Effects of *Meloidogyne incognita* and *Fusarium oxysporum* f. sp. *vasinfectum* on Plant Mortality and Yield of Cotton

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ABSTRACT

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The effects of population densities of *Meloidogyne incognita* and *Fusarium oxysporum* f. sp. *vasinfectum* on growth, mortality, and yield of cotton were examined in a factorial experiment in field microplots. Both *Fusarium* and *Meloidogyne* had significant main effects on cotton mortality. At initial populations of *Fusarium* of 2.3–4.2 × 10^3 colony-forming units per gram of soil and initial populations of *Meloidogyne* of 10–50 eggs and juveniles per 100 cm^3, a significant *Fusarium* × nematode interaction was observed. No interaction was observed at lower nematode populations or at higher populations of *Fusarium*. Populations of *Meloidogyne* had significant effects on cotton growth measured qualitatively as a growth index; the growth index was increased by low initial nematode populations and reduced by high initial nematode populations. *Fusarium* had no effect on the growth index but did tend to negate the effects of *Meloidogyne*. A repeated-measures analysis was used to identify significant effects of time on the growth indices and plant mortality. The time × nematode interactions were significant for both of these parameters. Only *Meloidogyne* had significant effects on seed cotton yields; the treatments with *Fusarium* and the fungus × nematode interactions were not significant. When yield responses to nematode populations at different levels of *Fusarium* were analyzed by the Seinhorst model, *Fusarium* consistently reduced the minimum yield parameter. The lack of significant effects of *Fusarium* on yield were believed to be due to constraints of the microplot system.

Additional keywords: Fusarium wilt, population dynamics, root-knot, stunting.

Disease complexes involving root-knot nematodes (*Meloidogyne* species) and vascular wilt *Fusarium* species have been recognized for many years. As early as 1892, Atkinson (2) observed that severity of Fusarium wilt of cotton was greater when plants also were infected by *Meloidogyne incognita* (Kofoid & White) Chitwood. In field and greenhouse studies (9,10), little or no wilt symptoms were observed on cotton in the absence of the nematode unless populations of *Fusarium oxysporum* f. sp. *vasinfectum* (Atk) Synd. & Hans. were very high. Numerous studies in the greenhouse have characterized the Fusarium wilt/root-knot disease complex of cotton and other crops as being a synergistic interaction (13,18). In most instances, the presence of the nematode resulted in earlier expression of wilt symptoms and an increased incidence of wilt. The effects of root-knot nematodes on Fusarium wilt diseases generally are more pronounced when infection of the roots by the nematodes precedes infection by the wilt pathogen by 3–4 wk. For some crops (including cotton, tomato, and squash), root-knot nematodes were reported to induce susceptibility in cultivars normally resistant to the wilt pathogen (6,13,18). More recent studies, however, indicate that the nematodes may not be able to overcome resistance to *Fusarium* in all situations, especially in cultivars possessing high levels of resistance to the wilt pathogen (1,6).

M. incognita alone is an important pathogen of cotton. Orr and Robinson (17) estimated that annual losses of cotton due to the nematode in a 17-county region of Texas were 10% of potential yield. Roberts and Matthews (19) have documented the effects of nematode parasitism on yield of cotton. Starr and Veech (25,26) demonstrated a negative, linear relation between cotton yield and initial nematode populations. There are few studies, however, that have examined the epidemiology of Fusarium wilt/root-knot complex under field conditions. Roberts et al (20) reported that the negative slope parameter of the regression equation for the relationship between initial nematode populations and cotton yield was of greater magnitude when the fungal pathogen also was present. Thus, the incremental effect of increasing nematode population was greater in the presence of *Fusarium*.

The objectives of our study were to further examine the effects of *F. o. vasinfectum* on the yield response of cotton at different initial population levels of *M. incognita*. Further, we examined the development of the disease complex through sequential analysis of plant growth in height, plant mortality, and the effects of the disease complex on the populations of each pathogen.

MATERIALS AND METHODS

All tests were conducted in field microplots (55 cm diameter × 45 cm deep) containing a loamy sand soil (91% sand, 2% silt, 7% clay, and <1% organic matter, pH 8.2). Microplots were fumigated each year with methyl bromide (1 kg/10 m^2) under a tarp for 48 hr and allowed to aerate for 2 wk before infesting with *F. o. vasinfectum*. Two weeks after the microplots were infested with the fungal pathogen, they were infested with *M. incognita* and planted to cotton.

Race 1 of *F. o. vasinfectum* (supplied by J. E. DeVay) was subcultured by monoconidial isolations, increased in a modified mineral salts broth (FLC broth) (7), and stored in soil-tubes (15). Primary inoculum for the microplots was started by placing a few granules of *F. o. vasinfectum* from a soil-tube into flasks containing 50 ml of FLC broth and incubating it under continuous fluorescent lighting (56 $\mu E/m^2/sec$) at 24 C for 3 days. The contents of the flasks then were filtered through eight layers of sterile cheesecloth. The predominantly microconidial suspension was adjusted to 1 × 10^6 conidia per milliliter, and 100 ml was mixed with 7 kg of a twice-autoclaved sand:cornmeal (4:1, v/v) mixture, which was incubated at 22 C to allow colonization of the medium. After 8 wk, the contents of one or more bags of colonized sand:cornmeal inoculum mix were blended together, and duplicate soil-dilution plates were made onto Komada's medium (11). Resultant estimates of colony-forming units per

gram of soil (cfu/g) were used to determine amounts of inoculum to be added to the microplots to achieve desired population densities.

