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Predisposition of Broadleaf Tobacco to Fusarium Wilt by Early Infection with *Globodera tabacum tabacum* or *Meloidogyne hapla*

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Abstract: In greenhouse experiments, broadleaf tobacco plants were inoculated with tobacco cyst (*Globodera tabacum tabacum*) or root-knot (*Meloidogyne hapla*) nematodes 3, 2, or 1 week before or at the same time as *Fusarium oxysporum*. Plants infected with nematodes prior to fungal inoculation had greater Fusarium wilt incidence and severity than those simultaneously inoculated. *G. t. tabacum* increased wilt incidence and severity more than did *M. hapla*. Mechanical root wounding within 1 week of *F. oxysporum* inoculation increased wilt severity. In field experiments, early-season *G. t. tabacum* control by preplant soil application of oxamyl indirectly limited the incidence and severity of wilt. Wilt incidence was 48%, 23%, and 8% in 1989 and 64%, 60%, and 19% in 1990 for 0.0, 2.2, and 6.7 kg oxamyl/ha, respectively. Early infection of tobacco by *G. t. tabacum* predisposed broadleaf tobacco to wilt by *F. oxysporum*.

Key words: Disease complex, *Fusarium oxysporum*, Fusarium wilt, *Globodera tabacum tabacum*, interaction, *Meloidogyne hapla*, nematode, *Nicotiana tabacum*, predisposition, root-knot nematode, tobacco, tobacco cyst nematode.

Fusarium wilt caused by *Fusarium oxysporum* (Schlecht) Wr. is the most destructive disease of broadleaf tobacco in Connecticut. The tobacco cyst nematode, *Globodera tabacum tabacum* (Lownsbery & Lownsbery) Behrens, is reported to increase the incidence and severity of this wilt disease (11). This enhanced disease severity appears similar to previously demonstrated associations of root-knot nematodes (*Meloidogyne* spp.) with Fusarium wilts of tobacco and other crops (15,16).

The mechanism of the interaction between *G. t. tabacum* and *F. oxysporum* is not known but may be similar to that described for the wilt fungus and *Meloidogyne* spp. (13,16). Increased wilt of tobacco occurred when *F. oxysporum* and *Meloidogyne* spp. were added simultaneously, but disease was greatest when the fungus was added 3–4 weeks after nematode infection (17). It has been suggested that the specialized, nutrient-rich giant cells induced by root-knot nematodes contribute to this interaction (14). Cyst nematodes, sedentary endoparasites that induce somewhat similar feeding cells, also have been implicated in disease complexes (4,5,18). Additionally, the timing of the interaction, as determined by sequential inoculation of pathogens, may have an impact on the efficacy of Fusarium wilt management through control of the nematode component of the complex.

The objectives of this study were to determine i) if infection by *G. t. tabacum* prior to inoculation with *F. oxysporum* predisposes plants to increased disease, ii) response of tobacco cyst and root-knot nematodes, and iii) if early-season tobacco cyst nematode control is effective in restricting the incidence of Fusarium wilt under field conditions.

Materials and Methods

The effects of inoculating wilt-susceptible broadleaf tobacco with *G. t. tabacum* before inoculation with *F. oxysporum* were investigated in repeated factorial design greenhouse experiments. Sixty-day-old 'CT 86-4' wilt-susceptible broadleaf tobacco was transplanted to 10-cm-d plastic pots containing 450 cm^3 of a 1:1 mixture of Sunshine potting mix and fumigated field soil (86.8% sand, 10% silt, 3.2% clay, 1.6% organic matter). Suspensions of 20,000 second-stage juveniles (J2) in eggs of *G. t. tabacum* or 20,000 eggs and juveniles of *M. hapla* were added to each pot 3, 2, or 1 week before inoculation with *F. oxy-*

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sporum, or both nematode and fungus were inoculated at the same time.

Fusarium oxysporum inoculum was prepared by incubating PDA plugs colonized by the fungus in a liquid medium of potato–carrot broth on a shaker for 4 days. The medium was filtered through cheesecloth, and the fungal suspension diluted to allow inoculation of 1.0×10^7 microconidia per pot. *G. t. tabacum* inoculum was prepared by crushing cysts in water to release eggs and juveniles. Nematodes in suspension were passed through a 0.35-mm-pore sieve to remove uncrushed cysts. The suspension was calibrated and diluted to result in a Pi (initial inoculum) of 20,000 juveniles per pot. *Meloidogyne hapla* inoculum (20,000 eggs and juveniles per pot) was prepared by NaOCl extraction of eggs from infected 'Rutgers' tomato roots.

