Influence of Resistant Tobacco and Tobacco Cyst Nematodes on Root Infection and Secondary Inoculum of *Fusarium oxysporum* f. sp. *nicotianae*

J. A. LaMONDIA, Department of Plant Pathology and Ecology, Connecticut Agricultural Experiment Station, Valley Laboratory, P.O. Box 248, Windsor 06095

ABSTRACT

LaMondia, J. A. 1995. Influence of resistant tobacco and tobacco cyst nematodes on root infection and secondary inoculum of *Fusarium oxysporum* f. sp. *nicotianae*. Plant Dis. 79:337-340.

The influence of Fusarium wilt-resistant broadleaf tobacco and *Globodera tabacum tabacum* on infection and secondary inoculum production by *Fusarium oxysporum* f. sp. *nicotianae* was investigated under greenhouse and field microplot conditions. Wilt severity and postharvest *F. oxysporum* density in soil was greater for wilt-susceptible than wilt-resistant tobacco in all experiments. *G. t. tabacum* increased the number of *F. oxysporum* colonies recovered per centimeter of root for wilt-susceptible but not for resistant tobacco after 8 wk. *F. oxysporum* levels in soil were greater after plant infection by both *F. oxysporum* and *G. t. tabacum* than after plant infection by *F. oxysporum* alone. Wilt-resistant tobacco supported *F. oxysporum* densities that were intermediate between susceptible tobacco and fallow and significantly greater than fallow only after more than one season of production, regardless of nematode infection, under both field and greenhouse conditions.

Fusarium wilt of broadleaf tobacco (*Nicotiana tabacum* L.), caused by *Fusarium oxysporum* Schlechtend.:Fr. f. sp. *nicotianae* (J. Johnson) W.C. Snyder & H.N. Hans., is the most important disease of broadleaf tobacco in Connecticut and Massachusetts. The tobacco cyst nematode, *Globodera tabacum tabacum* (Lownsberry & Lownsberry) Behrens, has been demonstrated to increase the severity of wilt (10,11). Early season nematode control has reduced both the incidence and the severity of wilt (10).

The most effective control of Fusarium wilt has been achieved through the development and use of wilt-resistant broadleaf tobacco cultivars (2,12,14). These resistant cultivars are not immune to *Fusarium* infection and will develop wilt symptoms under high inoculum potential (11).

The effect of wilt-resistant cultivars on *F. oxysporum* populations and the influence of tobacco cyst nematodes on these populations are important in evaluating the long-term effectiveness of wilt resistance as a control tactic against this disease. The objectives of this research were to determine 1) the extent of *F. oxysporum* infection and root colonization of resistant cultivars, 2) the influence of *G. t. tabacum* infection on this colonization, and 3) the effect of growing resistant cultivars on residual inoculum densities of *F. oxysporum* in soil.

Accepted for publication 4 January 1995.

MATERIALS AND METHODS

Greenhouse experiments. The isolate of *F. oxysporum* used in these experiments was recovered from wilt-symptomatic tobacco in 1986 and maintained by serial transfer on potato-dextrose agar (PDA). *F. oxysporum* was grown for 2 days in potato-carrot broth (prepared by autoclaving 10 g of potato tissue, 10 g of carrot, and 10 g of sucrose in 1 L of water for 15 min, filtering through cheesecloth, and autoclaving again). The broth culture was added to 1,000 cm^3 of milled straw (previously moistened with 250 ml of water and autoclaved two times for 1 h at 121 C on successive days). After 2 wk incubation, the infested straw was dried to stimulate chlamydospore formation, mixed, and used as inoculum.

G. t. tabacum cysts collected from tobacco grown in pasteurized soil in the greenhouse were soaked overnight in water. Soaked cysts were crushed and passed through a 0.25-mm-pore sieve in water to collect second-stage juveniles and juveniles in eggs, which were used as inoculum.

Pasteurized Merrimac fine sandy loam field soil (450 cm^3 per pot: 73.4% sand, 21.4% silt, 5.2% clay, 3.2% organic matter, pH 6.1) was infested or not infested with *F. oxysporum* and/or *G. t. tabacum*. *F. oxysporum* inoculum levels were 500 cfu/cm^3 of soil, determined by dilution plating onto *Fusarium*-selective Komada medium (8). The fungus was mixed with soil prior to potting. *G. t. tabacum* inoculum levels were 10,000 juveniles per pot (22 juveniles per cubic centimeter of soil). Two-month-old wilt-susceptible 86-4 or wilt-resistant C8 or C9 broadleaf tobacco plants were transplanted to pots, and nematodes were added in suspension to four 1-cm-diameter, 5-cm-deep holes per pot outside the root ball to avoid root injury. All cultivars were susceptible to *G. t. tabacum*.