Composite soil samples (eight 2.5 cm diameter × 25–30 cm deep cores per plot) were collected from the microplots 2 wk after infestation and assayed for the established levels of *Fusarium* on duplicate soil-dilution plates as described previously (14). Table 1 lists amounts of inoculum added to each microplot and the resultant established populations of *F. o. vasinfectum*. No *F. oxysporum* was detected in the noninfested fumigated microplots in 1985. In 1986, however, low populations survived the fumigation treatment (Table 1).

Race 3 of *M. incognita* was isolated from cotton and maintained on *Lycopersicon esculentum* Mill. 'Rutgers.' Inoculum of *M. incognita* was prepared by mixing infested soil and infected tomato root fragments from greenhouse cultures with pasteurized river sand (1:1, v/v). Numbers of eggs and infective juveniles (J_2) in the inoculum mix was determined by elutriation and centrifugation (3,5) of triplicate 500-cm^3 samples. Extraction efficiencies were 90% for eggs and 20% for J_2, with the population being 92% eggs. Inoculum was added to individual microplots and thoroughly mixed to establish desired nematode populations in the upper 25 cm of soil (Table 1). Immediately after plots were infested with nematodes, 10 cotton seeds were planted in each microplot in a single row. Two weeks after emergence, plots were thinned to five or six plants per microplot. All plots were irrigated as required, fertilized with NPK according to soil test recommendations, and treated with insecticides to control insects and mites.

Composite soil samples (eight 2.5 cm diameter × 25–30 cm deep cores per plot) were collected 6–8 wk after planting and at crop maturity to determine population densities of nematodes and *Fusarium*. Egg and J_2 populations were estimated based on extraction of 500-cm^3 subsamples by elutriation and centrifugation (3,5). Samples (10 g) of air-dried soil were used to determine population densities of *Fusarium* by soil dilution techniques on Komada's selective medium (11).

In 1985, the experimental design was a randomized complete block with one cultivar (Tamcot SP37, susceptible to both *M. incognita* and *F. o. vasinfectum*), three levels of *Fusarium* (F_0, F_1, and F_2), and five levels of nematode (N_0–N_4). There were six replicates of each treatment. Plant mortality was assessed at biweekly intervals beginning 1 wk after initial wilt symptoms. In 1986, the experimental design was altered to minimize possible cross-contamination of *Fusarium* into uninfested plots and to accommodate two cotton cultivars (Tamcot SP37 and Tamcot CAB-CS, susceptible and resistant to the Fusarium wilt/root-knot complex, respectively). A split-split-plot design was used with the three levels of *Fusarium* as main plots randomized within six replicate blocks, and 10 subplots within main plots to accommodate the two cotton cultivars and five levels of nematode. Mortality was assessed at weekly intervals beginning 1 wk after initial symptoms. Plots were hand-harvested at maturity each year to determine seed cotton yields.

A qualitative growth index was used in 1986 to determine effect of treatments on plant height (degree of stunting). At weekly intervals, from first appearance of wilt symptoms, the height of the control plants (F_0N_0 treatments) was measured from the soil surface to the apical bud, and a mean height was calculated. Subsequently, each plant of every treatment was measured and assigned a growth index value based on whether its height was one standard deviation (SD) above or below that of the control plants. A value of −1 was assigned to plants whose height was more than one SD value below the mean of the control plants, 0 for plants within one SD value of the mean, and +1 for plants greater than one SD value above the mean. Individual plant values were summed to obtain a growth index for each microplot.

All data were subjected to analysis of variance and regression analysis with the SAS statistical package (21). Nematode population estimates were log transformed to stabilize variances. Yield data were fitted to the Seinhorst model (23) by the method of Ferris et al (8).

TABLE 1. Treatment levels for *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* in the 1985 and 1986 microplot experiments

Treatment	1985		1986	
	Total amount added[a]	Population at planting[b]	Total amount added[a]	Population at planting[b]
F. o. vasinfectum				
F_0	0	0	0	0.1×10^3
F_1	1.1×10^8	1.4×10^4	3.0×10^7	2.3×10^3
F_2	2.6×10^8	2.1×10^4	1.5×10^8	4.2×10^3
M. incognita				
N_0	0	0	0	0
N_1	59	0.1	59	0.1
N_2	590	1.0	590	1.0
N_3	5,900	10.0	5,900	10.0
N_4	29,500	50.0	29,500	50.0

[a]Total inoculum added to each microplot; values for *F.o. vasinfectum* are total colony-forming units, and values for *M. incognita* are total eggs and juveniles.

[b]Inoculum present at planting; values for *F. o. vasinfectum* are colony-forming units per gram air dried soils, and values for *M. incognita* are eggs and juveniles per 100 cm^3 soil.

