Yield-loss Models for Tobacco Infected with *Meloidogyne incognita* as Affected by Soil Moisture

T. A. Wheeler,[1] K. R. Barker,[2] and S. M. Schneider[3]

Abstract: Yield-loss models were developed for tobacco infected with *Meloidogyne incognita* grown in microplots under various irrigation regimes. The rate of relative yield loss per initial nematode density (Pi), where relative yield is a proportion of the value of the harvested leaves in uninfected plants with the same irrigation treatment, was greater under conditions of water stress or with high irrigation than at an intermediate level of soil moisture. The maximum rate of plant growth per degree-day (base 10 C) was reduced as nematode Pi increased when plots contained adequate water. When plants were under water stress, increasing Pi did not further reduce the maximum rate of plant growth (water stress was the limiting factor). Cumulative soil matric potential values were calculated to describe the relationship between available water in the soil (matric potential) due to the irrigation treatments and subsequent plant growth.

Key words: *Meloidogyne incognita*, nematode, *Nicotiana tabacum*, yield-loss model, soil matric potential, tobacco.

Yield-loss models as a function of the initial population density (Pi) of root-knot nematodes, *Meloidogyne* spp., have been developed for many crops (2,6). In tobacco (*Nicotiana tabacum*) losses due to *M. incognita* (Kofoid & White) Chitwood have been well documented (1). Microplot studies used to develop predictive yield-loss models often are irrigated so that growing conditions are more favorable to the plant than in commercial fields. Models developed from such data may be insensitive to water stress. Plants that are both water stressed and infected with root-knot nematodes may behave differently from those that are parasitized but not subjected to water stress.

Soil moisture stress to a plant is a dynamic process. Stress at certain points in the season may be critical to high yields. A cumulative measurement of soil moisture may be more useful to quantify irrigation procedures than an average measure of soil moisture matric potential. Fitting the water history of the plant over time to a model allows for a distinction to be made between early season drought or late season drought, though the cumulative value may be similar at the end of the season.

Second-stage juveniles of *Meloidogyne* spp. move through moisture films in pores between soil particles (13). Restricted mobility can occur at high soil matric potentials (13,14). The root system of water-stressed tobacco is smaller than that of plants with adequate water (14). The probability of a nematode encountering a root under such conditions may be reduced because of both a smaller root system and restricted mobility. If the factors of soil moisture deficit and nematode damage combine additively, then there is no advantage in allowing plants to be water stressed in order to limit the rate of root-knot infection. However, if yield loss due to root-knot nematode is diminished by soil moisture stress, then yield suppression due to inadequate water could be less than the yield loss associated with the same nematode level plus irrigation costs. Alternatively, the combination of *M. incognita* infection and water stress could be synergistic (5) and could increase yield loss over the sum of loss due to both factors separately.

The objectives of this study were to examine the effects of soil moisture and root-knot nematode in tobacco growth and yield. In addition, a dynamic indication of soil moisture matric potential was developed.

[1] Former graduate student, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695-7616. Current address: Ohio Agricultural Research and Development Center, Wooster, OH 44691.

[2] Professor, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695-7616.

[3] Assistant professor, North Carolina State University, USDA ARS Crops Research Laboratory, Oxford, NC 27565.

MATERIALS AND METHODS

Field-plot design: Microplots (100 cm × 80 cm or 77 cm d) located at the Central Crops Research Station at Clayton, North Carolina, with a Fuquay sand (91% sand, 3% clay, 6% silt; 0.6% OM) were fumigated in the fall of each year with methyl bromide + 2% chloropicrin (c.a. 1.13 g a.i./m²). The experiment was established in a randomized complete block design with a factorial treatment arrangement consisting of soil moisture and nematode initial population density (Pi). In the spring of 1988 and 1989 the plots were inoculated with eggs of *M. incognita* (race 3), extracted from tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) roots with NaOCl (4). Initial population densities were 0, 750, 1,500, 5,000, 10,000, and 20,000 eggs/500 cm³ soil in 1988 and 0, 1,000, and 10,000 eggs/500 cm³ soil in 1989. The endomycorrhizal fungus *Glomus macrocarpus* Tul. & Tul. was added to each microplot with the nematode inoculum. The organisms were introduced into the plots in 1,000 ml water with a watering can and incorporated to a depth of 15 cm. One day after infesting the plots, tobacco transplants of the cultivar NC27-NF (two plants per plot in 1988 and one plant per plot in 1989) were placed in the plots. Normal cultural practices for tobacco were followed. Amounts of nitrogen added during the season were based on leaf color for each irrigation treatment. This adjustment was necessary because of the high potential for leaching in the sandy soil.

