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Broadleaf Tobacco Yield Loss in Relation to Initial *Globodera tabacum tabacum* Population Density

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Abstract: Field microplot experiments were conducted from 1995 to 1998 to determine the relationship between fresh shoot weight of stalk-cut broadleaf and shade-grown cigar wrapper tobacco types (*Nicotiana tabacum* L.) and initial density of *Globodera tabacum tabacum* second stage juveniles (J2) per cm^3 soil. Total shoot weight was negatively correlated with initial nematode densities of 12.3 to 747.3 J2/cm^3 soil ($r = -0.53$ and -0.70 for broadleaf and shade-grown tobacco, respectively). Nonlinear damage functions were used to relate initial *G. t. tabacum* densities to shoot weight. The models described shoot weight losses of less than 14% or 39% for broadleaf and shade tobacco, respectively, at *G. t. tabacum* densities below 50 J2/cm^3 soil. Total shoot weights were reduced by 40% and 60% of uninfested plots as preplant nematode densities approached maximum levels (>600 J2/cm^3 soil) for broadleaf and shade tobacco, respectively. *Globodera t. tabacum* population increase over a growing season was described by a linear relation on a log/log plot ($R^2 = 0.07$ and 0.61 for broadleaf and shade, respectively). These experiments demonstrate that *G. t. tabacum* can directly reduce shoot weight of stalk-cut broadleaf tobacco. Broadleaf is more tolerant to nematode infection than shade tobacco, as shade tobacco shoot weight reductions were greater at the same initial nematode densities in the same years.

Key words: damage function, nematode, *Nicotiana tabacum,* population dynamics, tobacco cyst nematode.

The tobacco cyst nematode, *Globodera tabacum tabacum* (Lownsbery & Lownsbery) Behrens, is an important pathogen of cigar wrapper tobacco (*Nicotiana tabacum* L.) types in the Connecticut River Valley of Connecticut and Massachusetts. The nematode has most often been associated with direct effects such as stunting and yield reductions in shade-grown tobacco. Early-season stunting is often dramatic, and losses may approach 40% at high nematode densities (LaMondia, 1995; Lownsbery and Peters, 1955). *Globodera t. tabacum* affects stalk-cut broadleaf cigar wrapper tobacco by increasing the incidence and severity of Fusarium wilt (LaMondia and Taylor, 1987). Losses due to Fusarium wilt in broadleaf production fields infested with both *G. t. tabacum* and *F. oxysporum* were often high. The introduction and widespread use of *F. oxysporum*-resistant broadleaf tobacco cultivars has greatly reduced the extent of losses due to Fusarium wilt (LaMondia and Taylor, 1992). Although infection with *G. t. tabacum* may result in increased wilt, the nematode does not alter cultivar resistance to *F. oxysporum* (LaMondia, 1992; LaMondia and Taylor, 1987).

Since the release of wilt-resistant cultivars, *G. t. tabacum* populations have been increasing in broadleaf tobacco fields and apparent yield losses due to nematode infection have been observed. The objectives of this study were to determine: (i) the effects of soil densities of *G. t. tabacum* at planting (Pi) on broadleaf tobacco shoot growth and (ii) the relationship between nematode population changes and Pi.

Materials and Methods

Microplots consisting of plastic waste cans (37.5-cm top diam., 30-cm bottom diam., and 45 cm deep, open at the bottom) filled with fumigated field soil were established in Windsor, Connecticut. The Merrimac fine sandy loam field soil (Entic Haplorthod; 71.8% sand, 23.0% silt, 5.2% clay; pH 6.2, 4.0% organic matter), typical of Connecticut River Valley tobacco soils, was fumigated with methyl bromide (0.45 kg a.i./72 m^2, 20 cm deep under sheets of plastic). Sixty microplots were placed 0.3 m apart in a single row. Microplots were infested in 1987 with *G. t. tabacum* cysts extracted from infested field soil by flotation in water with a modified Fenwick can. Infested soil in the microplots was mixed annually to 20 cm deep with a trowel, and plots were planted with tobacco or nonhost rotation crops to establish a range of nematode densities. In these experiments, broadleaf tobacco cultivar C9 was grown each year from 1995 to 1998. In 1995 and 1996, half of the plots were planted to the shade tobacco cultivar O-40 for comparison. Fertilizer and pesticides were applied as per commercial practice. All microplots received nitrogen incorporated preplant (225 kg/ha) and nitrogen side-dressed (56 kg/ha) 24 days after transplanting (5.9-2.8-6.1 N-P-K cottonseed meal base). Preplant applications of chlorpyrifos (7.0 liters Lorsban 4E/ha) and metalaxyl (1.2 liters Ridomil Gold EC/ha) were incorporated in all plots 24 hours before transplanting. Seedlings of the tobacco cultivars 0-40 and C9, 60 to 70 days old, were transplanted to each microplot, between microplots, and in border rows 1 m to either side of microplot centers, with 35 cm between plants in rows. Foliar insects were controlled by acephate (1 kg a.i./ha) applied to all plots as needed.