Three greenhouse experiments were performed. In the first, wilt-susceptible 86-4 and wilt-resistant C8 broadleaf tobacco were evaluated. In the second, 86-4 and wilt-resistant C9 were compared. The third experiment evaluated all three cultivars. There were five, five, and 10 replicate pots, respectively, of each factorial treatment in a randomized complete block design for the three experiments. Fallow pots, which were infested with *F. oxysporum* but not planted to tobacco, were used as controls in the first two experiments to determine *F. oxysporum* densities in soil alone at transplanting and again after 8 wk. Plants were maintained in the greenhouse on propagation mats set at 25 C. Plants were grown for 8 wk after transplanting to approximate the time required to produce a crop under field conditions.

After 8 wk, plants were rated for foliar wilt symptoms on a scale of 0–4 (0 = healthy plants, 1 = stunted or off-color plants, 2 = plants with one symptomatic leaf, 3 = more than one symptomatic leaf, and 4 = dead plants) (11). Root systems were split in half, and in one half, roots were washed free of soil, surface disinfested for 1 min in 0.5% NaOCl, and rinsed twice in sterile distilled water, and 100–200 cm of root was spread over four plates of Komada medium. Root length was determined using a modified line intersect method (18). The number of *F. oxysporum* colonies on roots was counted after 10 days. Roots and soil from the second half of the root system were air-dried to stimulate chlamydospore formation, sieved, and mixed. *F. oxysporum* populations were estimated by dilution plating onto Komada medium. Wilt rating data were transformed by square root of $X+1$ to stabilize the variance prior to analysis.

Field microplots. The effect of *F. oxysporum*-resistant tobacco on *F. oxysporum* densities in soil was investigated in open bottom field microplots con-

structed from Rubbermaid waste cans (Model 2947) containing 30 L of Merrimac fine sandy loam soil (71.8% sand, 23.0% silt, 5.2% clay, and 2.2% organic matter, pH 6.2) typical of Connecticut Valley tobacco soils. The microplots were placed 37 cm deep in rows 1 m apart, and 2.4 m apart within rows. Field soil naturally infested with both *F. oxysporum* and *G. t. tabacum* was fumigated with methyl bromide (1 kg/20 m^2 of soil) and placed in the plots. Fumigation reduced both nematode and fungal pathogens to below levels detectable by soil dilution and cyst extraction techniques. In a previous experiment, the microplots were inoculated with 0, 24,000, or 162,000 encysted juveniles of *G. t. tabacum* and/or 0 (20 g of autoclaved straw), 5, 10, or 20 g of *F. oxysporum*-infested straw per microplot in 1987 (five replicates of each factorial treatment). The microplots were planted to wilt-susceptible 86-4 broadleaf tobacco in 1987 to investigate the interaction of the two pathogens (11), resulting in a range of *F. oxysporum* and *G. t. tabacum* densities after harvest, which were used as initial population densities in the experiments reported in this paper.

In this experiment, microplots were planted on 22 June 1988 with the wilt-resistant broadleaf tobacco cultivar C8. Preplant and postharvest *F. oxysporum* populations were determined by dilution plating of soil taken from 10 2.5-cm-diameter cores per plot onto Komada medium. *G. t. tabacum* densities were determined by extracting cysts from soil using a modified Fenwick can, crushing cysts, and counting encysted juveniles. Wilt symptoms were recorded on 17 August prior to harvest.

In 1989, preplant and postharvest *F. oxysporum* and *G. t. tabacum* densities in microplots were determined as above. However, all microplots were found to be infested with both pathogens by 1989. *F. oxysporum* preplant densities ranged from 10 to 230 cfu/g of soil. Initial *G. t. tabacum* densities in microplots ranged from 45 to 118 juveniles per cubic centimeter of soil. Microplots were blocked for *F. oxysporum* soil density based on preplant dilution plating and wilt severity on a previous susceptible tobacco crop in 1987. Six or seven replicate microplots per block (1 = low-density *F. oxysporum* cfu per gram of soil and 1987 wilt rating of 0–1; 2 = intermediate *F. oxysporum* density and 1987 wilt rating of 2–3; 3 = high *F. oxysporum* densities in soil and 1987 wilt ratings of 4) were planted on 15 June 1989 to either wilt-resistant C8 or wilt-susceptible 86-4, or were left fallow. Tobacco plants were rated for wilt severity. In 1990, wilt-susceptible tobacco was planted on 18 June and grown in all plots as a bioassay of *F. oxysporum* soil densities.