Plastic covers were placed on top of each of the microplots to minimize intrusion of rain. Drip irrigation provided four different levels of water. In 1988 water treatments were DRY, LOW, MOD, and HIGH with emitter rates of 0, 4, 8, and 16 liters/hour, respectively. All plots were irrigated when plants in the MOD treatments began to wilt or when soil moisture tension in the MOD treatments reached a matric potential of −40 kilopascals (KPa). Length of irrigation for all plots was based on the time required to bring the soil in MOD plots to saturation. Evapotranspiration conditions were high in 1988, and a moisture gradient was established by 19 days after transplanting, as measured by size of plants in the uninfected controls of each irrigation treatment. In 1989 the water treatments were DRY, LOW, MOD, and alternating MOD-DRY with emitter rates of 0, 4, 8, and 8 liters/hour. Alternating MOD-DRY was irrigated similarly to MOD, except irrigation was withheld when the influx of second-stage juveniles (J2) for the second generation was anticipated and for the last month of the season. Soil moisture was monitored using a Troxler Series 2000 neutron probe at depths of 30 and 60 cm. Four (1988) and two (1989) replications per treatment were averaged for each biweekly reading. A soil moisture release curve had been previously developed to relate soil moisture (percent by weight) to matric potential (KPa) in the Fuquay sand and to relate the neutron probe readings to soil moisture (14). A cumulative measure of soil moisture availability was obtained by using trapezoidal integration (10) of matric potential over time (degree-days with a base of 10 C) (9). Soil temperature was monitored with a thermograph at a depth of 20 cm, and a daily measure was obtained by averaging readings from every 6 hours.

Ten blocks were used for destructive sampling to monitor plant growth. Fresh leaf weight was determined at weekly intervals in 1988 from day 12 to day 47 after transplanting and then every 2 weeks until day 105. In 1989, blocks were sampled starting at day 35 at 5-day intervals for 25 days and then at days 66, 80, 87, 92, and 100. The number of plots was not sufficient for sampling all treatments at all 10 sampling periods in 1988. Thus on days 12, 26, 40, 61, 75, 89, and 105, one water treatment (six Pi levels) was not sampled. A rotation was used to alternate the water treatment not sampled. Samples from the initial five sampling periods in 1988 were taken from plants in 18.9-liter buckets which were embedded in microplots and contained Pi and water levels similar to

those of the plants growing directly in microplots.

Leaves from the tobacco plants were harvested three or four times over the growing season with final harvesting occurring at day 110 in 1988 and day 100 in 1989. Leaves from each harvest were cured and a quality grade was assigned. Yield was obtained by multiplying the price per grade by the cured leaf weight. Yield was measured for four replications for each treatment combination.

Analyses: The cumulative soil matric potential (CSMP) values were fitted to the following equation:

$$CSMP = b0 + b1(Pi) + b2(DD) + b3(Pi \times DD)$$

where Pi is the initial nematode density, DD is time in degree-days, and Pi × DD represents the interaction between Pi and DD. The coefficients define the water availability pattern for each irrigation treatment.

Leaf growth for each Pi level and water treatment as a function of DD was fitted to a logistic equation (9):

$$RLW = k/(1 + [\{k - L_i\}/L_i]exp[-rDD])$$

where RLW is the relative leaf weight, with fresh leaf weight as a proportion of the highest fresh leaf weight recorded by the control plant in that water level all season; k is the relative final leaf weight (at harvest) for the water treatment combination, as a proportion of the control final leaf weight for that irrigation treatment; L_i is the initial leaf weight (relative to highest leaf weight) at transplanting and was taken to be 0.0025; r is a leaf growth parameter to be estimated; and DD is degree-days.

The leaf-growth parameters were regressed against the initial nematode density for each water treatment with both linear and quadratic models. The slopes were tested with a *t*-test (*P* = 0.05). The pattern of residuals was used to determine if either model was appropriate. An interaction was assumed to occur if any nonparallel response was observed. Only data

from 1988 were used because the sampling periods in 1989 started at day 35, which was after the period of maximum rate of plant growth.

