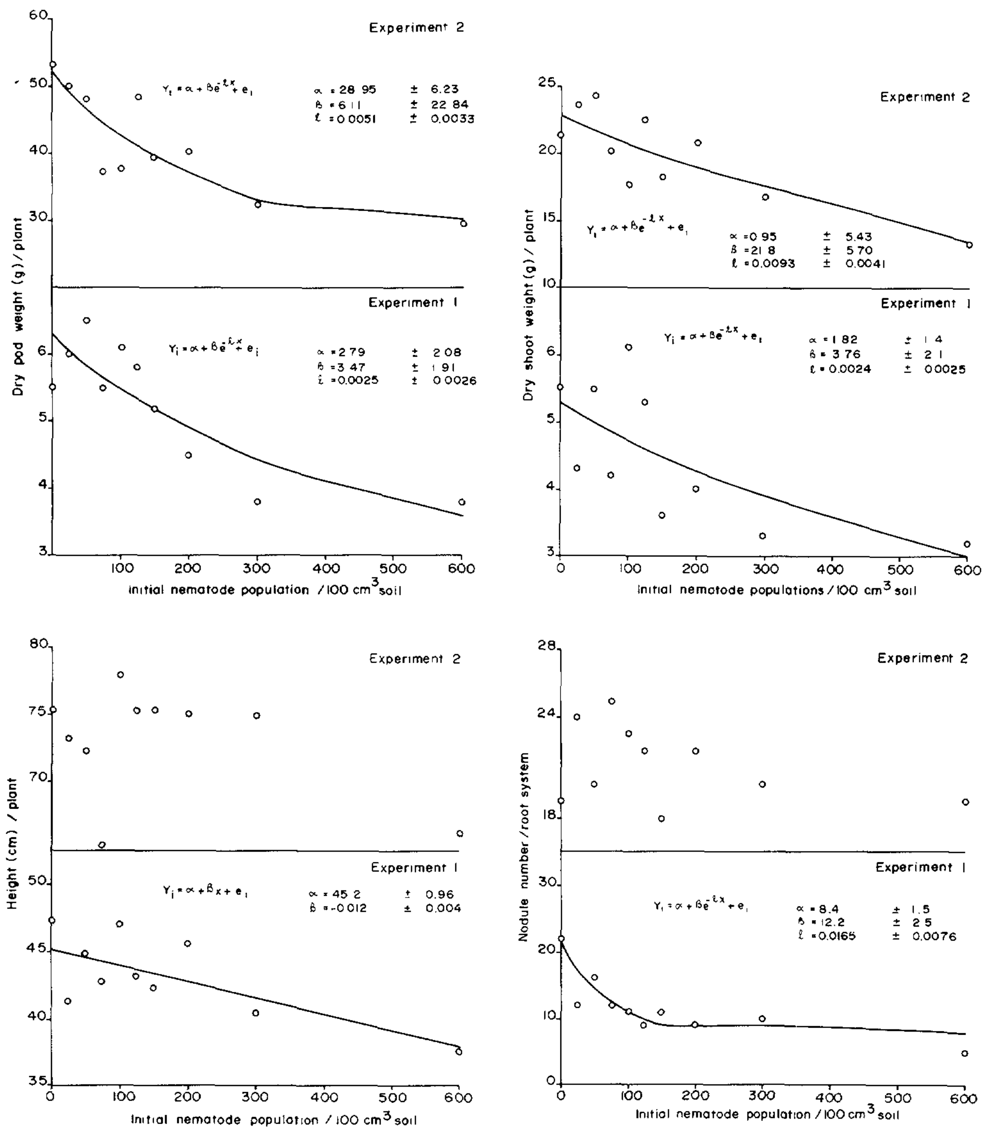

FIG. 2. Relationships of height, nodules per root system, and shoot and pod weights of 'Davis' soybean to initial populations of *Meloidogyne incognita* in microplots.

growth were found in field two. Initial and final populations of *H. columbus* were not highly correlated.

DISCUSSION

A declining asymptotic exponential relationship exists between soybean growth and increasing P_is of *M. incognita* and *H. columbus*. The curves imply that yield suppression is proportionally greater at smaller than at larger P_is. This effect could result from feeding site overlap, progressive unattractiveness of root tissue as nematode numbers increase, or associated micro-organisms.