On 12 June 1991, plots were sampled to determine *F. oxysporum* population densities in soil and again planted to the same resistant or susceptible tobacco cultivar or left fallow as in 1989. Microplots were not re-randomized, but were reblocked for wilt severity based on 1990 data (20 microplots per block, six or seven replicates per treatment). After sampling soil to determine postharvest *F. oxysporum* cfu/g of soil on 26 August, wilt-susceptible 86-4 tobacco was grown for 8 wk as a bioassay.

Data were analyzed by analysis of variance. Wilt-rating data were transformed by the square root of $X+1$ to stabilize the variance prior to analysis. Selected treatments were compared with linear contrasts.

RESULTS

Wilt severity was greater for wilt-susceptible than wilt-resistant tobacco in all greenhouse experiments. Wilt ratings were low for both resistant cultivars. No wilt symptoms were evident in the *F. oxysporum*-uninfested control pots, and *F. o. nicotianae* was not isolated from roots of uninfested control plants. Fallow pot data were excluded from the analysis of variance for wilt severity and cfu per 10-cm root variables. The tobacco cyst nematode did not increase final wilt severity in two of the three experiments (Tables 1–3).

Root infection by *F. oxysporum*, determined by the number of *F. oxysporum* colonies recovered per 10 cm surface sterilized root, was greater for wilt-susceptible than resistant tobacco. *G. t. tabacum* infection increased *F. oxysporum* root colonization of wilt-susceptible tobacco at 8 wk after transplanting for two of the three experiments (Tables 1–3). Trends were similar in the third experiment, but means were not significantly different.

F. oxysporum cfu per gram of soil after 8 wk was greater for wilt-susceptible tobacco than for resistant tobacco or fallow, which did not differ (Tables 1–3). *G. t. tabacum* infection significantly increased final *F. oxysporum* densities in soil in two of three experiments. *F. oxysporum* densities after 8 wk of fallow were unchanged from initial inoculum levels.

Wilt-resistant C8 broadleaf tobacco grown in field microplots in 1988 did not develop significant wilt symptoms. A paired *t* test between preplant and postharvest *F. oxysporum* densities (means

Table 1. The effects of wilt-susceptible tobacco, C8 wilt-resistant tobacco or fallow and *Globodera tabacum tabacum* (Gtt) infection on Fusarium wilt severity, *Fusarium oxysporum* root colonization, and soil density after 8 wk under greenhouse conditions (Experiment 1)

Host	Gtt	Wilt severity rating[a]		Cfu per 10 cm root		Cfu × 10^2 per g soil	
86-4[b]	+[c]	4.0		9.4		69.3	
	−	3.7		4.8		19.5	
C8	+	1.3		1.7		11.1	
	−	1.2		1.7		8.9	
Fallow		...		...		4.9	
Source of variation	df	*P*	df	*P*	df	*P*	
Host	1	0.001	1	0.001	2	0.001	
Gtt	1	NS	1	0.01	1	0.02	
Host × Gtt	1	NS	1	0.01	2	0.01	
Error	16		16		24		

[a] Wilt rating: 0 = healthy to 4 = plant dead. Data analyzed after $X + 1$ transformation.
[b] Wilt-susceptible 86-4, wilt-resistant C8 and C9.
[c] *G. t. tabacum* inoculum density = 22 juveniles per cubic centimeter of soil, *F. oxysporum* inoculum = 500 cfu/cm^3 soil.

