Journal of Nematology 27(1):114–119. 1995.

Shade Tobacco Yield Loss and *Globodera tabacum tabacum* Population Changes in Relation to Initial Nematode Density

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Abstract: Field microplot experiments were conducted from 1987 to 1992 to determine the relationship between fresh weight leaf yield of shade tobacco (*Nicotiana tabacum*) and initial density of *Globodera tabacum tabacum* (encysted J2 per cm^3 soil). Initial nematode densities of 0.1 to 1,097 J2/cm^3 soil were negatively correlated with leaf yield, total shoot weight, and normalized plant height 5 to 6 weeks after transplanting ($r = -0.73$, -0.73, and -0.52, respectively). Nonlinear damage functions were used to relate initial *G. t. tabacum* densities to the yield and shoot weight data. The model described leaf yield losses of <5% for initial nematode densities of less than 100 J2/cm^3 soil. Densities above 100 J2 resulted in yields decreasing exponentially to a maximum yield loss of >40% at 500 to 1,000 J2/cm^3 soil. A similar initial density tolerance threshold relationship was observed for total shoot weight. No threshold effect was evident for standardized plant height, which was a poor predictor of leaf yield. *Globodera tabacum tabacum* population increase over a growing season was described by a linear relation on a log/log plot ($R^2 = 0.73$).

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

The tobacco cyst nematode, *Globodera tabacum tabacum* (Lownsbery & Lownsbery) Behrens, is widely distributed in shade tobacco (*Nicotiana tabacum* L.) production fields in the Connecticut River Valley of Connecticut and Massachusetts. When first identified, this nematode was demonstrated to reduce shade tobacco height and shoot weight in pot and small plot experiments (8). Early-season nematode control by oxamyl application was shown to increase shade leaf yields by 10–21% when nematode densities were 33–154 J2/cm^3 soil (6). The effects of *G. t. tabacum* initial densities on leaf yield and quality were not determined.

Shade tobacco is a high-value crop and is commonly grown with little or no rotation, due to the input required to establish a shade tent (12). As a result, the tobacco cyst nematode has been intensively managed by fumigant and nonfumigant nematicides to keep nematode levels as low as possible. As management options become less available, the need for threshold levels and damage functions (an understanding of the relationship between nematode numbers and crop yield) increases. Damage functions based on critical point initial density models have been developed for a number of cyst and root-knot nematodes (3,5,9,13,16). In addition, because field sampling is costly and time consuming, a means of predicting nematode population changes would also prove useful in a management system.

The objectives of this study were as follows: i) to determine the effects of initial soil densities of *G. t. tabacum* on shade tobacco yield and ii) to determine the relationship between nematode population changes and initial density.

Materials and Methods

In 1987, microplots consisting of plastic waste cans (37.5 cm top diameter, 30 cm bottom diameter, and 45 cm deep, open at the bottom) (7) 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 between sheets of plastic). Sixty microplots

Received for publication 13 April 1994.
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The author thanks Jane Canepa-Morrison and Rich Horvath for technical assistance.

were placed 0.3 m apart in a single row in the center of a cloth-covered shade tent (12). Plots were initially infested in 1987 with *G. t. tabacum* cysts recovered from infested field soil by flotation in water using a modified Fenwick can. Nematodes were mixed to 20 cm deep with a trowel to establish a range of inoculum densities. Fertilization and pesticide applications were performed as per commercial practice. Each year from 1987 to 1992, all plots received nitrogen incorporated preplant (224 kg/ha) and nitrogen side-dressed (56 kg/ha) at 24 days after transplanting (5.9-2.8-6.1 N-P-K cottonseed meal base). A preplant application of diazinon (2.2 kg a.i./ha) and metalaxyl (0.2 liter a.i./ha) was incorporated in all plots 24 hours before transplanting (6). Seedlings of the shade tobacco cultivar 0-40-A, 60–70 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 sampled by removing 10 2.5-cm-d cores to 15 cm deep per plot. All soil samples 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 determine the number of free *G. t. tabacum* second-stage juveniles (J2) and eggs per cubic centimeter of soil. Initial *G. t. tabacum* densities ranged from 0.1 to 1,097 J2/cm^3 soil over the 6 years of the experiment. Nematode populations were allowed to increase naturally in microplots from 1987 to 1992. 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, 1992. These reductions were achieved by removing and pasteurizing 50 to 90% of the designated microplot soil for 2 hours at 77 C.