Globodera tabacum tabacum populations were estimated each year before transplanting and again after harvest. Soil in microplots was thoroughly mixed to 20 cm deep with a trowel, and ten 2.5-cm-diam. cores were collected 15 cm deep from each plot. All soil samples

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were air dried, and *G. t. tabacum* cysts were extracted from the soil with a modified Fenwick can and crushed in water. Two aliquots of nematodes in water suspension were counted to estimate the number of *G. t. tabacum* second-stage juveniles (J2) and eggs per cm^3 of soil. Initial *G. t. tabacum* population densities ranged from 12.3 to 747.3 J2/cm^3 soil over the 4 years of the experiment. Nematode populations were allowed to increase naturally in microplots. However, to maintain a range of densities in each year, nematode densities were deliberately reduced in 16 to 22 plots per year in 1990, 1991, and 1992. These reductions were achieved by removing and pasteurizing a portion of up to 75% of the designated microplot soil for 2 hours at 77°C prior to planting in 1997 and 1998.

Entire plant shoots consisting of leaves and stalks were removed and weighed after 70 days to determine total aboveground fresh weight. Microplots were sampled again after harvest, and final *G. t. tabacum* densities were determined as described.

An inverse logistic function (Noe, 1993; Noe et al., 1991) previously used for shade-grown tobacco (LaMondia, 1995) was used to represent the relationship between total shoot weight and initial *G. t. tabacum* density for each tobacco type:

$$Y = m + ((M-m)/(1 + (Pi/u)^b))$$

where Y = harvested leaf weight or total shoot weight; Pi = initial *G. t. tabacum* density in J2 and eggs per cm^3 soil; M = maximum yield or shoot weight; m = minimum yield or shoot weight; and the parameters u and b determine the shape of the curve.

Shoot weight and nematode density data were also fit to the Seinhorst equation (Seinhorst, 1965) by means of the SeinFit computer program (Viaene et al., 1997).

The relationship between plant height and *G. t. tabacum* Pi and the relationship between $\log_{10}$ final density (Pf) and $\log_{10}$ Pi were best represented by linear regression and correlation.

Results

Globodera t. tabacum Pi was negatively correlated with total shoot weight of broadleaf and shade tobacco types ($r = -0.53$ and -0.70, $P = 0.001$ and 0.001, respectively). The inverse logistic function effectively described the relation between Pi and shoot weight for all 4 years of both broadleaf and shade tobacco growth ($R^2 = 0.28$, $P = 0.001$, and $R^2 = 0.49$, $P = 0.001$, respectively) (Table 1, Fig. 1). *Globodera t. tabacum* densities below 50 J2/cm^3 soil resulted in predicted shoot weight losses less than 14% and 39% for broadleaf and shade tobacco, respectively. Shoot weights predicted by the model decreased exponentially at densities of 100 to 300 J2/cm^3 soil (Table 2). Maximum shoot weights (M) in microplots were approximately 959 g/plant, and minimum weights (m) were approximately 577 g/plant for broadleaf and 2,064 and 811 g/plant for shade. Shoot weights were approximately 60% and 40% of uninfested plots as preplant nematode densities approached maximum levels (>600 J2/cm^3 soil) for broadleaf and shade tobacco, respectively.

TABLE 1. Parameter estimates and nonlinear regression statistics for initial *Globodera tabacum tabacum* population density effects on broadleaf and shade tobacco total shoot weight in microplots, 1995 to 1998.