Table 2. The effects of wilt-susceptible tobacco, C9 wilt-resistant tobacco or fallow and *Globodera tabacum tabacum* (Gtt) infection on Fusarium wilt severity, *Fusarium oxysporum* root colonization, and soil density after 8 wk under greenhouse conditions (Experiment 2)

Host	Gtt	Wilt severity rating[a]		Cfu per 10 cm root		Cfu × 10^2 per g soil	
86-4[b]	+[c]	3.0		5.0		34.9	
	−	3.0		2.4		26.2	
C9	+	0.0		1.2		15.6	
	−	0.0		1.2		17.5	
Fallow		...		...		11.9	
Source of variation	df	*P*	df	*P*	df	*P*	
Host	1	0.001	1	0.001	2	0.02	
Gtt	1	NS	1	0.02	1	NS	
Host × Gtt	1	NS	1	0.02	2	NS	
Error	16		16		24		

[a] Wilt rating: 0 = healthy to 4 = plant dead. Data analyzed after $X + 1$ transformation.
[b] Wilt-susceptible 86-4, wilt-resistant C8 and C9.
[c] *G. t. tabacum* inoculum density = 22 juveniles per cubic centimeter of soil, *F. oxysporum* inoculum = 500 cfu/cm^3 soil.

= 71 and 65 cfu/g of soil, respectively) indicated that densities were not different after production of wilt-resistant tobacco ($t = 0.52$; $P = 0.61$).

In 1989, wilt ratings for susceptible tobacco ranged from 0 to 4 (mean = 2.2). Resistant plants did not exhibit wilt symptoms. *F. oxysporum* cfu per gram of microplot soil were not affected by the production of wilt-susceptible or wilt-resistant tobacco, or by fallowing plots (Table 4). However, *F. oxysporum* inoculum potential, as determined by a wilt-susceptible bioassay crop produced in the microplots in 1990, was greater for microplots planted to wilt-susceptible tobacco in 1989 than to wilt-resistant tobacco or fallow.

In 1991, preplant *F. oxysporum* cfu per gram of microplot soil was higher as a result of the production of wilt-susceptible tobacco in 1990 (Table 4). *F. oxysporum* soil densities after growing wilt-resistant tobacco were greater than in fallow soil and less than after wilt-susceptible tobacco. Wilt symptoms in a wilt-susceptible tobacco bioassay grown in fall 1991 were consistent with soil dilution results that susceptible tobacco increased *Fusarium* soil densities more than did wilt-resistant tobacco or fallow.

DISCUSSION

Wilt-resistant tobacco is not immune to *F. oxysporum* infection (11). *F. oxysporum* has been isolated repeatedly from wilt-resistant broadleaf tobacco (9,11). Resistance to *F. oxysporum* in other crops has been correlated with a lack of infection, or with reduced infection, of vascular tissues above the soil line (1,2,11).

Root colonization of susceptible, nonhost, or resistant plants can contribute to the increase or persistence of *F. oxysporum* in soil (4,6,7,13,15). Because resistant tobacco can be infected by the pathogen and may become diseased at extremely high inoculum densities (11), there have been concerns that resistant tobacco cultivars might increase *F. oxysporum* densities to levels sufficient to cause failure of a wilt-resistant crop. Additionally, because *G. t. tabacum* has been associated with increased wilt severity (10,11), infection with this nematode was included in the experiments.

Fusarium wilt severity, as determined by ratings of visible symptoms, was much greater for wilt-susceptible 86-4 than for wilt-resistant C8 or C9 tobacco. Resistance to *F. oxysporum* is quantitatively inherited (5). C8 has consistently been less resistant to wilt than C9, both in commercial production fields and in greenhouse screens at higher *F. oxysporum* inoculum levels, suggesting that C8 may contain fewer or less effective wilt resistance genes. Previous observations in field and greenhouse experiments, as well as in commercial production, have shown that wilt expression on wilt-resistant plants is often mild and that plants often outgrow early symptoms (11,12). Differences in wilt severity between C8 and C9 were not large enough to be of practical concern.

In these experiments, *F. oxysporum* root colonization and final levels in soil were greater for wilt-susceptible than for wilt-resistant tobacco. While *G. t. tabacum* increases wilt severity, previously demonstrated in field and greenhouse experiments (10,11), root colonization was increased only for susceptible tobacco at 8 wk after transplanting. Final *F. oxysporum* levels in soil were higher for wilt-susceptible than -resistant plants, and nematodes increased fungal densities in two of three experiments. Similar trends were seen in the third experiment.

Dilution plating to determine cfu per gram of soil could not distinguish pathogenic from nonpathogenic isolates of *F. oxysporum*. This limitation was greater in field microplots than in greenhouse experiments. Microplot soil had greater numbers of *Fusarium* species and variation in *F. oxysporum* isolates than did the pasteurized soil used in greenhouse experiments. As a result, a bioassay using wilt-susceptible tobacco was probably a better indicator of pathogenic *F. oxysporum* density in microplot soil than dilution plating.