RESULTS

Plant mortality. No effect of either *F. o. vasinfectum* or *M. incognita* was observed on cotton stand establishment in either 1985 or 1986. The mean number of cotton seedlings emerging per plot at 2 wk after planting was 7.9 over both years and all treatments.

In 1985, the first symptoms of Fusarium wilt (chlorosis and

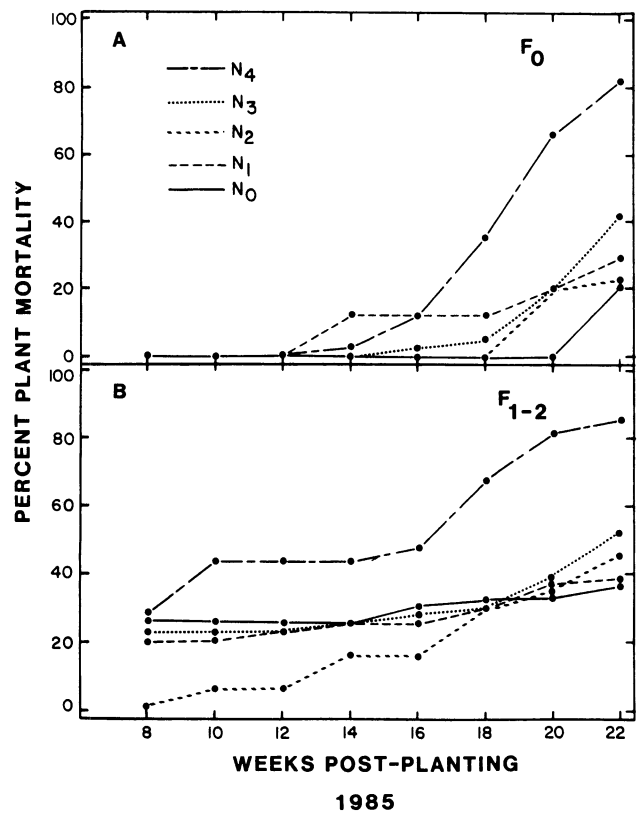

Fig. 1. Effects of population densities of *Meloidogyne incognita* ($N_0 = 0$, $N_1 = 0.1$, $N_2 = 1.0$, $N_3 = 10$, and $N_4 = 50$ eggs and J_2/100 cm^3 of soil at planting) and *Fusarium oxysporum* f. sp. *vasinfectum* on mortality of cotton in microplots in 1985. **A,** In the absence of *Fusarium* ($F_0 = 0$ cfu/g of soil). **B,** Combined data from treatments having initial populations of *Fusarium* of 1.4×10^4 (F_1) and 2.1×10^4 (F_2) cfu/g of soil.

wilting of the foliage) and some plant mortality were observed 7 wk after planting. There was 20–30% mortality in the F_1 and F_2 treatments at week 8 across all nematode treatments, except for the N_2 treatment (Fig. 1). At nematode treatments of N_0, N_1, and N_3, mortality in the F_1 and F_2 treatments with *Fusarium* increased slowly from week 8 through the end of the season (week 22). The amount of mortality in the F_1 and F_2 treatments was much greater in the N_4 treatments than that in all other nematode treatments. In the absence of *Fusarium* (F_0 treatment) there was no nematode-induced mortality until week 14 (Fig. 1). Final mortality values for the N_4 treatments were similar, regardless of the treatment with *Fusarium*. At the N_0–N_3 nematode levels, the final mortality values were slightly higher for the F_1 and F_2 treatments than for the F_0 treatment. Plants in the control plots (N_0F_0) began to senesce at week 20. This was due to contamination of these plots with *Fusarium* during the later part of the season, which lead to a change in the experimental design for 1986.

Univariate analysis of variance at each assessment time indicated a significant effect of *Fusarium* on plant mortality at weeks 8 through 18 (Table 2), but the F_1 and F_2 treatments were not different. *M. incognita* had a significant effect on plant mortality at weeks 16 through 22 (Table 2). At no assessment time was there a highly significant Fusarium × nematode interaction; however, at week 12 the Fusarium × nematode interaction was significant at $P = 0.075$. The repeated-measures analysis of variance (12) allows a valid comparison of treatment effects with time where repeated assessments are made on the same experimental unit. With this analysis, there was a significant increase in mortality with time ($P = 0.001$). The time × *Fusarium* and time × *Fusarium* × nematode interactions were not significant.

Because of the lack of a significant effect in mortality between the F_1 and F_2 treatments in 1985, the populations of *Fusarium* were decreased in 1986 for the F_1 and F_2 treatments (Table 1). Although the cultivar Tamcot CAB-CS is reported to be more resistant to the Fusarium wilt/root-knot complex than Tamcot SP37 (4), no significant difference in mortality or yield responses between the two cultivars was observed. Therefore, all data reported for 1986 are the combined results from the two cultivars.