Pathogens were introduced either with or without root wounding. Root wounding in conjunction with inoculation was done by placing nematodes and (or) fungi in four 0.5-cm-d holes created by a glass rod placed 5 cm deep in the soil, 2.5 cm from the edge of the pot. Conversely, plants were inoculated without wounding by adding suspensions of nematodes or fungi to the soil surface and covering with 1 cm of moist soil.

Plants were randomly placed on low watt propagation mats (Olson Products, Medina, OH) and root systems were maintained at 25 C. Plants were rated for developing Fusarium wilt symptoms on a scale of 0–4 (0 = healthy, 1 = off color, 2 = one leaf symptomatic, 3 = two or more leaves symptomatic, 4 = plant dead) when wilt incidence was approximately 50% (2.5 or 5 weeks in these experiments) (11). There were five replications of each treatment combination.

Wilt ratings and fresh shoot weights were analyzed by factorial ANOVA and means were separated by linear contrasts. Both greenhouse experiments were repeated once.

The effects of early-season *G. t. tabacum* control on wilt development in wilt-susceptible 86-4 broadleaf tobacco were investigated in field experiments in 1989 and 1990. Broadleaf tobacco was transplanted in single-row plots 1 m wide and 6.5 m long naturally infested with both *G. t. tabacum* and *F. oxysporum*. Twenty-four hours before transplanting, plots were treated with 0.0, 2.2, or 6.7 kg a.i. oxamyl (Vydate L) per ha. The appropriate amount of oxamyl for each lot was diluted in water (400 liters/ha) and repeatedly applied to the soil surface with a backpack sprayer with a KCL-5 nozzle until expended. Plots were immediately tilled to 10 cm depth with a spring tooth harrow. There were 10 tobacco plants transplanted to each plot and 10 replicate plots per treatment. All field plots were cultivated between rows 1 and 3 weeks after transplanting with tractor-drawn shanks to control weeds as per commercial production practices. Plants from border plots were removed to examine the extent of root growth and damage by cultivation. Initial (Pi) and final (Pf) *G. t. tabacum* population densities were determined by taking ten 2.5-cm-diameter cores per plot to a depth of 15 cm before transplanting and again after harvest. Plants were rated for wilt symptoms (0–4) before harvests, and total green shoot weight was determined for five healthy plants per plot. Marketable leaf yields were determined after air-curing. Wilt ratings and yields were analyzed by ANOVA and means separated by LSD.

In both 1989 and 1990, four plants of each treatment from plots treated but not included in the 10 replicates were destructively sampled to determine the effects of oxamyl on *G. t. tabacum* infection and development in roots. Roots were washed free of soil, and two 1-g samples from each plant were stained with glycerine acid fuchsin (3).

Results

In greenhouse experiments in which roots were wounded or not at the time of nematode inoculation, both recent wounding and nematode infection of roots before

F. oxysporum inoculation increased wilt incidence and severity. Fusarium wilt severity was greater and fresh shoot weights were lower for broadleaf tobacco plants infected with tobacco cyst nematodes than for plants wounded but not inoculated with nematodes 2 weeks before *F. oxysporum* inoculation (Table 1). Wilt severity was not increased by nematode infection of roots alone 1 week before or at the same time as *F. oxysporum* inoculation. *Globodera tabacum tabacum* increased wilt ratings and decreased shoot weights more than did *M. hapla*. *Meloidogyne hapla*-infected plants were not different from uninfected plants ($P = 0.05$).

Tobacco-cyst or root-knot nematode infection increased Fusarium wilt incidence when nematodes were inoculated before *F. oxysporum* microconidia and both nematodes and fungi were added to plants without wounding (Table 2). *Globodera tabacum tabacum* increased wilt severity more than *M. hapla* or plants without nematodes, which were not different ($P = 0.05$). Wilt incidence and severity 5 weeks after inoculation was greater for plants inoculated with nematodes 1–3 weeks prior to *F. oxysporum* than for plants inoculated with nematodes and fungi simultaneously, or with *F. oxysporum* alone. Similar results were obtained from both repetitions of greenhouse experiments.