Parameter estimate[a]	Standard error	Least-squares analysis			
		Source	df	Mean square	F
		Broadleaf shoot weight (g)			
m = 577.0	32.7	model	3	382,964.1	21.9
M = 958.7	121.2	error	171	17,510.2	
u = 69.7	28.1	total	174		
b = 1.8	1.0				
		Shade shoot weight (g)			
m = 811.3	95.6	model	3	673,220.1	18.0
M = 2.064.3	913.3	error	350	37,414.5	
u = 30.8	39.6	total	353		
b = 1.2	0.9				

[a] Plant shoot weight = m+((M-m)/(1+(Pi/u)^b)), where m = minimum yield (g/plant), M = maximum yield (g/plant), and u and b are parameters that determine the curve shape.

Globodera t. tabacum Pf each season were related to Pi for both tobacco types. For broadleaf tobacco, $\log_{10}$ Pf = 2.05 + 0.17 $\log_{10}$ Pi ($R^2 = 0.07$, $P = 0.001$); for shade tobacco, $\log_{10}$ Pf = 1.75 + 0.421 $\log_{10}$ Pi ($R^2 = 0.61$, $P = 0.001$). Pi increased rapidly to a Pf equilibrium density of more than 500 J2/cm^3 soil at harvest (Fig. 2). Equilibrium densities of 300 to 500 J2/cm^3 soil were achieved in broadleaf tobacco microplots within a few seasons.

Discussion

Historically, *G. t. tabacum* has been perceived as directly affecting shade tobacco growth and yield

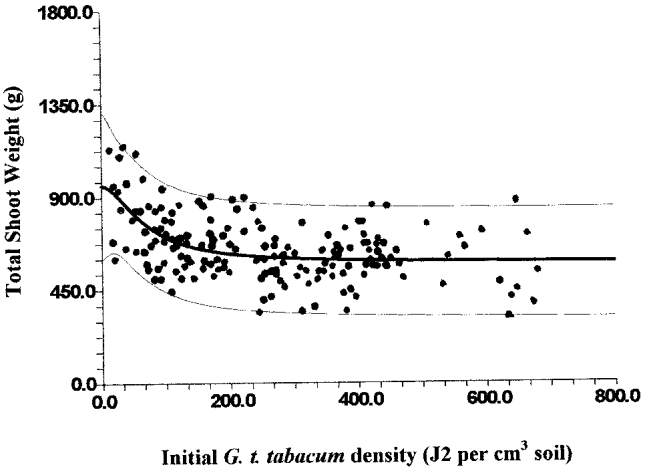

FIG. 1. The effect of initial *Globodera tabacum tabacum* population density in soil on broadleaf tobacco shoot weight (g) in microplots, 1995 to 1996. Equation statistics for curve in Table 1.

TABLE 2. The influence of *Globodera tabacum tabacum* initial population density in soil on actual and predicted broadleaf tobacco shoot fresh weight in field microplots, 1995 to 1998.

G. t. tabacum Pi[a]	Number in class	Actual	Predicted[b]
Broadleaf shoot weight (g), R^2 predicted vs. actual = 0.28			
0–75	44	838.3	831.5
76–150	49	675.8	698.2
151–225	40	691.5	633.7
226–300	57	589.1	608.4
301–375	39	566.3	597.4
376–450	28	612.1	591.7
>450	46	576.3	585.4
Shade shoot weight (g), R^2 predicted vs. actual = 0.49			
0–100	13	1,238.5	1,249.8
101–200	13	1,011.8	982.2
201–350	9	888.0	892.4
351–500	13	835.7	862.7
>500	12	861.7	843.5

[a] J2 and eggs per cm^3 soil prior to transplanting.
[b] Predicted by equation in Table 1.

(LaMondia, 1995) and only indirectly affecting broadleaf tobacco by increasing Fusarium wilt severity (LaMondia and Taylor, 1987). Broadleaf tobacco was thought to be tolerant of cyst nematode infection. *Globodera t. tabacum* Pi of 0 to 28 J2/cm^3 soil, typical of populations in broadleaf fields at that time, were sufficient to contribute to severe wilt and plant death but did not result in differential effects on broadleaf tobacco growth (LaMondia and Taylor, 1987).