In 1986, the first symptoms of Fusarium wilt were observed at week 6, with limited mortality in the F_1N_4, F_1N_3, and F_2N_4 treatments (Fig. 2). In the absence of *Fusarium*, plant mortality first was observed at week 8 at the N_4 nematode level. As in 1985, the greatest total mortality was observed in the F_2N_4 treatment. The univariate analysis of variance indicated a significant effect of *Fusarium* and nematodes on mortality at each assessment time (Table 3). Additionally, at each assessment, the *Fusarium* × nematode interaction was significant. In contrast to the 1985 experiment, the F_1 and F_2 treatments clearly were separated in 1986, and the N_4 and N_3 nematode treatments were separated from the N_0–N_2 treatments. The repeated-measures analysis again revealed significant increase in mortality with time ($P = 0.001$) and a significant time × nematode interaction ($P = 0.01$). As in the 1985 experiment, neither the time × *Fusarium* nor the time × *Fusarium* × nematode interactions were significant.

Population dynamics. The population dynamics of *F. o. vasinfectum* and *M. incognita* were similar in the 1985 and the 1986 experiments, respectively. Populations of *Fusarium* generally were stable throughout each growing season, with little change in population levels from planting to crop harvest (Fig. 3). The

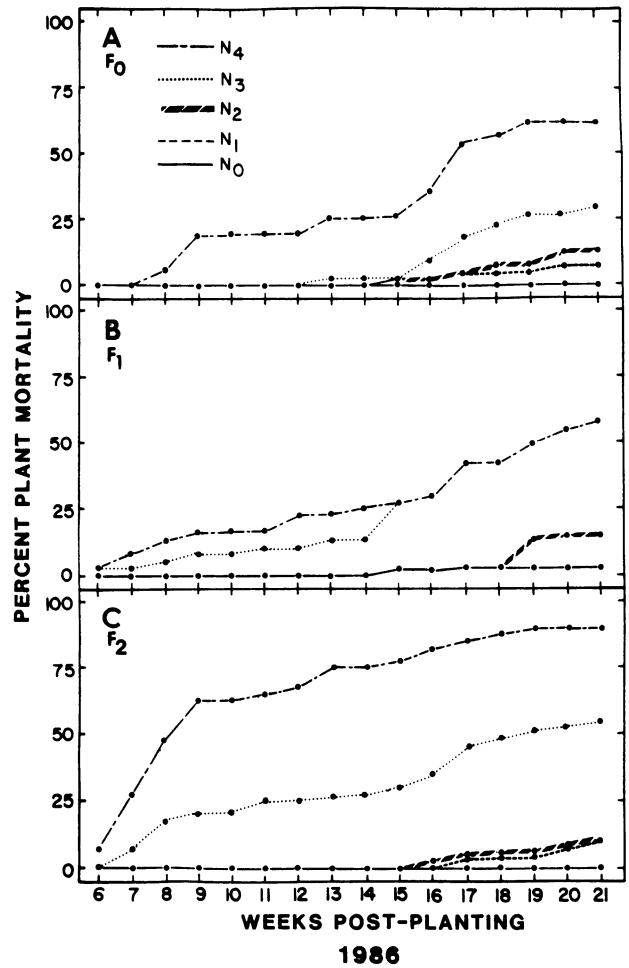

Fig. 2. Effects of population densities of *Meloidogyne incognita* ($N_0 = 0$, $N_1 = 0.1$, $N_2 = 1.0$, $N_3 = 10$, and $N_4 = 50$ eggs and J_2/100 cm^3 of soil) and *Fusarium oxysporum* f. sp. *vasinfectum* on mortality of cotton in microplots in 1986. **A,** Initial population of *Fusarium* of 0.1×10^3 cfu/g of soil (F_0). **B,** Initial population of *Fusarium* of 2.3×10^3 cfu/g soil (F_1) and **C,** initial population of *Fusarium* of 4.2×10^3 cfu/g of soil (F_2).

TABLE 2. Mean squares from analysis of mortality of cotton in microplots infested with different populations of *Fusarium oxysporum* f. sp. *vasinfectum* (FOV) and *Meloidogyne incognita*; values in parentheses are degrees of freedom for *F*-test (data from 1985 test)

Weeks after planting	Error (75)	FOV[a] (2)	Nematode[a] (4)	FOV × nematode (8)
8	2.496	8.011*	3.306	2.872
10	2.778	9.878*	6.850	4.725
12	2.802	17.478*	3.711	5.061
14	3.236	9.544*	5.150	4.683
16	3.147	11.678*	6.928*	1.844
18	2.962	12.544*	14.567**	0.850
20	2.756	5.433	15.794***	1.711
22	2.864	3.078	21.900***	0.717

[a]Probability levels for main effects at $P = 0.05$ (*), 0.01 (**), and 0.001 (***).

