# Interactions of Concomitant Species of Nematodes and Fusarium oxysporum f. sp. vasinfectum on Cotton<sup>1</sup>

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Abstract: Meloidogyne incognita, Hoplolaimus galeatus, and North Carolina and Georgia populations of Belonolaimus longicaudatus were introduced singly and in various combinations with Fusarium oxysporum f. sp. vasinfectum on wilt-susceptible 'Rowden' cotton. Of all the nematodes, the combination of the N. C. population of B. longicaudatus with Fusarium promoted greatest wilt development. H. galeatus had no effect on wilt. With Fusarium plus M. incognita or B. longicaudatus, high nematode levels promoted greater wilt than low levels. The combination of either population of B. longicaudatus with M. incognita and Fusarium induced greater wilt development than comparable inoculum densities of either nematode alone or where H. galeatus was substituted for either of these nematodes. Nematode reproduction was inversely related to wilt development. Without Fusarium, however, the high inoculum level resulted in greater reproduction of all nematode species on cotton. Combining M. incognita with B. longicaudatus or H. galeatus gave mutually depressive effects on final nematode populations. The interactions of H. galeatus with B. longicaudatus varied with two populations of the latter. Key Words: Gossypium hirsutum, Meloidogyne incognita, Belonolaimus longicaudatus and Hoplolaimus galeatus.

Diseases of cotton, Gossypium hirsutum L., involving nematodes and Fusarium, were recently reviewed by Sasser (16), who indicated that root-knot caused by Meloidogyne incognita (Kofoid & White) Chitwood is the most important nematode disease of cotton. Belonolaimus longicaudatus Rau, however, is probably the most devastating

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nematode parasite of cotton. Yet, the greatest damage with either of these nematodes occurs in association with Fusarium oxysporum f. sp. vasinfectum (ATK) Snyd. & Hans. Martin et al. (11) studied the development of Fusarium wilt in cotton infected with several populations of M. incognita and found differences in their ability to increase incidence of wilt. Recently, Robbins & Barker (14), in studying the morphology and ecology of the sting nematode, B. longicaudatus, found that a North Carolina population (Tarboro) and Georgia population (Tifton) varied in host range as well as in reproductive capabilities. They suggested that these are either different physiological races or species. Hoplolaimus galeatus Cobb also damages cotton (8, 9). With high population densities in the rhizosphere, roots were severely stunted, resulting in severe defoliation. Yet, there are no reports implicating this pest in Fusarium-nematode interactions.

Although plants in the field may be infected with only a single nematode species, Oostenbrink (12) and others have found that most nematodes occur in polyspecific communities. Most investigations of nematode-fungus interactions have concerned monospecific nematode populations. The few investigations concerning interactions among plant-parasitic nematodes suggest that competition, antagonism, synergism and other associated effects occur between two or more nematode species which occupy the same niche and share a common food supply (4, 7, 8, 15, 18). Whether these effects enhance or inhibit the interactions with pathogenic fungi is important to understanding disease complexes in nature. Therefore, this investigation was designed to determine: (i) the magnitude of interactions of nematodes of different feeding habits with Fusarium on cotton [M. incognita (gall-inducing, sedentary endoparasite), B. longicaudatus (ectoparasite with very long stylet), and H. galeatus (migratory endoparasite)]; and (ii) the concomitant interactions of these nematodes with and without Fusarium.