Application of oxamyl at rates of 0.0, 2.2, or 6.7 kg a.i./ha suppressed early-season root infection by *G. t. tabacum* in 1989 ($P = 0.05$) (Table 3). Both rates of oxamyl restricted the numbers of *G. t. tabacum* infective J2 and developing third-stage (J3) to adult nematodes in roots at 3 weeks after transplanting in 1989. The number of J2 in roots increased 5 weeks after transplanting in oxamyl-treated plots, and further invasion and development to J3-adult stages occurred by week 6. In 1990, invasion of tobacco roots by J2 was less in oxamyl-treated plots than in nontreated plots during the first 2 weeks, but not different thereafter (Table 4). Fewer J3-adult nematodes were present in

TABLE 1. Effects of prior inoculation with nematodes and root wounding on Fusarium wilt severity and fresh shoot weight of broadleaf tobacco.

Nematode treatment	Wilt rating†			Shoot weight (g)		
	2 weeks§	1 week	0 week	2 weeks	1 week	0 week
TCN	2.3	1.6	1.6	13.8	23.2	21.3
RKN	1.8	0.9	0.4	22.3	37.0	37.6
None	0.0	1.2	1.2	40.4	32.8	34.7
Source of variation:						
Nematode			*		***	
Timing			ns		ns	
Nematode × timing			*		ns	
Contrasts:‖						
Nematode vs. none			**		**	
TCN vs. RKN			*		**	
TCN vs. none			**		***	
RKN vs. none			ns		ns	
0 vs. 1 & 2			ns		ns	
2 vs. 1 & 0			ns		ns	
2 vs. 1 & 0 (nem)			*		**	
2 vs. 1 & 0 (none)			*		ns	

Data are means of 5 replicates. *, **, *** = significant at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively, based on analysis of variance. ns = not significant at $P \leq 0.05$.

† Wilt severity scale of 0–4 (0 = healthy, 4 = dead) 2.5 weeks after inoculation with *F. oxysporum*.

‡ TCN = tobacco cyst nematode, RKN = root-knot nematode, and None = inoculation wounding only (four holes per pot at time of nematode inoculation).

§ Nematodes inoculated 2 or 1 week before, or at the same time as *F. oxysporum*.

‖ 0 = 0 weeks; 1 = 1 week; 2 = 2 weeks; (nem) = nematode-inoculated only; (none) = non-inoculated only.

TABLE 2. Influence of prior inoculation with nematodes without root wounding on Fusarium wilt incidence and severity of broadleaf tobacco.

Nematode treatment	Wilt rating†				Wilt incidence‡			
	3 weeks	2 weeks	1 week	0 week	3 weeks	2 weeks	1 week	0 week
TCN§	1.3	1.9	1.7	0.2	6	7	7	1
RKN	0.9	1.1	0.9	0.0	4	5	3	0
None	0.3	0.0	0.5	0.1	1	0	1	1
Source of variation:								
Nematode					***		***	
Timing					**		**	
Nematode × timing					ns			
Contrasts:‖								
Nematode vs. none					*		***	
TCN vs. RKN					ns		*	
RKN vs. none					ns		*	
0 vs. 1, 2 & 3					**		**	
0 vs. 1, 2 & 3 (nem)					**		***	

Data are means of 10 replicates. *, **, *** = significant at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively, based on analysis of variance. ns = not significant at $P \leq 0.05$.

† Wilt severity scale of 0–4; 5 weeks after inoculation with *F. oxysporum*.

‡ Number of wilted plants.

§ TCN = tobacco cyst nematode, RKN = root-knot nematode, None = water alone.

‖ 0 = 0 weeks; 1 = 1 week; 2 = 2 weeks; 3 = 3 weeks; (nem) = nematode-inoculated only.

roots of plants in treated plots than in nontreated plots throughout the 6-week sampling period. Fewer cyst nematodes were present in roots of plants from plots treated with the higher rate of oxamyl than with the lower rate. The reduction in J3-adult nematodes over time reflects some loss of adult males by egress and adult females from roots to soil and solutions during the extraction and staining procedures, as well as changes in nematode numbers due to increased root growth.

Suppression of early *G. t. tabacum* infection and development in roots by preplant oxamyl treatment resulted in a decrease in Fusarium wilt incidence and severity in 1989 (Table 5). Broadleaf tobacco is pri-

TABLE 3. Influence of preplant oxamyl application on *Globodera tabacum tabacum* infection and development in field-grown broadleaf tobacco roots over time, 1989.