TABLE 3. Mean squares from analysis of mortality of cotton cultivar (CV) in microplots infested with different populations of *Fusarium oxysporum* f. sp. *vasinfectum* (FOV) and *Meloidogyne incognita* (N) (data from 1986 test)[a]

Weeks after planting	CV (1)[b]	FOV (2)	N (4)	FOV × N (8)	CV × FOV (8)
7	0.46	1.78***	2.43***	0.96***	0.20
9	0.12	7.84***	17.81***	4.00***	0.17
11	0.40	8.43***	19.88***	4.15***	0.36
13	0.17	9.42***	28.62***	4.99***	0.43
15	0.21	8.79***	33.30***	5.94***	0.41
17	0.10	5.59**	61.98***	3.87***	0.69
19	0.39	3.85**	77.75***	2.92***	1.26
21	1.01	3.79**	79.18***	2.67***	1.92

[a]Probability levels for main effects are $P = 0.05$ (*), 0.01 (**), and 0.001 (***).

[b]Values in parentheses are degrees of freedom.

F_2 treatment in 1986 was an exception, with an apparent decline of 57% from planting to harvest. There were no nematode or cultivar effects on populations of *Fusarium*.

In contrast to *Fusarium*, the populations of *M. incognita* exhibited major changes during the growing season. All treatments exhibited a population increase at the midseason assessment date. At the final assessment, populations in the N_1 and N_2 treatments exhibited further increase, whereas the N_3 and N_4 treatments were stable or decreased, respectively. At harvest, the ratio of the final populations to the initial populations (Pf/Pi) ranged from a mean of 3.9 for the N_4 treatments to 2,881 for the N_1 treatments. Regression analysis of the relationship between log Pi and log Pf/Pi revealed a significant, negative linear correlation (Fig. 4). In each year, the negative slope parameter of this relationship was greater as populations of *Fusarium* increased. Although the differences in slope were not significant, the trend was consistent over both years and all treatments with *Fusarium*.

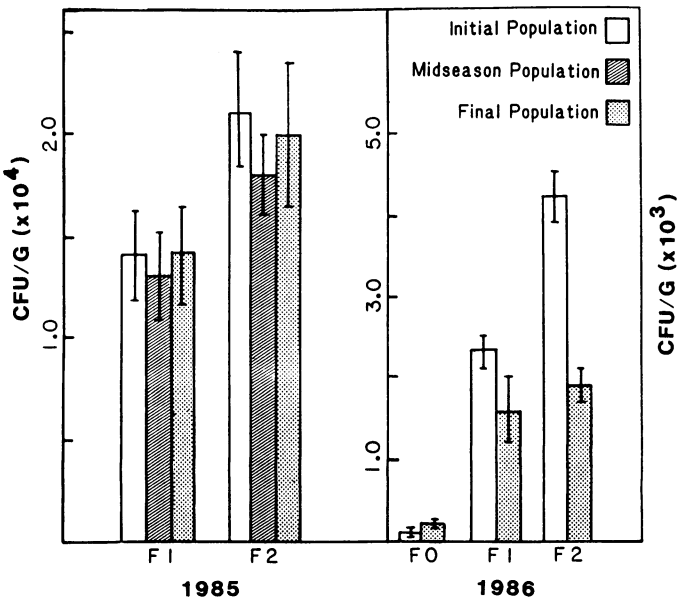

Fig. 3. Population dynamics of *Fusarium oxysporum* f. sp. *vasinfectum* in microplots planted to cotton. Initial population densities of *Fusarium* in 1985 were $F_1 = 1.4 \times 10^4$ and 2.1×10^4 cfu/g of soil. Initial population densities of *Fusarium* in 1986 were $F_0 = 0.1 \times 10^3$, $F_1 = 2.3 \times 10^3$, and $F_2 = 4.2 \times 10^3$ cfu/g of soil.

Seed cotton yields. Seed cotton yields were highly variable in both years; however, analysis of variance indicated a highly significant nematode effect ($P = 0.01$) in 1985 and 1986. There was no effect of *Fusarium* on yield in either year, nor were the Fusarium × nematode interactions significant. When yield data were analyzed by the Seinhorst model (8,23), slightly different effects were noted for 1985 and 1986. In 1985, only the F_0 and F_1 treatments were judged to have acceptable fits to the model ($r^2 > 0.30$); at F_1 the threshold value (T) and the minimum yield (M) parameters were decreased relative to the F_0 treatment (Table 4). In 1986, all treatments with *Fusarium* gave good fits to the model ($r^2 > 0.84$) (Table 4). Both F_1 and F_2 treatments resulted in decreased values of M relative to F_0 but there was no effect on T. When yield data were subjected to linear regression analysis, there was a general trend of increasing slope values (more negative) as populations of *Fusarium* increased (analysis not shown).