## MATERIALS AND METHODS

Nematode and fungal inocula: The population of M. incognita from North

Carolina (N. C. State University population #186, designated Mi) was maintained on 'Rowden' cotton. For inoculum the nematode was increased on 'Manapal' tomato (Lycopersicon esculentum Mill.). Egg suspensions were used as inoculum (6). The two populations of B. longicaudatus used were originally collected from a cotton field near Tarboro, North Carolina (NC) and from a millet field near Tifton, Georgia (GA). Each population was increased on 'Lee' soybean, Glycine max (L.) Merr., grown in 65-mesh silica sand. A greenhouse culture of H. galeatus (HG) was increased on 'Rowden' cotton grown in 2:1 mixture of sandy loam soil and sand. These two species were collected by decanting and sieving aqueous suspensions through a 40-mesh sieve nested on a 325-mesh sieve. Separan® (Dow Chemical Co., Midland, Mich.) was added to the water at 12.5  $\mu$ g/ml before stirring to induce flocculation of soil colloids, thereby giving cleaner nematode suspensions. Nematode inoculum levels, utilizing mixtures of larvae and adults, except eggs for Mi, were 5,000 and 10,000/pot, referred to as "5" and "10," respectively.

F. oxysporum f. sp. vasinfectum (F), maintained on a mixture of soil, peat moss and perlite (17), was grown for  $\overline{7}$  days on potato-dextrose agar (PDA). Two discs cut with a size 3 cork borer were transferred to 1-liter flasks containing 500 ml of a basal medium consisting of 5 g of glucose and 25 ml of stock solution [29.16 g Ca(NO<sub>3</sub>)<sub>2</sub>. 4H<sub>2</sub>O, 2.19 g KNO<sub>3</sub>, 31.18 g Mg(NO<sub>3</sub>)<sub>2</sub>. 6H<sub>2</sub>O, 5.75 g KH<sub>2</sub>PO<sub>4</sub>, 3.03 g MgSO<sub>4</sub>•4H<sub>2</sub>O and 0.56 g H<sub>3</sub>BO<sub>4</sub>] per liter of distilled water. After the flasks were shaken on a rotary shaker at 25 C for 7 days, the culture medium was filtered through four layers of cheesecloth to remove the mycelium. The liquid containing the spores which passed through the filter was then centrifuged at 2,000 g at 4 C for 15 min. The supernatant was discarded, and the spore sediment was suspended in 500 ml of distilled water for a second centrifugation. The fungal inoculum was then standardized with a hemacytometer so that 3x107 fungal spores were used per plant.

Culture of plants and experimental design: Test plants (G. hirsutum 'Rowden') were seeded singly in 15-cm clay pots partially filled with a 1:1 mixture of 35-mesh silica sand and sandy loam soil previously fumigated with methyl bromide. Plants were grown in the greenhouse with one-half of the replicates receiving 12 h supplement light of 8,600 lx from GE Lucalox® and mercury lamps to promote better plant growth. Inoculations were made by pouring nematode and/or fungal suspensions around 1-week old seedlings. Additional soil-sand mixture was added to fill each pot. Pots were watered immediately to insure egg, nematode, and spore dispersal. To wound plants in the wounding + Fusarium treatment (W + F), roots were partially cut by gently moving a knife through the soil. Plant nutrients [VHPF® (Miller Chem. & Fertilizer Corp., Hanover, Pa.) supplemented with  $KNO_3 + MgSO_4$ ] were provided as needed to support good plant growth.

There were six replications of each treatment in randomized complete blocks (Table 1). The experiment was terminated 63 days following inoculation. Parameters measured included plant height, fresh top and root weights, and wilt and gall development.

The two experiments, one with single nematode populations or species  $\pm$  Fusarium and one with two species of nematodes  $\pm$  Fusarium, were conducted concurrently in order to facilitate comparisons across experiments (Tables 1, 2).

Wilt development was rated from 0 to 5 as follows: class 0 = no wilt symptoms; class 1 = trace with 1 or 2 leaves showing epinasty; class 2 = half of the leaves with epinasty and beginning to yellow; class 3 =three-fourths of the leaves on plants with epinasty and yellowing portion of the leaf beginning to dry; class 4 = all the leaves showing epinasty and lower leaves beginning to fall off; class 5 = plant dead. Wilt indices for each treatment were calculated by the following formula (13):

TABLE	1. Descriptive	key to the	inoculations
of 'Rowden	seedlings with	Meloidogy	ne incognita
(Mi), Hoplo	laimus galeatus	s (HG), No	rth Carolina
and Georgia	populations of	Belonolain	ius longicau-
datus (NČ, )	GA) alone and i	in combinat	ion with Fu-
sarium oxys	borum f. sp. vas	infectum (F	).