The difficulties in controlling these

Table 3. The effects of C8 or C9 wilt-susceptible tobacco, wilt-susceptible tobacco and *Globodera tabacum tabacum* (Gtt) infection on Fusarium wilt severity, *Fusarium oxysporum* root colonization, and soil density after 8 wk under greenhouse conditions (Experiment 3)

Host	Gtt	Wilt severity rating[a]		Cfu per 10 cm root		Cfu × 10^2 per g soil	
86-4[b]	+[c]	3.1		12.8		30.1	
	−	1.7		5.8		20.1	
C8	+	0.8		1.1		20.8	
	−	0.0		0.5		14.5	
C9	+	0.2		1.8		17.1	
	−	0.0		2.2		13.3	
Source of variation	df	*P*	df	*P*	df	*P*	
Host	2	0.001	2	0.001	2	0.02	
Gtt	1	0.005	1	NS	1	0.03	
Host × Gtt	2	NS	2	NS	2	NS	
Error	54		54		54		

[a] Wilt rating: 0 = healthy to 4 = plant dead. Data analyzed after $X + 1$ transformation.
[b] Wilt-susceptible 86-4, wilt-resistant C8 and C9.
[c] *G. t. tabacum* inoculum density = 22 juveniles per cubic centimeter of soil, *F. oxysporum* inoculum = 500 cfu/cm^3 soil.

Table 4. The influence of initial *Fusarium oxysporum* soil density and wilt-susceptible tobacco, wilt-resistant tobacco, or fallow on *F. oxysporum* density and inoculum potential in microplots

Treatment[a]	*F. oxysporum* initial density	Cfu/g soil[b]	Bioassay[c]	1991 Cfu/g soil	1991 Bioassay[d]
		(1989)	(1990)		
Wilt-S	Low	80	0.6	700	1.1
	Med	150	3.3	720	2.3
	High	90	1.7	660	2.7
Wilt-R	Low	130	0.9	320	0.0
	Med	110	0.5	500	0.7
	High	70	1.1	560	1.7
Fallow	Low	90	0.0	130	0.0
	Med	90	0.0	380	1.3
	High	60	0.6	340	0.9
Source of variation (*P*)		(1989)	(1989)		
Host		NS	0.001	0.01	0.01
Inoculum level		NS	NS	NS	0.02
Host × inoc.		NS	0.01	NS	NS
Contrasts (*P*)					
Tobacco vs. fallow		NS	0.001	0.001	NS
Wilt-S vs. wilt-R		NS	0.01	0.01	0.05
Wilt-R vs. fallow		NS	NS	0.05	NS
Wilt-S vs. fallow		NS	0.01	0.001	0.05

[a] Wilt-susceptible = 86-4; wilt-resistant = C8 tobacco.
[b] Cfu per g soil determined by dilution plating onto Komada medium.
[c] Bioassay = wilt-susceptible 86-4 tobacco grown June to August 1990, wilt rating of 0 (healthy) to 4 (dead).
[d] Bioassay = wilt-susceptible 86-4 tobacco grown August to October 1991, wilt rating of 0 (healthy) to 4 (dead).

soilborne pathogens were demonstrated by the reinfestation of fumigated soil in the microplots between 1987 and 1989, despite efforts such as surface-disinfestation of trowels and core samplers used in the plots. Pathogens either increased from undetectable levels in soil after fumigation, or were introduced to plots from surrounding soil, or both. Nematodes and fungi present below the plow layer were accessible to microplots through the open bottoms required for drainage. Because of reinfestation with *G. t. tabacum*, microplot experiments were not intended to determine the role of the nematode in disease. Rather, the microplot experiments were conducted to examine the effect of resistant or susceptible tobacco on *F. oxysporum* densities under wilt complex conditions.

Fusarium spp. are well-adapted for long-term persistence in soils in the absence of a host. *F. oxysporum* may survive in fallow soil as chlamydospores (16), by colonizing crop residues (3), or by asymptomatically colonizing roots of various wild or cultivated plants (4,7,15). Fallowing soil infested with *F. oxysporum* did not significantly change soil densities in greenhouse pots or field microplots after 8 wk. In the microplot experiments, cfu per gram of soil were slightly higher for wilt-resistant tobacco than for fallow after the first year, but these differences were not significant. *Fusarium* densities in soil were greater for wilt-resistant tobacco than for fallow after the second year of production. Wilt-resistant broadleaf tobacco cultivars appear to minimize increases in *F. oxysporum* population densities in soil, even in the presence of *G. t. tabacum*. These results are similar to the effects of wilt-resistant watermelon, pea, or tomato on densities of pathogenic *F. oxysporum* in soil (13,17). Wilt-resistant tobacco, while not providing a means of eliminating the pathogen from soil, should continue to allow the successful production of broadleaf tobacco in fields infested with both *F. oxysporum* and *G. t. tabacum* (12).