M. incognita was more virulent than *H. columbus* on Davis soybean, causing substantial growth suppression both years in microplots. Although the rate of decline (ℓ) of dry pod weight in Experiment 1 (1980) was five times greater due to 25–100 *H. columbus* than to the same numbers of *M. incognita*, the latter caused a 45% yield suppression compared to 35% by *H.*

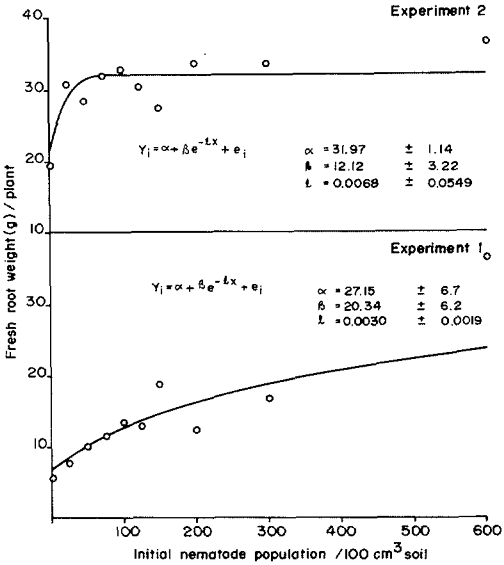

FIG. 3. Relationship of fresh root weight of 'Davis' soybean to initial populations of *Meloidogyne incognita* in microplots.

TABLE 2. Final microplot populations of *Meloidogyne incognita* in relation to initial populations in Experiments 1 and 2 (1980 and 1981).

	Experiment 1		Experiment 2	
P_i*	P_f*	R_f*	P_f	R_f
0	0†	0	0	0
25	1,500	60	1,675	67
50	2,400	48	2,850	57
75	3,300	44	4,050	54
100	4,200	42	5,400	54
125	5,125	41	6,625	53
150	6,000	40	7,350	49
200	7,800	39	9,000	45
300	11,400	38	12,000	40
600	18,000	30	16,200	27

* P_i = initial population (eggs)/100 cm³ soil. P_f = final population (eggs and second-stage juveniles)/100 cm³ soil and roots predicted from fitted curves obtained by least-squares estimations ($P = 0.01$) calculated from numbers of nematodes in soil and roots. R_f = reproduction factor, P_f/P_i.

† Analysis of variance F value significant for P_i effect on P_f, $P = 0.01$.

columbus at the largest P_i. In Experiment 2 (1981), when plants were not under moisture stress, the effect of *H. columbus* was minimal while *M. incognita* suppressed pod weight 31%. Increased fresh root weight indicated a diversion of photosynthate from the shoot to the root system. When pod weights and P_is were related, so were shoot weights and P_is, which suggests photosynthetic area was reduced with less photosynthate available for podset and podfill.

The correlations of *H. columbus* populations with growth of Davis soybean were not as evident in the field as in microplots. At one site P_is were negatively correlated with plant growth, but the association was weak. Small P_is with no moisture stress and the inherently high variability among field plots explain the low correlations.

The relationship of soybean growth and P_i of *M. incognita* and *H. columbus* is an ex-

TABLE 1. Final microplot populations of *Hoplolaimus columbus* in relation to initial populations in Experiment 2 (1981).

P_i*	P_f*	R_f*
0	0†	0
25	118	4.7
50	180	3.6
75	248	3.3
100	330	3.3
125	400	3.2
150	480	3.2
200	600	3.0
300	900	3.0
600	1,260	2.1

* P_i = initial population (adults and juveniles)/100 cm³ soil. P_f = final population (adults and juveniles)/100 cm³ soil and roots predicted from fitted curves obtained by least-squares estimations ($P = 0.01$) calculated from numbers of nematodes in soil and roots. R_f = reproduction factor, P_f/P_i.

† Analysis of variance F value significant for P_i effect on P_f, $P = 0.01$.

TABLE 3. Correlations of 'Davis' soybean growth to initial populations of *Hoplolaimus columbus* in two fields near Blackville, South Carolina, in 1981.