Plant height (cm) was measured 5 to 6 weeks after transplanting in 1987, 1988, 1989, and 1990. Height was standardized by dividing by the mean height of plants in uninfested plots in the same year. Three leaves per plant were harvested for each of the plants on each of six occasions starting 55 days after transplanting and weekly thereafter for all 6 years. Remaining leaves and stalks from the plants were removed and weighed after the last harvest to determine total above-ground fresh weight. Plots were sampled again after the last harvest, and final *G. t. tabacum* densities were determined as described.

An inverse logistic function (10,11) was used to represent the relationship between leaf yield and initial *G. t. tabacum* density and total shoot weight and initial *G. t. tabacum* density.

$$Y = m + ((M - m)/(1 + (Pi/u)^\wedge b)) \quad \text{(eq. 1)}$$

where Y = harvested leaf weight or total shoot weight; Pi = initial *G. t. tabacum* density in encysted second-stage juveniles (J2) and J2 in 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.

The relationship between plant height and initial *G. t. tabacum* density and the relationship between log initial density and log final density were best represented by linear regression and correlation.

Results

Initial *G. t. tabacum* density was negatively correlated with leaf yield, total shoot weight, and height of shade tobacco (r = -0.73, -0.73, and -0.52, P = 0.001, 0.001, and 0.001, respectively, Table 1.). The nonlinear function (eq. 1) effectively described the relation between shoot weight or leaf yield for all 6 years (R^2 = 0.61 P = 0.0001, Table 2, Fig. 1). *G. t. tabacum* densities below 50 or 100 J2/cm^3 soil resulted in predicted leaf yield losses less than 1 or 5%, respectively, but yields predicted by the model decreased expo-

TABLE 1. Correlations among plant parameters and *Globodera tabacum tabacum* soil densities before transplanting and after harvest in field microplots, 1987 to 1992.

	Correlation coefficients†				
	Pi‡	Pf	Yield	Shoot weight	Height
Pi	1.00				
Pf	0.49	1.00			
Yield	−0.73	−0.41	1.00		
Shoot weight	−0.73	−0.38	0.95	1.00	
Height	−0.52	−0.36	0.51	0.52	1.00

† df = 352; all correlations significant at $P = 0.001$.
‡ Pi = initial *G. t. tabacum* per cm^3 soil before transplanting. Pf = final *G. t. tabacum*/cm^3 soil after harvest. Yield = fresh weight (g) leaf harvest 18 leaves per plant. Shoot weight = total shoot fresh weight (g) after the last harvest. Height = standardized shoot height 5–6 weeks after transplanting.

nentially at densities of 100 to 300 J2/cm^3 soil (Table 3). Maximum leaf yields (M) in microplots were approximately 445 g/plant and minimum yields (m) were approximately 243 g/plant. Yields reached a minimum level of 55% of uninfested plots as preplant nematode densities approached maximum levels (>600 J2/cm^3 soil). The relation between total shoot weight and initial *G. t. tabacum* density was similar to that for leaf yield. Total shoot weight was highly correlated ($r = 0.95$) with harvested leaf yield, and the relationship between nematode density and total shoot weight was similar to that for harvested leaf weight.

Globodera tabacum tabacum population densities after harvest each season were related to initial densities such that

$$\log_{10} \text{Pf} = 1.96 + 0.29 \log_{10} \text{Pi} \; (R^2 = 0.73, P = 0.001) \qquad \text{(eq. 2)}$$

Low initial densities increased rapidly to a maximum of 1,000 J2/cm^3 soil at harvest (Fig. 2).

DISCUSSION

These data demonstrate that *Globodera tabacum tabacum* can reduce shade tobacco leaf yields by up to 45% compared with uninfested plants. Yield reduction was minimal at low densities but dropped off quickly to very significant losses at high densities, differing from the linear relationship between height or weight and nematode density reported by Lownsbery and Peters (8). This asymptotic yield, at or near equilibrium densities, was predicted by Seinhorst (15), who emphasized the importance of testing plant growth against a wide range of nematode densities. Densities examined in these experiments ranged from 0.1 to 1,097 J2/cm^3 soil. The model

TABLE 2. Parameter estimates and nonlinear regression statistics for initial *Globodera tabacum tabacum* density effects on shade tobacco leaf yield and total shoot weight in microplots, 1987–1992.