These experiments demonstrate that *G. t. tabacum* can directly affect stalk-cut broadleaf tobacco and reduce shoot weight by up to 40% at high Pi as the cultivar used was wilt-resistant and *Fusarium oxysporum* was not present in the microplots. However, the current study demonstrated that broadleaf is apparently more tolerant to infection than shade tobacco, as maximum shade tobacco shoot weight reductions of 61% and 62% were observed in the same experiments or in previous years (LaMondia, 1995). Shoot weight reductions were consistently much greater in shade tobacco than in broadleaf in these experiments. The model used here predicted losses at initial *G. t. tabacum* densities of 10 J2/cm^3 soil of 1.1% for broadleaf and 12% for shade. At 50 J2/cm^3 soil, losses would be expected to be 14.1% for broadleaf and approximately 39% for shade.

The model damage function used to fit these data was originally developed (Noe, 1993; Noe et al., 1991) to describe yield loss of cotton and soybean as a result of migratory endoparasite infection (*Hoplolaimus columbus*). This model adequately described damage to both shade and broadleaf tobacco by the sedentary endoparasitic tobacco cyst nematode and therefore may

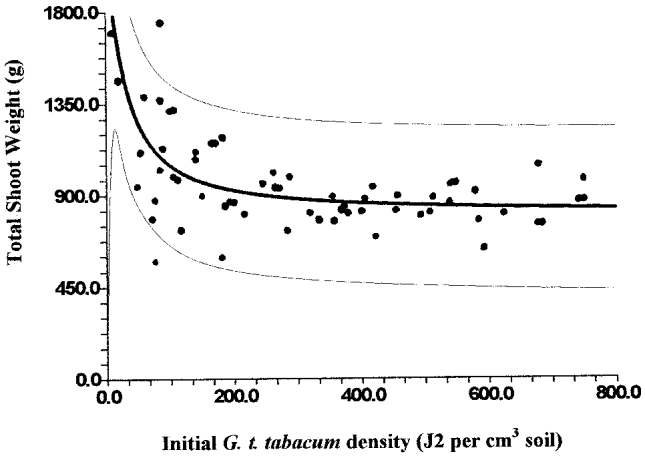

FIG. 2. The effect of initial *Globodera tabacum tabacum* population density in soil on shade tobacco shoot weight (g) in microplots, 1995 to 1998. Equation statistics for curve in Table 1.