	P_i*	Pod (g)	Shoot (g)	Seed (g)	Height (cm)
Field one					
Mean	27	10.40	5.60	6.80	57.80
Min.	0	0.90	0.60	1.00	32.60
Max.	127	24.90	15.50	16.40	90.00
R		−0.30	−0.32	−0.29	−0.48
Prob.†		0.02	0.01	0.03	0.01
Field two					
Mean	45	15.30	9.40	9.80	65.70
Min.	2	1.20	0.70	0.60	21.30
Max.	140	33.40	22.00	23.80	99.00
R		0.05	−0.04	0.05	−0.16
Prob.†		0.73	0.76	0.72	0.26

* P_i = initial population (adults and juveniles)/100 cm³ soil.
† Rho value significant at 0.05.

ponential of the general equation $y(x) = \alpha + \beta e^{-\ell x}$ where y = growth parameter; α = the asymptote (minimum yield); β = the difference between the minimum and maximum yield; and e = the base of the natural logarithm, 2.72; ℓ = the rate parameter (slope); and x = the nematode density. The general equation above invokes concepts of a maximum yield where x = 0, and a minimum yield, α, and also has a function $e^{-\ell x}$ which describes the pattern of yield decline. The yield decline in relation to increasing P_i followed a logistic ogive with four parameter estimates (minimum yield, maximum yield, the P_i inducing a yield loss halfway between minimum and maximum yield, and the steepness of yield decline) obtained by least-squares routines. The resulting curve implies that the rate of decline in yield with increasing P_i is very slow at small P_is, then increases smoothly to a maximum at intermediate P_is before decreasing at larger densities. These logistic curves are continuous formulations and do not allow for tolerance, a discontinuity in plant growth. The concept of tolerance may still have some utility from a management viewpoint, but it is not a biological phenomenon, a point recognized by Seinhorst (13).

Current management of *H. columbus* and *M. incognita* in soybean fields involves nematicides, resistant varieties, and subsoiling tillage. The loss of income from a soybean field with 20% suppression of yield depends on the price of soybeans and the yield potential of the field. The loss is \$81.50/ha (\$33.00/A) at current market price in a field with a small yield potential of 1,333 kg/ha (22 bu/A) and \$148.20/ha (\$60.00/A) in a field with a yield potential of 2,424 kg/ha (40 bu/A). The cost of the chemical alone would not generally be recovered by the yield increase in *M. incognita*-infested fields with a small yield potential but would be in fields with *H. columbus* since this species requires a lower application rate of nematicide. In fields with the larger yield potential, nematicide costs for both species would be recovered. Additional costs would have to be considered if the nematicide was applied separately. A yield suppression of 20% in 1980 resulted from an *H. columbus* P_i of 50/100 cm^3 and from an *M. incognita* P_i of 150 in both years.

The number of *M. incognita* eggs and juveniles added to microplots and resulting in 20% yield suppression of susceptible soybean is similar, by our calculations, to the number of soil-extracted juveniles (125/100 cm^3 soil) causing a predicted yield loss of 20% at planting time in Florida (9). The similarity of the results is more obvious if egg hatch in the microplot inoculum is assumed to be approximately 80%.

The use of yield response curves and equations for management of *M. incognita* on susceptible soybean varieties is plausible since the percentage yield suppression was similar in both experimental years and similar to results found in another region (9). Percentage yield suppression by *M. incognita* may be similar in irrigated or nonirrigated soybeans and should be investigated. Since most growing seasons have an extended (4–8 weeks) dry period, the ability of *H. columbus* to cause significant yield suppression under these conditions would indicate control in every year in which populations are about 50/100 cm^3 soil and an intolerant cultivar is planted.

The ecological success of plant feeding nematodes such as *H. columbus* and *M. incognita* is attributable to their utilization of a food source subjected to frequent and severe changes (15) and to their survival in fluctuating temperature and moisture conditions. The two species resemble K and r strategists in their ability to survive and persist. Both reproduced well, but the maximum R_f of *Meloidogyne* was 14 times greater than that of *Hoplolaimus*. An r-strategist is a good colonizer, matures quickly, and produces many offspring. These are adaptations to density-independent factors, such as severe environmental conditions (14). *M. incognita* populations fall drastically (90%+) during the spring prior to planting, especially when no host is present (9). *H. columbus* matures slowly, produces relatively few offspring, declines only about 20% during winter and is therefore typical of K strategists; in addition, it withstands large osmotic pressure changes, desiccation for more than 1 year in dry soil (0.2–0.3% soil moisture), and 70 C for 1 hour with more than 64% survival after 1 week in water (4). Unlike *Meloidogyne, H. columbus* is not committed to the plant after beginning a feeding relationship; this allows survival when feeding is interrupted, such as when the host dies. The optimum control procedures are related to the life histories of these two species. The close association of *M. incognita* with the host for feeding, reproduction, and ultimate survival indicates that varietal resistance is a good long-term control method, while nematicides and tolerant varieties are more useful control tactics for *H. columbus*.

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