In both years, it was observed that the N_1 treatments yielded more seed cotton than did the N_0 treatments (Table 5). The highest populations of *Fusarium* (F_2) negated the stimulatory effect of the low nematode populations. These responses were not

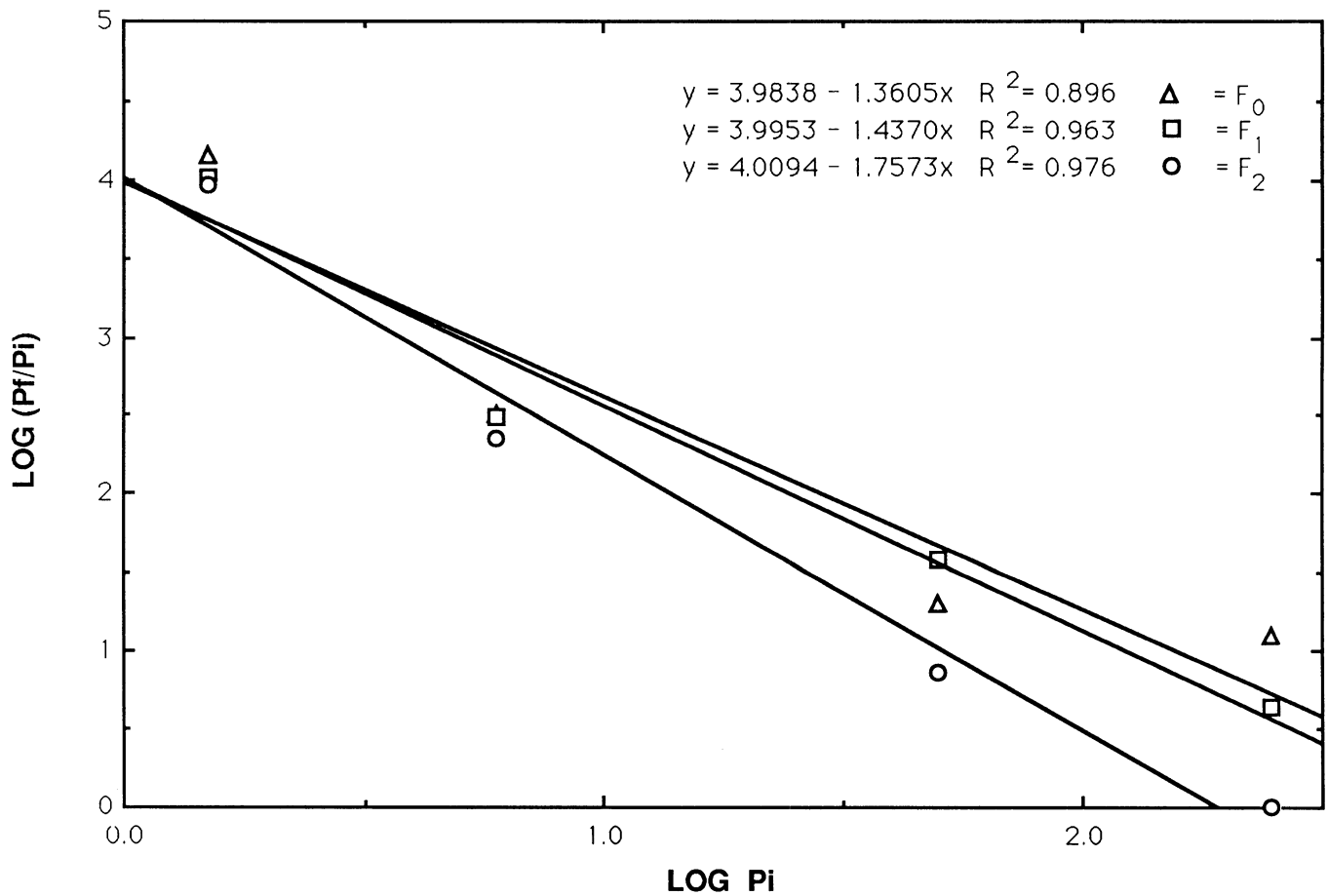

Fig. 4. The relationship of initial population densities (log P_i) of *Meloidognyne incognita* on the development of nematode populations (log PF/P_i) at three different initial populations of *Fusarium oxysporum* f. sp. *vasinfectum* ($F_0 = 0.1 \times 10^3$, $F_1 = 2.3 \times 10^3$, and $F_3 = 4.2 \times 10^3$ cfu/g of soil). Data are from a 1986 microplot experiment.

significant at $P = 0.05$.

Plant growth index. The growth index measurement in 1986 revealed a general stimulation of plant growth by the N_1 treatments at F_0 and a suppression of plant growth by the N_4 treatments (Fig. 5). The N_2 and N_3 treatments were not consistently different from N_0. The F_1 and F_2 treatments appeared to negate the growth stimulation of N_1, and the F_2 treatment negated the growth suppression observed at the N_4 treatment during the latter part of the season (Fig. 5). Analysis of variance at each assessment time revealed a highly significant effect of the nematode, but not of *Fusarium*; the *Fusarium* × nematode interaction also was not significant (Table 6). Growth indices generally were stable over time, except for the F_0N_1 and the F_2N_4 treatments. The stimulatory and suppressive responses, respectively, for these treatments that were observed early in the season decreased with time. A significant time × nematode interaction ($P = 0.05$) in the repeated-measures analysis confirmed these observed changes over time.