Yield-loss models as a function of Pi were developed for each irrigation treatment. Yield was converted to relative yield as a proportion of the uninfected nematode controls for each irrigation regime. A number of models were fitted to each irrigation treatment and four criteria were used to select the best model. The model had to be significant at *P* = 0.05 using an *F*-test; a lack-of-fit test was used to reject nonrandom patterns of residuals (*P* = 0.05: *R²* > 50%; and if coefficients of variation were similar among different models (for a single irrigation treatment), then the model which was "best" for all or most of the irrigation treatments was selected so comparisons between damage functions could be made. The models tested for each of the irrigation treatments were

1) y = a + b(Pi)
2) y = a + b(Pi) + c(Pi²) (1988 only)
3) y = a + b(log [Pi + 1])
4) y = log (a + b(Pi))
5) log (y) = log (a) + b(log [Pi + 1])
6) 1/y = a + b(Pi)

where a, b, and c were parameters to be estimated and y was the yield. If the same model was selected for different irrigation treatments, then the null hypothesis that the slopes were the same was tested with a *t*-test (*P* = 0.05). If different models were fitted to the water treatments, then nonparallel response (interaction) was assumed. These models were chosen as likely candidates because of the minimal number of parameters to be estimated.

RESULTS

Soil moisture: The CSMP values were fitted by regression to Pi, DD, and Pi × DD. The CSMP was higher (*P* = 0.05) for the DRY water treatments in 1988 and 1989 than the other water treatments (Table 1). There was a trend for a decrease in CSMP

as Pi increased. The equations which defined CSMP are

DRY-1988:

$$CSMP = -844 + 0.31(Pi) + 2.55(DD) - 9.0 \times 10^{-5}(Pi \times DD),$$
$$R^2 = 0.94$$

LOW-1988:

$$CSMP = -346 + 0.12(Pi) + 1.17(DD) - 3.9 \times 10^{-5}(Pi \times DD),$$
$$R^2 = 0.87$$

MOD-1988:

$$CSMP = -214 + 0.76(DD) - 2.2 \times 10^{-5}(Pi \times DD),$$
$$R^2 = 0.66$$

HIGH-1988:

$$CSMP = -43 + 0.21(DD) - 6.1 \times 10^{-6}(Pi \times DD),$$
$$R^2 = 0.83$$

DRY-1989:

$$CSMP = -145 + 0.41(DD) - 8.9 \times 10^{-6}(Pi \times DD),$$
$$R^2 = 0.69$$

LOW-1989:

$$CSMP = -52 - 0.0055(Pi) + 0.13(DD) + 1.3 \times 10^{-5}(Pi \times DD),$$
$$R^2 = 0.77$$

MOD-1989:

$$CSMP = -133 - 0.012(Pi) + 0.33(DD) - 2.9 \times 10^{-5}(Pi \times DD),$$
$$R^2 = 0.59$$

MOD-DRY-1989:

$$CSMP = -129 + 0.0099(Pi) + 0.34(DD) - 2.5 \times 10^{-5}(Pi \times DD),$$
$$R^2 = 0.84$$

Rate of leaf growth: The rate of leaf growth was estimated by using the logistic equation for each of the Pi × irrigation combinations in 1988 (Table 2). These rate values represent the maximum rate of leaf growth. Use of the logistic model assumes that rate is not constant but decreases over time as the leaf approaches its final size. In both the DRY and LOW water treatments in 1988, there was no effect ($P = 0.05$) of

Pi on maximum rate of leaf growth per degree (r) (Fig. 1). The scatter pattern of the rate values for LOW water treatments do suggest a curvilinear pattern (data not presented), but lack of replication, along with possible outliers, caused a nonsignificant fit for the models tested. With MOD and HIGH water levels the change in rate with respect to Pi was significant ($P = 0.05$) when fitted with a quadratic model (Fig. 1). The leaf-growth rate in a moderate water treatment showed a weakly quadratic response with respect to Pi. There was a strong curvilinear response of leaf growth in the HIGH water treatment as a function of Pi.

Yield: There was no single function that could be used to describe the yield-loss relation for all water treatments in 1988 and 1989. In 1988 a linear model was significant for all water treatments and the response of yield loss to nematode Pi in DRY and HIGH water treatments was approximately 1.5 times that in MOD and LOW water treatments (Fig. 2). The MOD water treatment supported greater yield ($P = 0.05$) than the other water treatments in 1988.