Parameter estimate†	Standard error	Least-squares analysis			
		Source	df	Mean square	*F*
			Leaf yield (g)		
m = 243.62	12.6	model	3	720,996.3	183.7
M = 445.02	6.2	error	350	3,925.7	
u = 220.35	17.6	total	353	10,019.8	
b = 2.75	0.5				
			Total shoot weight (g)		
m = 474.87	105.7	model	3	6,137,584.0	161.8
M = 1,242.39	21.8	error	350	37,921.7	
u = 299.98	57.3	total	353	89,760.2	
b = 1.66	0.4				

† m = minimum yield (g/plant); M = maximum yield (g/plant); u and b are parameters that determine the curve shape.

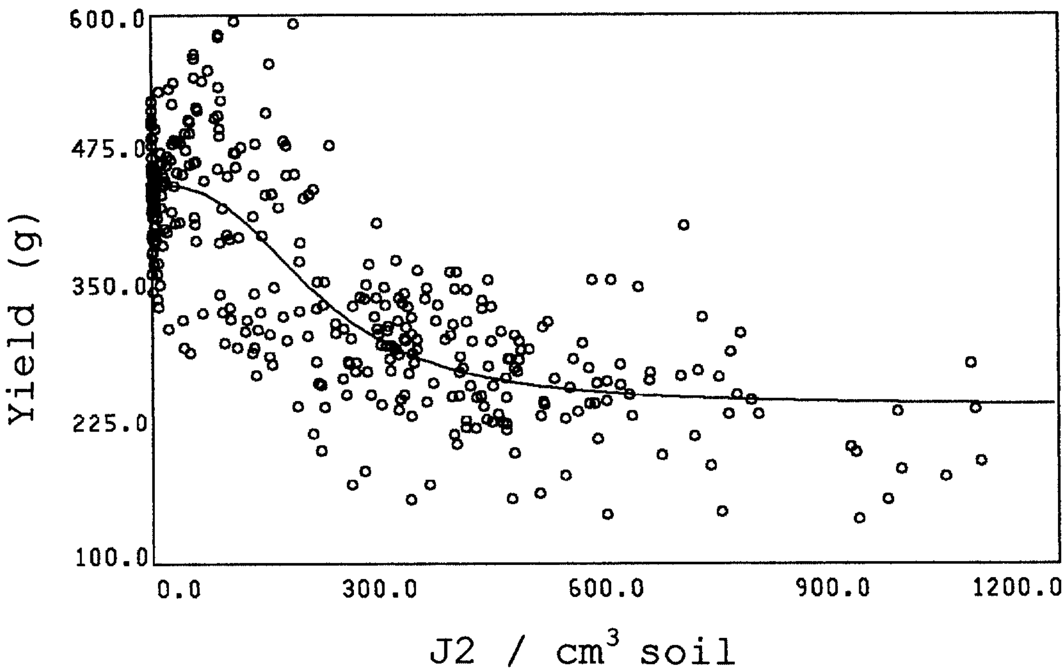

FIG. 1. Effect of initial *Globodera tabacum tabacum* density in soil on shade tobacco leaf yield (g) in microplots, 1987 to 1992. Equation statistics for curve in Table 2.

damage function used to fit these data was presented by Noe et al. (10,11) to describe yield reduction of cotton and soybean as a result of migratory endoparasite infection, e.g., *Hoplolaimus columbus*. This model adequately described damage to tobacco by the sedentary endoparasitic tobacco cyst nematode and therefore may have wide utility in describing nematode damage to crops.

TABLE 3. Influence of *Globodera tabacum tabacum* initial density in soil on actual and predicted harvested leaf fresh weight in field microplots, 1987 to 1992.

G. t. tabacum Pi‡	No. in class	Leaf yield (g)†	
		Actual	Predicted
0–5	44	439.3	445.0
6–50	49	436.8	436.1
51–150	49	428.1	425.0
151–250	40	374.9	365.9
251–350	57	298.0	302.3
351–450	39	288.3	268.2
451–550	28	265.9	264.0
>550	46	250.7	252.1
R^2 predicted vs. actual = 0.61			

† Predicted by equation in Table 2.
‡ Encysted J2 per cm^3 soil before transplanting.