TABLE 4. Effect of *Fusarium oxysporum* f. sp. *vasinfectum* on the relation between populations of *Meloidogyne incognita* and yield of cotton based on the Seinhorst model[a]

Population of *Fusarium* (cfu/g)	Threshold level (nematodes/100 cm³)	Relative minimum yield	r^2
1985			
0	7.5	0.20	0.30
13.7×10^3	5.7	0.13	0.64
21.0×10^3	...[b]	...[b]	...[b]
1986			
1.1×10^2	9.4	0.23	0.89
2.3×10^3	9.5	0.11	0.90
4.3×10^3	9.4	0.16	0.84

[a]Seinhorst model: $y = M + (1 - M)\, z^{P-T}$, where y = relative yield, M = minimum yield, T = threshold level, P = nematode population density, and z = proportion of the root system not damaged by one nematode.
[b]Inadequate fit of data to model ($r^2 = 0.10$).

TABLE 5. Effects of low initial populations of *Meloidogyne incognita* on seed cotton yields in microplot experiments (1986)

Cotton cultivar	*Fusarium* treatment (cfu/g)[a]	Yield (g/plot) N_0[b]	Yield (g/plot) N_1[b]	Difference (%)
Tamcot Sp37	F_0–0.1×10^3	58.6	66.4	+13.3
	F_1–2.3×10^3	62.9	82.6	+31.3
	F_2–4.2×10^3	85.1	78.2	− 8.1
Tamcot CABCS	F_0–0.1×10^3	70.5	79.6	+12.9
	F_1–2.3×10^3	79.4	78.1	− 1.6
	F_2–4.2×10^3	75.8	75.4	− 0.5

[a]Initial population density of *Fusarium* in microplot soil.
[b]N_0 and N_1 are initial nematode population of 0 and 0.1 eggs and juveniles per 500 cm³ of soil.

DISCUSSION

This study involved a detailed analysis of the development of the Fusarium wilt/root-knot complex of cotton in field microplots, which more closely mimic field situations than typical greenhouse experiments. Plant mortality is a major component of the Fusarium wilt/root-knot complex. We used sequential observations of cotton mortality on the same experimental units to follow development of the complex over time. At high initial populations, each pathogen caused significant mortality; however, mortality due to *Fusarium* commenced earlier in the season than did mortality due to *Meloidogyne*. Further, mortality due to

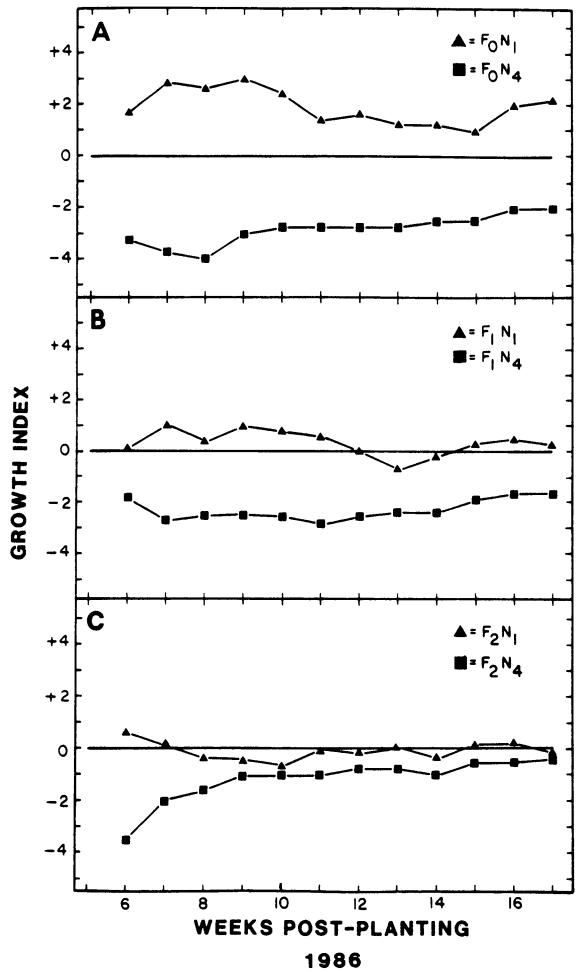

Fig. 5. Effects of *Meloidogyne incognita* and *Fusarium oxysporum* f. sp. *vasinfectum* on a qualitative growth index of cotton. Initial population densities of *Fusarium* were **A**, $F_0 = 0.1 \times 10^3$ cfu/g of soil; **B**, $F_1 = 2.3 \times 10^3$ cfu/g of soil; and **C**, $F_2 = 4.2 \times 10^3$ cfu/g of soil. Initial nematode population densities were $N_1 = 0.1$ and N_4 = eggs and J_2/100 cm³ of soil. The 0 line in each figure is the growth index for cotton in the absence of nematodes and *Fusarium*.

TABLE 6. Mean squares analysis of growth index of cotton cultivar (CV) in microplots infested with different populations of *Fusarium oxysporum* f. sp. *vasinfectum* (FOV) and *Meloidogyne incognita* (N) (1986); values in parentheses are degrees of freedom

Weeks after planting	FOV (2)	CV × FOV[a] (2)	N[a] (4)	CV × N (4)	FOV × N (8)	CV × FOV × N (8)
7	5.90	8.42	41.34***	3.29	6.65	3.79
9	0.06	5.92	33.04***	1.90	5.24	5.44
11	3.48	4.56	31.45***	2.59	4.22	4.88
13	3.84	9.88*	23.69***	1.26	2.37	1.10
15	2.17	5.07	24.18***	1.37	1.47	2.08
17	1.23	2.04	21.93***	2.61	3.15	1.96

[a]Probability levels for effects are $P = 0.05$ (*) and 0.001 (***).