Designation	
of treatments	Treatment description
Control	Noninoculated check
F	Fusariuma
W+F	Mech. wounded roots with Fusarium
HG5	5,000 H. galeatus
HGI0	10,000 H. galeatus
Mi5	5,000 M. incognita
Mil0	10,000 M. incognita
NC5	5,000 NC pop. of B. longicaudatus
NC10	10,000 NC pop. of B. longicaudatus
GA5	5,000 GA pop. of B. longicaudatus
GA10	10,000 GA pop. of B. longicaudatus
Mi5+HG5	5,000 M. incognita + 5,000 H. galeatus
Mi5+NC5	5,000 M. incognita + 5,000 NC pop.
	of B. longicaudatus
M15 + GA5	5,000 M. incognita + 5,000 GA pop. of B. longicaudatus
NC5+HG5	5,000 NC pop. of B. longicaudatus + 5,000 H. galeatus
GA5+HG5	5,000 GA pop. of B. longicaudatus + 5,000 H. galeatus
HG5+F	5,000 H. galeatus + Fusarium
HG10+F	10,000 H. galeatus + Fusarium
Mi5 + F	5,000 M. incognita + Fusarium
Mi10+F	10,000 M. incognita + Fusarium
NC5 + F	5,000 NC pop. of B. longicaudatus
	+ Fusarium
NC10+F	10,000 NC pop. of B. longicaudatus + Fusarium
GA5+F	5,000 GA pop. of B. longicaudatus
GA10+F	10,000 GA pop. of B. longicaudatus
Mi5 + HG5 + F	+ Fusarium 5,000 M. incognita + 5,000 H.
Mi5+NC5+F	galeatus + Fusarium 5,000 M. incognita + 5,000 NC pop.
Mi5+GA5+F	5,000 M. incognita + 5,000 GA pop.
NC5+HG5+F	ot B. longicaudatus + Fusarium 5,000 NC pop. of B. longicaudatus
GA5 + HG5 + F	+ 5,000 H. galeatus + Fusarium 5,000 GA pop. of B. longicaudatus + 5,000 H. galeatus + Fusarium
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<sup>a</sup>3 X 107 spores/plant (15-cm pot).



## Total No. plants in treatment x 5

Roots were washed and galling was rated according to the classification system used by Powell et al. (13). This system consists of: class 0 = no galls on roots; class 1 = less than 10% galled; class 2 = 11-25% galled; class 3 = 26-50% galled; class 4 = 51-75% galled; class 5 = 76-100% galled. The above formula used for computing wilt

#### Interactions of Concomitant: Yang et al. 77

TABLE 2. Effects of two inoculum levels of single and combined species of [Meloidogyne incognita (Mi), Hoplolaimus galeatus (HG) North Carolina and Georgia populations of Belonolaimus longicaudatus (NC, Ga)] with Fusarium oxysporum f. sp. vasinfectum (F) on wilt development in 'Rowden' cotton.