Weeks after transplanting	J2 per g root			J3-adult per g root		
	0.0 kg†	2.2 kg	6.7 kg	0.0 kg	2.2 kg	6.7 kg
3	103	14	0	76	4	0
5	66	45	24	23	12	1
6	5	7	30	57	32	16
Source of variation:						
Oxamyl rate			***		***	
Weeks			***		*	
Oxamyl rate × weeks			**		ns	
Contrasts:						
Oxamyl vs. none			**		***	
2.2 vs. 6.7 kg/ha			ns		ns	
Oxamyl vs. none (3 weeks)			***		***	
Oxamyl vs. none (5 weeks)			ns		ns	
Oxamyl vs. none (6 weeks)			ns		*	

Data are means of eight observations. *, **, *** = significant at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively, based on analysis of variance. ns = not significant at $P \leq 0.05$.

† Oxamyl rate in kg a.i./ha.

TABLE 4. Influence of preplant oxamyl application on *Globodera tabacum tabacum* infection and development in field-grown broadleaf tobacco roots over time, 1990.

Weeks after transplanting	J2 per g root			J3-adult per g root		
	0.0 kg†	2.2 kg	6.7 kg	0.0 kg	2.2 kg	6.7 kg
1	164	42	29	14	3	1
2	70	23	3	91	67	10
3	27	13	5	66	85	17
4	3	12	2	87	57	12
5	9	5	1	69	23	3
6	2	5	1	80	23	8

Source of variation:		
Oxamyl rate	***	***
Weeks	*	ns
Oxamyl rate × weeks	**	ns
Contrasts:		
Oxamyl vs. none	***	***
2.2 vs. 6.7 kg/ha	ns	**
Oxamyl vs. none (1 week)	***	ns
Oxamyl vs. none (2 weeks)	**	*
Oxamyl vs. none (3 weeks)	ns	ns
Oxamyl vs. none (5 weeks)	ns	*
Oxamyl vs. none (6 weeks)	ns	*

Data are means of eight observations. *, **, *** = significant at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively, based on analysis of variance. ns = not significant at $P \leq 0.05$.
† Oxamyl rate in kg a.i./ha.

marily a cigar-wrapper tobacco. Wilt-symptomatic plants are often of poor quality and may not justify the expense of harvesting, curing, and sorting. Harvested asymptomatic plants had decreased fresh shoot (leaves and stalk) weights, but cured weight leaf yields were not different (P = 0.05).

Initial wilt symptoms were first observed 4 weeks after transplanting in field experiments, and both incidence and severity increased after that time. Suppression of *G. t. tabacum* infection and development in roots resulted in a reduction in Fusarium wilt incidence and severity of plants treated with 6.7 kg per ha oxamyl as compared to no-nematicide controls in 1990. Fresh weight yield of wilt-asymptomatic plants was greater for plants from oxamyl-treated plots than those from untreated

TABLE 5. Effects of preplant oxamyl application on Fusarium wilt incidence and severity and broadleaf tobacco yield, 1989 and 1990.

Oxamyl kg a.i./ha	Wilt incidence†	Wilt severity‡	Fresh weight yield (kg)§	Cured weight yield (g)
		1989		
0.0	48	1.4	1.6	709
2.2	23	0.7	1.7	736
6.7	8	0.2	1.8	752
LSD	19	0.6	0.1	53
		1990		
0.0	64	1.9	1.6	666
2.2	60	1.8	1.8	744
6.7	19	0.5	1.8	706
LSD	23	0.9	0.2	68

† Wilt incidence (% symptomatic plants).
‡ Wilt severity scale of 0–4 (0 = healthy, 4 = dead).
§ Yield per five asymptomatic plants.

lots, but cured weight leaf yields were not different. Initial *G. t. tabacum* densities were 14 per cm^3 soil in 1989 and 33 per cm^3 soil in 1990. Both wilt incidence and severity increased from 1989 to 1990, probably due to increased *G. t. tabacum* and *F. oxysporum* inoculum levels in soil.

Cyst nematode reproduction, as measured by reproduction rates (Pf/Pi) was 9.8, 1.0, and 0.5 in 1989 and 8.0, 2.1, and 2.9 in 1990 for 0.0, 2.2, and 6.7 kg per ha oxamyl, respectively. Oxamyl application suppressed nematode increase, but there were no differences between low or high application rates.