Meloidogyne increased with time, but mortality due to *Fusarium* did not. No interaction was observed at very high levels of *Fusarium* or at the lowest levels of *Meloidogyne*, but a significant interaction was observed at intermediate populations of *Fusarium* and the higher populations of *Meloidogyne*. This interaction was evident in the time of occurrence of initial mortality and in final levels of mortality.

In the 1986 experiment, a qualitative growth index was used as an additional variable to further characterize the effect of the disease complex on cotton growth. These observations revealed that the lowest nematode initial population levels stimulated cotton growth, whereas growth was stunted at the highest nematode population. Cotton growth was not affected at the intermediate nematode populations. Interestingly, the presence of *Fusarium* tended to negate both of these plant responses to the nematode. The lack of growth stimulation by low nematode numbers in the presence of *Fusarium* is believed to be due to the pathological effects of *Fusarium* on cotton. However, the apparent lack of plant stunting by high numbers of nematodes in the presence of *Fusarium* is believed to be an artifact of the experimental system. In the F_2N_4 treatment, the reduction in stunting paralleled the increase in mortality. Thus, at the end of the season, the few plants that survived also were only slightly stunted and probably were disease escapes. Although they were not significant, we believe the consistent effect of *Fusarium* on the growth index, either as a main effect or in the interaction, represents a real phenomenon.

Although yield data were highly variable, and it would be difficult to extrapolate yield values from these microplot studies to actual field situations, we did observe significant effects of *M. incognita* on yield. We did not, however, detect any effect of *Fusarium* or a *Fusarium* × nematode interaction on yield. The lack of significant effects of *Fusarium* on seed cotton yields is believed to be an artifact of the microplot system. In these experiments, the principal effect of *Fusarium* was on cotton mortality and, hence, plant spacing. Cotton, however, exhibits a great deal of plasticity with respect to the effect of plant spacing on yield. Smith et al (24) reported that a 66% reduction in plant density resulted in only a 14% yield reduction. Thus, a 20% reduction in plant population per microplot due to mortality induced by *Fusarium* is unlikely to cause a significant yield loss.

The Seinhorst model (23) estimates a threshold value T (the minimum nematode population at which yield suppression occurs) and a minimum relative yield value M (the lowest possible yield, regardless of the nematode population). Using this model, we were able to detect an effect of *Fusarium* on the relationship between initial nematode populations and seed cotton yields; *Fusarium* consistently resulted in a reduction in the minimum relative yield value. In only one instance was the threshold value affected. The effect on the minimum relative yield value is consistent with the results of Roberts et al (20) where they reported that, in the presence of *Fusarium*, the negative slope of the linear model of the relationship between populations of *M. incognita* and yield of cotton was more negative than in the absence of *Fusarium*.

Other studies (16,22), involving other nematode species and crop combinations, have reported that crop yield and/or plant growth is stimulated at low initial nematode populations. We also observed a stimulation of cotton yield at the N_1 nematode treatments. This stimulation was similar to that observed for growth index, and also was negated by the presence of *Fusarium*. Such stimulation generally is believed to be due to overcompensation by the host for minor amounts of damage; however, data to support this hypothesis are lacking.

With regard to the population of the two pathogens, it was noted that the populations of *Fusarium* were more stable during the growing season than were the populations of *Meloidogyne*. Further, the nematodes had no apparent effect on populations of *Fusarium*, whereas the presence of *Fusarium* did affect populations of *Meloidogyne*. This difference probably is due to *M. incognita* being an obligate biotroph and would be expected to be affected by mortality of the host. *F. o. vasinfectum*, as a transitory biotroph, would not be expected to be affected greatly by the death of the host. The negative relationship between initial nematode populations and the ratio of the final to initial populations previously has been reported for the *M. incognita*/cotton system (25,26) and represents, in part, the effects of decreased host resources available to support development of nematode populations. That this relationship is more pronounced (more negative slope) in the presence of *Fusarium* is consistent with the expected affect of increased plant mortality.

In summary, this study of the Fusarium wilt/root knot complex has provided a greater understanding of the disease than could be obtained from greenhouse studies. Based on the data presented, we believe that most of the yield loss and suppression of cotton growth are due to the effects of *M. incognita*. However, we do believe that under more natural field conditions a greater effect of *F. o. vasinfectum* would be evident. We further believe that there is no advantage in attempting to classify this, or other similar disease complexes, as being a synergistic or additive relationship. Previous attempts to arrive at such a classification frequently were based on inappropriate experimental designs. As this and other studies (1,9) have shown, the population of the participants in such disease complexes strongly influences the nature of the relationship. Rather than attempting to categorize a disease complex as a synergistic or additive relationship, one should attempt to illucidate the effects of each participant on the others at different population levels and how disease progress is affected over time.

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