			Rate of	wilt devel	opment/d	ays after i	noculation	I	
Treatment <sup>a</sup>	21	25	28	31	35	42	49	56	63
			Levels o	f single sp	ecies of ne	ematodes	+ fungus <sup>b</sup>		
F	0e	0d	0d	0e	0d	0f	4e	6dc	14c
W+F	56a	66a	74a	84a	84b	84b	84b	84b	84b
HG5+F	0e	$0\mathbf{d}$	0d	0e	0d	0f	0e	0e	0d
HG10+F	0e	$\mathbf{0d}$	$0\mathbf{d}$	0e	0d	$0\mathbf{f}$	0e	0d	0d
Mi5 + F	0e	$0\mathbf{d}$	6d	10e	16d	34e	54d	66b	76b
Mi10+F	10cde	14c	24c	<b>34d</b>	40c	60d	70c	74b	80b
GA5 + F	6ed	14c	26c	40c	46c	70c	84b	94a	96a
GA10+F	4ed	16c	26c	46c	56c	76c	96a	100a	100a
NC5+F	14cd	24c	46b	74b	90a	100a	100a	100a	100a
NC10+F	16b	40b	64a	84a	94a	100a	100a	100a	100a
			Combinatio	ons of two	species of	nematod	es + fungi	ısb	
Mi5+HG5+F	4d	4d	6cd	10c	14d	30d	46c	 60c	76b
GA5 + HG5 + F	10c	24c	36b	40b	50bc	74b	90a	96a	100a
NC5 + HG5 + F	6d	14cd	34bc	46b	56b	84b	94a	96a	100a
Mi5 + GA5 + F	30b	56a	76a	94a	96a	100a	100a	100a	100a
Mi5 + NC5 + F	30b	50a	70a	90a	96a	100a	100a	100a	100a

<sup>a</sup>Nematode inoculum levels: 5=5,000; 10=10,000 (eggs of *M. incognita* were used as inoculum). Wilt indices: 0=no wilt; 100=maximum wilt or dead plant (See Table 1 for descriptions of treatments). <sup>b</sup>Data analyzed by Duncan's new multiple range; data in given column with common letters are not significantly different at 5% level.

indices was also utilized for calculating gall indices.

Final numbers of nematodes in soil were extracted by sugar-flotation-sieving (1). Egg numbers of M. incognita were determined by the method of Byrd et al. (2), except that entire root systems were used rather than 10-g samples. H. galeatus was extracted from roots by incubating the latter in a mist chamber for 14 days. The numbers obtained from the roots were combined with the respective number obtained from soil. For treatments involving both M. incognita and H. galeatus, one-half of the root system was used to determine the number of the Mi eggs and the other half was placed in a mist chamber to determine the number of H. galeatus in the roots.

Duncan's new multiple range test values were calculated for individual comparisons of means on all characteristics, including each date of wilt readings.

#### RESULTS

Wilt development: Up to 28 days, plants wounded and inoculated with Fusarium

(W+F) showed more wilt than other treatments (Table 2). From 28-31 days, plants inoculated with NC10+F exhibited wilt comparable to W+F. The greatest wilt development after 35-42 days was observed in NC10+F and NC5+F. After 49 days, wilt indices were comparable in all treatments with B. longicaudatus (NC & Ga). Plants inoculated with the higher inoculum level of M. incognita with Fusarium (Mi10+F)had more severe wilt development than plants which received the lower inoculum level of Mi + F between 25 and 49 days after inoculation. H. galeatus did not interact with Fusarium at either inoculum level, and Fusarium alone caused only slight wilt development to appear 49 days after inoculation.

When comparing the influence of the concomitant species of nematodes + Fusarium on cotton, no treatment gave early wilt equal to wounded plants + fungus (Table 2). However, by 25 days after inoculation, wilt in this treatment did not differ from plants receiving Mi5+FA5+F or Mi5+NC5+F. By 28-35 days after inoculation, wilt in treatment NC10+F was comparable to that of the three treatments above. All plants receiving NC10+F, Mi5+NC5+F and Mi5+FA5+F were dead by the 42nd day after inoculation. Beyond the 49th day after inoculation, there were no differences in wilt development on plants receiving the following treatments: FA10+F, NC10+F, HG5+FA5+F, NG5+NC5+F, Mi5+FA5 +F and Mi5+NC5+F. Plants inoculated with Mi10+F and Mi5+HG5+F had less wilt than the above treatments and had not reached 100% wilt when the experiment was terminated.