Many previous studies have used class frequency data to reduce error in estimating initial nematode density (2,9–11,13). The use of microplots and intensive mixing and sampling of microplot soil can result in relatively uniform nematode distribution and reasonably accurate initial density estimates. As a result, raw data, rather than class frequency data, were used to fit the damage function. In addition, plant growth and yield reduction due to *G. t. tabacum* were quite consistent over the 6 years tested, thereby avoiding the need to standardize the data. This may have been due to crop production in cloth-covered shade tents, which reduce wind, evaporation, changes in temperature, humidity, and light intensity (17), and the use of overhead irrigation (12). While standardized plant height at 5 to 6 weeks after transplanting was correlated with leaf yield, it was not as good a predictor of yield or total shoot weight as was *G. t. tabacum* initial density. *Globodera tabacum tabacum* initial density was better correlated with leaf yield and shoot weight than plant height, differing from an earlier report (8). This may be due to a number of fac-

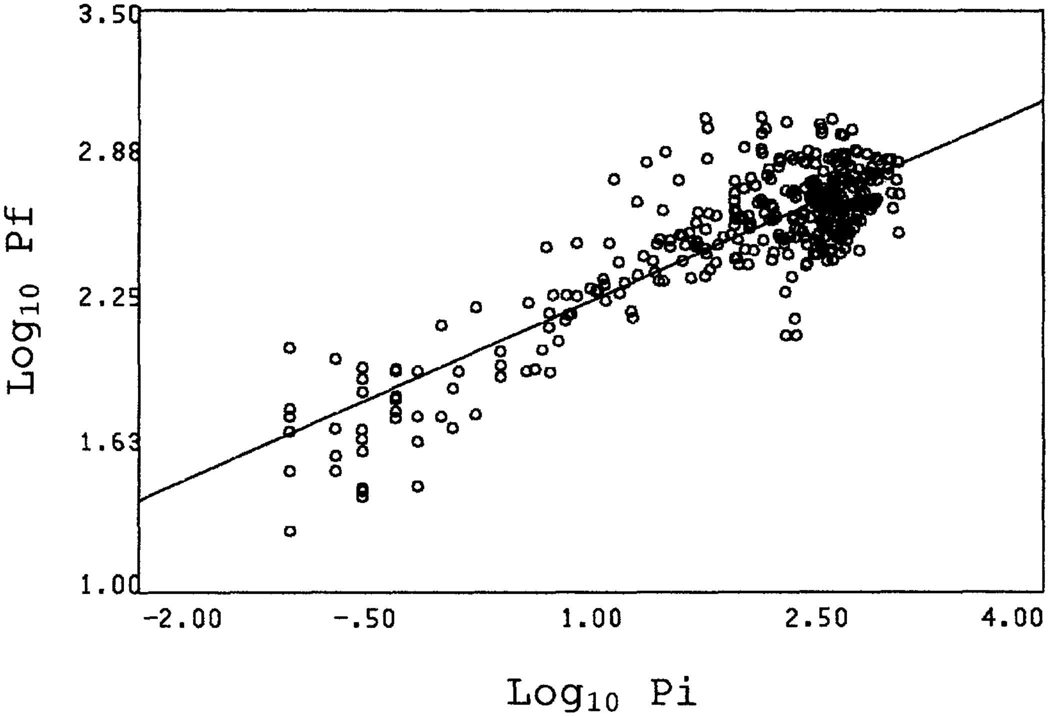

FIG. 2. Relation between $\log_{10}$ initial and $\log_{10}$ final *Globodera tabacum tabacum* densities in soil (seasonal increase in encysted eggs and J2 per cm^3 soil) in microplots, 1987 to 1992; $\log_{10}$ Pf = 1.96 + 0.29 $\log_{10}$ Pi (R^2 = 0.73, P = 0.001).

tors, including tobacco cultivar, growth of plants in pots versus microplots, and single-year versus multiple-year experiments.

Globodera tabacum tabacum population increases occurred exponentially at low densities but stabilized at 600 to 1,000 J2/cm^3 soil. This trend was consistent with the results of Lownsbery and Peters (8), who found that the highest density that maintained itself was 1,000 J2/g soil. This density is approximately equivalent to 900 J2/cm^3 soil in typical loamy sand tobacco soils in Connecticut. The tobacco cyst nematode can develop from a J2 to a female with eggs in 5–6 weeks (6), indicating that two generations may be completed per growing season on shade tobacco in Connecticut.

The damage function and *G. t. tabacum* population increase model developed as a result of these microplot evaluations will be 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 (1,2,4,14). In addition, yield reduction was determined as a simple reduction 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 reduction 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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