Discussion

Fusarium oxysporum alone is capable of causing wilt of broadleaf tobacco, but severe wilt has been associated with *G. t. tabacum* infection (11). In addition to nematode infection, *F. oxysporum* ingress may be aided by mechanical wounding of roots during cultivation.

Broadleaf tobacco seems more susceptible and does not appear as dependent on nematodes for wilt development as does flue-cured tobacco (10). Initial wilt symptoms developed as quickly as 2.5 weeks after Fusarium inoculation of broadleaf in my tests, compared to over 7 weeks for wilt to develop in flue-cured tobacco (17). Additionally, wilt was more severe on root-wounded broadleaf plants in my experiments than that reported for wounded plants of flue-cured tobacco (17).

The interaction of *Meloidogyne* spp. with Fusarium wilts of a number of crops have previously been described (13,15,16). The mechanism(s) of *Meloidogyne*–Fusarium wilt interactions, though extensively studied, are complex and not fully understood. Root-knot nematode infection of roots may change the amount or composition of root exudates (1,20) or may influence *F. oxysporum* penetration and pathogenesis. *Fusarium oxysporum* can readily infect roots by direct penetration, but wilt can be increased by root wounding (13). It has also been proposed that nematode invasion of roots creates wounds that allow *F. oxysporum* ingress (19). In my experiments mechanical wounding of roots increased wilt severity when wounding was at the same time or within 1 week of *F. oxysporum* inoculation. Inoculation with *G. t. tabacum* or *M. hapla* 2 or more weeks before *F. oxysporum* inoculation was more efficient than mechanical wounding in increasing wilt development. *Globodera tabacum tabacum* infection of broadleaf tobacco roots resulted in greater wilt incidence and severity than did *M. hapla* infection.

The fact that wilt increased in plants inoculated with nematodes prior to *F. oxysporum* inoculation supports the general theory that the mechanism of nematode-wilt interaction is complex and involves a modification of host physiology rather than simple wounding due to juvenile invasion (13,16). Sedentary endoparasites such as *Meloidogyne* and *Globodera* stimulate the production of giant cells or syncytia in xylem parenchyma cells adjacent to xylem vessels (2,6) that act as nutrient sinks (7). Because sedentary endoparasitic nematodes influence the production and accumulation of various minerals and plant metabolites such as indole-acetic acid and other growth factors (8,21), the extended juvenile state of these cells may facilitate *F. oxysporum* infection of xylem elements. Nutrients may also leak from roots, causing increased *F. oxysporum* density in the rhizosphere of tomato roots infected by *M. incognita* (20) or *M. javanica* (1). Tobacco roots infected with *Meloidogyne* spp. also had extensive *F. oxysporum* colonization of giant cells and nearby vessel elements, and the maximum development of the fungus in galled roots occurred 3–4 weeks after infection of roots by *Meloidogyne* spp. (14).

Previous work showed that root-knot nematode control with fumigant nematicides greatly limits Fusarium wilts of a number of crops (15). Control of *G. t. tabacum* by fumigation with dichloropropene and methyl isothiocyanate also has restricted the incidence of Fusarium wilt of broadleaf tobacco (11). Preplant applications of oxamyl to shade tobacco in Con-

necticut have previously resulted in an early-season inhibition of *G. t. tabacum* invasion and development in roots (9). The results in the present experiments are consistent with that observation. The use of oxamyl as an experimental tool to limit or delay early-season *G. t. tabacum* infection indicates the importance of *G. t. tabacum* predisposition in the development of wilt. At moderate *F. oxysporum* inoculum densities in 1989, a delay of 3 weeks in significant *G. t. tabacum* infection and development limited Fusarium wilt incidence and severity. At higher *F. oxysporum* levels in 1990, wilt incidence was 64% in untreated plots, and nematode control alone was not as effective in reducing losses due to wilt.

Control of *G. t. tabacum* alone does not consistently suppress wilt in broadleaf tobacco, especially after repeated tobacco crops. This problem reflects the importance of developing and integrating additional tactics for Fusarium wilt management. Wilt-resistant cultivars have been developed that substantially limit the incidence of disease in fields heavily infested with both pathogens (12). Although *G. t. tabacum* may result in increased wilt severity in these cultivars, symptoms are typically mild, and the nematode does not alter the resistance to *F. oxysporum* (11).