ACKNOWLEDGMENTS

I thank J. Canepa-Morrison, R. Horvath, and J. Winiarski for technical assistance.

LITERATURE CITED

1. Elgersma, D. M., MacHardy, W. E., and Beckman, C. H. 1972. Growth and distribution of *Fusarium oxysporum* f. sp. *lycopersica* in near-isogenic lines of tomato resistant or susceptible to wilt. Phytopathology 62:1232-1237.
2. Gordon, T. R., Jacobson, D. J., May, D. M., Tyler, K. B., and Zink, F. W. 1990. Fruit yield, disease incidence, and root colonization of hybrid muskmelons resistant to Fusarium wilt. Plant Dis. 74:778-781.
3. Gordon, T. R., and Okamoto, D. 1990. Colonization of crop residue by *Fusarium oxysporum* f. sp. *melonis* and other species of *Fusarium*. Phytopathology 80:381-386.
4. Gordon, T. R., Okamoto, D., and Jacobson, D. J. 1989. Colonization of muskmelon and nonsusceptible crops by *Fusarium oxysporum* f. sp. *melonis*, and other species of *Fusarium*. Phytopathology 79:1095-1100.
5. Gritton, E. T., Jones, G. L., Powell, N. T., and Matzinger, D. F. 1965. Inheritance of resistance to Fusarium wilt in flue-cured tobacco. Crop Sci. 5:547-550.
6. Huisman, O. C. 1988. Colonization of field-grown cotton roots by pathogenic and saprophytic soilborne fungi. Phytopathology 78:716-722.
7. Katan, J. 1971. Symptomless carriers of the tomato Fusarium wilt pathogen. Phytopathology 61:1213-1217.
8. Komada, H. 1975. Development of a selective medium for quantitative isolation of *Fusarium oxysporum* from natural soil. Rev. Plant Prot. Res. 8:114-124.
9. LaMondia, J. A. 1990. Pathogenicity and vegetative compatibility of *Fusarium oxysporum* isolated from tobacco. Tob. Sci. 34:105-108.
10. LaMondia, J. A. 1992. Predisposition of broadleaf tobacco to Fusarium wilt by early infection with *Globodera tabacum tabacum* or *Meloidogyne hapla*. J. Nematol. 24:425-431.
11. LaMondia, J. A., and Taylor, G. S. 1987. Influence of the tobacco cyst nematode (*Globodera tabacum*) on Fusarium wilt of Connecticut broadleaf tobacco. Plant Dis. 71:1129-1132.
12. LaMondia, J. A., and Taylor, G. S. 1991. New Fusarium wilt-resistant Connecticut broadleaf tobacco varieties. Conn. Agric. Exp. Stn. Bull. 891.
13. Larkin, R. P., Hopkins, D. L., and Martin, F. N. 1993. Effect of successive watermelon plantings on *Fusarium oxysporum* and other microorganisms in soils suppressive and conducive to Fusarium wilt of watermelon. Phytopathology 83:1097-1105.
14. Lucas, G. B. 1975. Diseases of Tobacco. 3rd ed. H. E. Parker and Sons, Fuquay-Varina, NC.
15. Nash, S. M., and Snyder, W. C. 1967. Comparative ability of pathogenic and saprophytic *Fusaria* to colonize primary lesions. Phytopathology 57:293-296.
16. Nelson, P. E. 1981. Life cycle and epidemiology of *Fusarium oxysporum*. Pages 51-80 in: Fungal Wilt Diseases of Plants. M. E. Mace, A. A. Bell, and C. H. Beckman, eds. Academic Press, New York.
17. Reyes, A. A., and Mitchell, J. E. 1962. Growth response of several isolates of *Fusarium* in rhizospheres of host and nonhost plants. Phytopathology 52:1196-1200.
18. Tennant, D. 1975. A test of a modified line intersect method of estimating root length. J. Ecol. 63:996-1001.