Effects of concomitant nematode species with Fusarium on nematode increase: The introduction of other nematodes (HG, Mi) with B. longicaudatus (NC, GA) on cotton had variable effects on the reproduction of the latter whether expressed as numbers of nematodes per pot or per g root (Table 3). The high levels of NC and GA alone resulted in the greatest numbers/pot. Mi suppressed the reproduction of GA, but had no significant interaction with NC. Inoculation

TABLE 3. Reproduction of North Carolina or Georgia populations of *Belonolaimus longicaudatus* (NC, GA), and *Hoplolaimus galeatus* (HG) as affected by *Fusarium oxysporum* f. sp. vasinfectum (F) and *Meloidogyne incognita* (Mi) on 'Rowden' cotton.

	Nemato (X	odes/pot 103)	Nematodes/g root			
Nematode combination	Fungus	+ Fungus	Fungus	+ Fungus		
	B. longicaudatusa					
NC5	5.6ef	1.7f	306d	584c		
NC10	25.4a	5.1ef	1359ab	1881a		
GA5	11.6bc	3.2ef	583c	468d		
GA10	16.2b	2.9f	901b	507cd		
Mi5+NC5	8.1cde	2.4f	509cd	904b		
Mi5+GA5	5.2ef	6.2ef	279d	1711a		
GA5+HG5	10.5cd	1.1f	539c	635c		
NC5+HG5	11.8bc	4.8ef	655c	820bc		
	H. galeatusa					
HG5	7.2c	7.7c	345c	428c		
HG10	15.9a	16.0a	748ab	828a		
Mi5 + HG5	4.5de	3.0e	186d	184d		
GA5 + HG5	6.0cd	3.7e	305cd	619bc		
NC5+HG5	10.0b	3.3e	550c	923a		

<sup>a</sup>Data analyzed by Duncan's new multiple range; numbers in given column for a given nematode with common letters are not significant at the 5%level. Nematode inoculum levels: 5=5,000; 10=10,000.

TABLE 4. Interactions of Meloidogyne incognita (Mi) with Hoplolaimus galeatus (HG) with North Carolina or Georgia populations of Belonolaimus longicaudatus (NC, GA) as affected by Fusarium oxysporum f. sp. vasinfectum (F) on 'Rowden' cotton.

Nematode combination	Larvae/ pot (X 103)	Larvae/ g root	Eggs/ plant (X 103)	Gall indices®
<b></b>	Nematodes onlyb			
Mi5	11. <b>4</b> b	473ab	123b	32c
Mi10	21.7a	763a	231a	55a
Mi5 + HG5	3.5c	145cde	50cd	23d
Mi5+NC5	0.6c	39e	14de	5e
Mi5+GA5	0.3c	15e	25de	5e
		Nematodes -	+ fungus	0
Mi5	3.5c	224bc	89bc	- 35c
Mil0	2.2c	211b	93bc	44b
Mi5+HG5	3.4c	202cd	34de	20d

aRoot gall indices: 0 = no galling; 100 = maximum galling.

95de

63e

le

1e

le

le

0.2c

0.1c

Mi5 + NC5

Mi5 + GA5

<sup>b</sup>Data analyzed by Duncan's new multiple range; numbers in given columns with common letter are not significant at 5% level. Nematode inoculums levels: 5=5,000; 10=10,000.

with Fusarium greatly depressed the increase of GA and NC in all treatments on a per plant basis, although numbers of nematodes/g root varied with treatments.

Of the three species of nematodes, populations of H. galeatus (HG) were affected least by the addition of Fusarium or other nematodes (Table 3). Mi had a slight depressive influence, whereas NC was stimulatory (NC5+HG5), compared to HG5 alone. On a per pot basis, final numbers of HG were negatively affected by Fusarium, but the opposite was sometimes true if nematode numbers were expressed on a per g root basis.

Major trends in population changes of Mi were evident in various combination treatments (Table 4). The presence of Fusarium resulted in fewer eggs and larvae in roots and soil, respectively in treatments with Mi as the only nematode. Fusarium did not affect the populations of Mi when other nematode species were present. In the absence of Fusarium, HG and B. longicaudatus (NC & GA) greatly inhibited the increase of Mi.