Literature Cited

1. Bergeson, G. B., S. D. Van Gundy, and I. J. Thomason. 1970. Effect of *Meloidogyne javanica* on rhizosphere microflora and Fusarium wilt of tomato. Phytopathology 60:1245–1249.

2. Bird, A. F. 1961. The ultrastructure and histochemistry of a nematode-induced giant cell. Journal of Biophysical and Biochemical Cytology 11:701–715.

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

4. Grant, C. E., J. J. Reilly, and A. P. Elliott. 1984. Interaction of *Globodera solanacearum* (= *G. tabacum solanacearum*) and *Phytophthora parasitica* var. *nicotianae* with flue-cured tobacco. Phytopathology 74:756–757 (Abstr.).

5. Harrison, J. A. C. 1971. Association between the potato cyst nematode *Heterodera rostochiensis* Woll. and *Verticillium dahliae* Kleb. in the early dying disease of potatoes. Annals of Applied Biology 67:185–193.

6. Jones, M. G. K., and V. H. Dropkin. 1975. Scanning electron microscopy of syncytial transfer cells induced in roots by cyst-nematodes. Physiological Plant Pathology 7:259–263.

7. Jones, M. G. K., and D. H. Northcote. 1972. Nematode induced syncytium—a multinucleate transfer call. Journal of Cell Science 10:789–809.

8. Kleineke-Borchers, A., and U. Wyss. 1982. Investigations on changes in susceptibility of tomato plants to *Fusarium oxysporum* f.sp. *lycopersici* after infection by *Meloidogyne incognita*. Zeitschrift fuer Pflanzenkrankheiten und Pflanzenschutz. 89:67–78.

9. LaMondia, J. A. 1990. Effect of oxamyl on *Globodera tabacum* population dynamics and shade tobacco growth and yield. Supplement to the Journal of Nematology 22:654–657.

10. LaMondia, J. A. 1990. Pathogenicity and vegetative compatibility of *Fusarium oxysporum* isolated from tobacco. Tobacco Science 34:105–108.

11. LaMondia, J. A., and G. S. Taylor. 1987. Influence of the tobacco cyst nematode (*Globodera tabacum*) on Fusarium wilt of Connecticut broadleaf tobacco. Plant Disease 71:1129–1132.

12. LaMondia, J. A., and G. S. Taylor. 1991. New Fusarium wilt-resistant Connecticut broadleaf tobacco varieties. Connecticut Agricultural Experiment Station Bulletin 891.

13. Mai, W. F., and G. S. Abawi. 1987. Interactions among root-knot nematodes and Fusarium wilt fungi on host plants. Annual Review of Phytopathology 25: 317–338.

14. Melendez, P. L., and N. T. Powell. 1967. Histological aspects of the Fusarium wilt-root knot complex in flue-cured tobacco. Phytopathology 57:286–292.

15. Powell, N. T. 1971. Interaction of plant parasitic nematodes with other disease-causing agents. Pp. 119–136 in B. M. Zuckerman, W. F. Mai, and R. A. Rohde, eds. Plant parasitic nematodes, vol. 2. New York: Academic Press.

16. Powell, N. T. 1971. Interactions between nematodes and fungi in disease complexes. Annual Review of Phytopathology 9:253–274.

17. Porter, D. M., and N. T. Powell. 1967. Influence of certain *Meloidogyne* species on Fusarium wilt development in flue-cured tobacco. Phytopathology 57:282–285.

18. Ross, J. P. 1965. Predisposition of soybeans to Fusarium wilt by *Heterodera glycines* and *Meloidogyne incognita*. Phytopathology 55:361–364.

19. Taylor, C. E. 1979. *Meloidogyne* interrelationships with microorganisms. Pp. 375–398 in F. Lamberti and C. E. Taylor, eds. Root-knot nematodes (*Meloidogyne* species), systematics, biology and control. London: Academic Press.

20. Van Gundy, S. D., J. D. Kirkpatrick, and J. Golden. 1977. The nature and role of metabolic leakage from root-knot nematode galls and infection by *Rhizoctonia solani*. Journal of Nematology 9:113–121.

21. Webster, J. M. 1985. Interaction of *Meloidogyne* with fungi on crop plants. Pp. 183–192 in J. N. Sasser and C. C. Carter, eds. An advanced treatise on *Meloidogyne*, vol. 1. Biology and control. Raleigh: North Carolina State University Graphics.