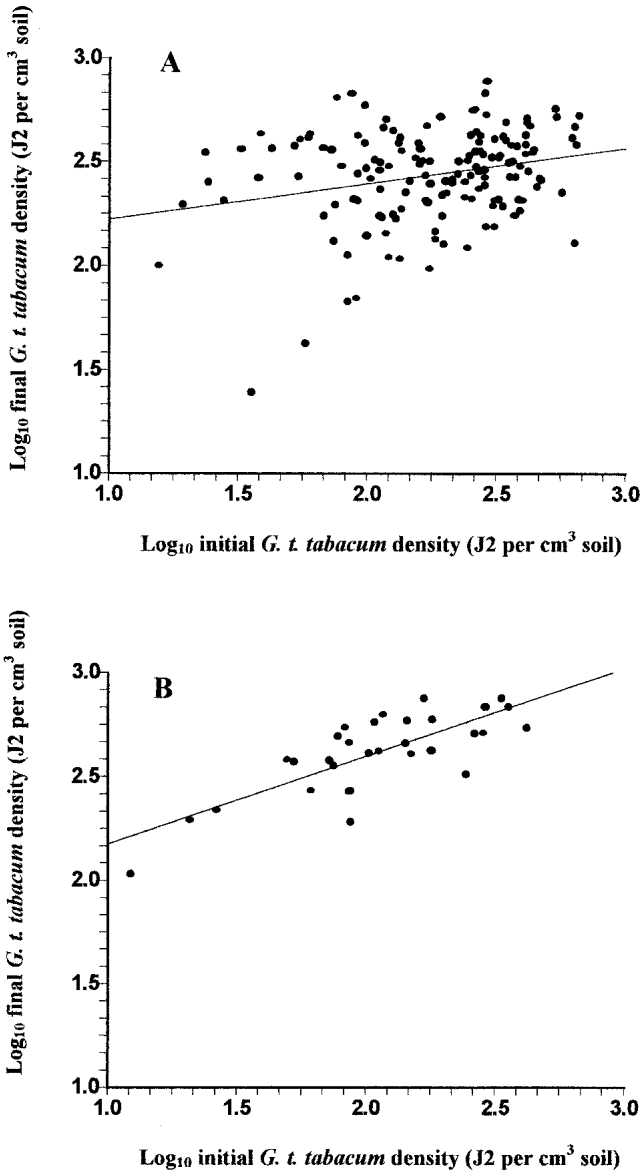

FIG. 3. The relation between $\log_{10}$ initial and $\log_{10}$ final *Globodera tabacum tabacum* population densities in soil (seasonal increase in J2 and eggs per cm^3 soil) in microplots: A) Broadleaf tobacco 1995 to 1998. $\log_{10}$ Pf = 2.05 + 0.17 $\log_{10}$ Pi (R^2 = 0.07, P = 0.001, n = 180). B) Shade tobacco 1995 to 1996. $\log_{10}$ Pf = 1.75 + 0.421 $\log_{10}$ Pi (R^2 = 0.61, P = 0.001, n = 60).

have wide use in describing nematode damage to many different crops. This model resulted in a better fit of the data than the Seinhorst equation (Seinhorst, 1965), as determined by the double partial derivative method in SeinFit (Viaene et al., 1997), which had an R^2 value of 0.26 ($P = 0.001$) for broadleaf tobacco data. The inverse logistic model was also more convenient to use, as it did not require a specific program such as SeinFit. Future studies are needed to validate the model for predicting damage under field conditions.

Damage functions based on critical-point initial nematode density models have been developed for a number of cyst and root-knot nematodes (Abdel-Momen and Starr, 1997; Ferris, 1981; Koenning and Barker, 1992; McSorley et al., 1992; Schmitt et al., 1987). Wang et al. (1999) determined that *G. t. solanacearum* populations sampled from roots over 11 weeks were inversely correlated with fresh leaf weight, feeder root weight, plant height, and leaf number. They concluded that Pi were inconsistent and not as well correlated with plant growth as number of nematodes in roots over time. This lack of utility as a critical point model may be due to the use of a contact nematicide to adjust nematode densities in soil, or to variation in nematode distribution in the field plots. Many researchers have used class frequency data to reduce error in estimating Pi (Ferris, 1984; McSorley et al., 1992; Noe, 1993; Noe et al., 1991; Schmitt et al., 1987). In the current study, the use of microplots and intensive mixing and sampling of microplot soil resulted in relatively uniform nematode distribution and reasonably accurate Pi estimates. As a result, raw data, rather than class frequency data, were used to fit the *G. t. tabacum* damage function. In addition, plant growth and the reduction due to *G. t. tabacum* were quite consistent over the 4 years tested, thereby obviating the need to standardize growth data.

In earlier experiments, *G. t. tabacum* population increases occurred exponentially at low Pi but stabilized at maximum populations of 600 to 1,000/cm^3 soil (LaMondia, 1995). This trend was consistent with the current results and those of Lownsbery and Peters (1955), who found that the highest density that maintained itself was 1,000/g soil. This density is approximately equivalent to 900/cm^3 soil in typical loamy sand tobacco soils in Connecticut. Broadleaf tobacco is grown for approximately 60 to 70 days, and shade tobacco is grown for 100 to 120 days. The tobacco cyst nematode can develop from J2 to a female with eggs in 5 to 6 weeks (LaMondia, 1990), and one or two generations may be completed per growing season on broadleaf or shade tobacco in Connecticut. Final nematode population densities in microplots planted to broadleaf tobacco were much more variable than in microplots planted to shade tobacco, perhaps due to the shorter growing season for broadleaf tobacco.

The damage function and *G. t. tabacum* population increase model developed as a result of these microplot evaluations, once validated, could become an important aid to tobacco cyst nematode management decisions in Connecticut. Damage functions can be used to predict yield losses and determine economic action thresholds. However, *G. t. tabacum* density was sampled intensively from relatively uniform distributions in microplots. The effect of aggregation and sampling intensity may change the interpretation of the damage or threshold level in production fields (Ferrandino, 1989; Ferris, 1984; Hughes, 1988). In addition, reductions in shoot weight were measured in these experiments. Total shoot weight was affected more than harvested leaf weight in previous experiments (LaMondia, 1995). For cigar wrapper tobacco, yield loss goes beyond a simple loss in harvested leaf weight. Practical losses to growers must eventually include leaf quality, a component not determined in these experiments. Further research is required to relate *G. t. tabacum* densities and leaf yield losses in microplots to population estimates from production fields, and to relate the effects of the tobacco cyst nematode on the leaf quality of field-grown shade tobacco.

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