#### DISCUSSION

The influence of nematodes on Fusarium wilt development of cotton was most pronounced with GA and NC populations of B. longicaudatus. The NC population plus F resulted in more rapid wilt development than the GA population at both levels. This supports the findings of Robbins & Barker (14) who detected differences between these two populations, including host range, morphology and rates of reproduction. A possible explanation for the greater interaction with NC-Fusarium, as compared to GA-Fusarium, is that the NC population was originally collected from a heavily infested cotton field, whereas the GA population was collected from millet. Although Cooper and Brodie (3) reported that B. longicaudatus is similar to root-knot nematodes in promoting wilt on cotton in field tests, our data indicate that both populations of B. longicaudatus, at the levels used, promoted greater wilt development than M. incognita. This apparent conflict can best be explained by the fact that the level of B. longicaudatus used in these experiments exceeds the usual density of this nematode found in infested fields (3, 5). Nevertheless, the ability of this nematode to promote a complex disease reaction should be emphasized.

Neither inoculum level of *H. galeatus* predisposed cotton plants to *Fusarium*. The failure of this migratory endoparasite, which feeds primarily on cortical tissue (9), to incite a positive disease interaction suggests that simple wounding in cortical tissues probably is not the primary mechanism permitting wilt development subsequent to parasitism by nematodes. For wounding to be important, it must permit *Fusarium* spores to gain access to the vascular tissues as apparently occurs with the long-styletbearing ectoparasite, *B. longicaudatus*.

Combinations of Mi with either GA or NC nematodes and *Fusarium* promoted earlier and more severe wilt development than either of these nematodes acting alone. This more rapid wilt development cannot be explained on the basis of nematode population densities since this association tends to be antagonistic to both nematodes. These two nematodes acting together may have created greater physiological and mechanical changes in the host, resulting in greater susceptibility to *Fusarium*. This finding may be especially significant since disease complexes in the field probably involve more than one nematode species. Since adding HG to other nematode species in combination with *Fusarium* failed to alter wilt on cotton, only combinations of nematodes which by themselves interact with *Fusarium* may result in greater wilt development.

The limited wilt development in the F treatment may be due to the methods used in growing and inoculating plants. The fungal spores and nematode suspensions were poured around established seedlings and covered with additional soil, without disturbing the roots of the seedlings.

Numerous workers (4, 7, 8, 15, 18) have found a general antagonistic interaction between nematodes. With our experiments, this effect is especially evident with the combination of any Mi and B. longicaudatus populations. The basic mechanism of antagonistic or stimulatory interactions in nematode combinations is not known. Based on these results, however, some inferences may be drawn. Both GA and NC cause severe inhibition of root growth. Since Mi penetrates mainly behind the root cap (10), populations may be limited by the few available sites for invasion. However, the addition of Fusarium to all nematode combination treatments also depresses their reproduction. This may be attributed to reduced food sources for the nematode since the wilted plant remains stunted and often dies.

The detrimental effect of *H. galeatus* (HG) on the reproduction of Mi may be due to HG, a migratory endoparasite, damaging the feeding sites of Mi. Reproduction of Mi on cotton also is suppressed by *Pratylenchus brachyurus* (Godfrey) T. Goodey (4). However, the feeding of HG may be beneficial to ectoparasitic nematodes such as *B. longicaudatus* since reproduction of the latter was affected little or increased in the presence of HG.

Regardless of whether there are one or many mechanisms involved in antagonistic or stimulatory effects of nematode combinations, the final population is important to the understanding of population dynamics of nematodes and their roles in disease complexes. These results show that combinations of two nematodes with *Fusarium* can cause greater wilt development than either nematode alone with this fungus. It would be especially useful to investigate this phenomenon on resistant varieties where qualitative and quantitative differences may be encountered.

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