The DRY water treatment had lower yields ($P = 0.05$) than the LOW, MOD, or alternating MOD-DRY water treatments in 1989 (Fig. 2). The only model that could be fitted to DRY-1989 was of the form: $1/y = a + b(Pi)$. For the LOW, MOD, and alternating MOD-DRY water treatments the model selected was $y = \log (a + b[Pi])$. There was no difference between the coefficient (b) of LOW, MOD, and MOD-DRY water treatments. The simple, linear model used in 1988 was rejected in 1989 based on an F-test. The response of yield to Pi was nonparallel or interactive in the DRY water treatment with respect to LOW, MOD, and alternating MOD-DRY in 1989 as shown by the different models required to fit the data.

DISCUSSION

Plant-response models were developed for specific growing conditions; however, repetition of specific environmental con-

TABLE 1. Cumulative soil matric potential values at end of the season for tobacco infected with *Meloidogyne incognita* at Pi† levels of 0 to 20,000 under different irrigation regimes.

Water	0	750	1,000	1,500	5,000	10,000	20,000
			1988				
DRY*	276	219		262	237	231	51
LOW	132	118		94	115	72	45
MOD	175	75		44	39	29	38
HIGH	19	28		30	17	10	11
			1989				
DRY*	35		60			28	
LOW	15		18			30	
MOD	49		18			5	
M-D‡	40		34			11	

Units are in MPa-degree-days (base 10 C). Dashes represent Pi levels which were not used in a given year.
* Significant treatment difference ($P = 0.05$).
† Initial nematode population density per 500 cm^3 soil.
‡ MOD-DRY water treatment.

ditions from one year to the next in field or microplots was difficult because of factors that could not be controlled consistently within a season (soil nitrogen levels), nor between seasons (temperature, wind, humidity, and rainfall). A basic question for optimization of yield of plants infected with the root-knot nematode is whether it is better to maximize plant growth or minimize the infection rate of the nematode. Although this experiment was not designed to answer the question, it did provide observations of yield under three basic conditions: water conditions favoring the plant (MOD-1988, LOW, MOD, and alternating MOD-DRY-1989); water conditions that may not favor nematode mobility in soil (DRY-1988); and water conditions that may favor nematode mobility but nutrient deficiency that was unfavorable for plant growth (HIGH-1988).

TABLE 2. Maximum rate of leaf growth for tobacco infected with *Meloidogyne incognita* at Pi† levels of 0 to 20,000 under different irrigation regimes for 1988.

Water	0	750	1,500	5,000	10,000	20,000
DRY	8.25	6.43	6.18	6.98	7.48	6.88
LOW	9.03	10.48	7.35	8.60	7.80	7.70
MOD	9.98	9.96	9.52	8.85	8.71	8.48
HIGH	10.63	8.61	10.25	7.42	5.61	5.82

Rate of leaf growth (g/DD × 10^{-3}) was fitted with a logistic growth curve (1988).
† Initial population density of *M. incognita* per 500 cm^3 soil.

Meloidogyne spp. limit the water absorption capacity of a root system, possibly through reduced number of fine roots and distortion of the vascular system (7,8,11). Excessively dry soil would limit the impact of the nematode on water uptake, because little water would be available, with or without the parasite. This effect may account for the lack of sensitivity of the intrinsic growth rate parameter (r) to nematode pathogenesis in DRY and LOW water treatments in 1988.

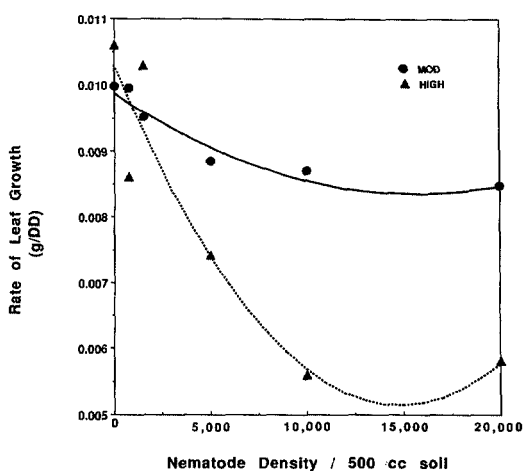If the growth of a plant is viewed as a

FIG. 1. Effects of *Meloidogyne incognita* on leaf growth. Moderate (MOD) = $0.00987 - 1.93 \times 10^{-7}(Pi) + 6.12 \times 10^{-12}(Pi)^2$, $R^2 = 0.93$; High = $0.0103 - 6.96 \times 10^{-7}(Pi) + 2.35 \times 10^{-11}(Pi)^2$, $R^2 = 0.90$. The DRY and LOW water treatments could not be fit to a function.
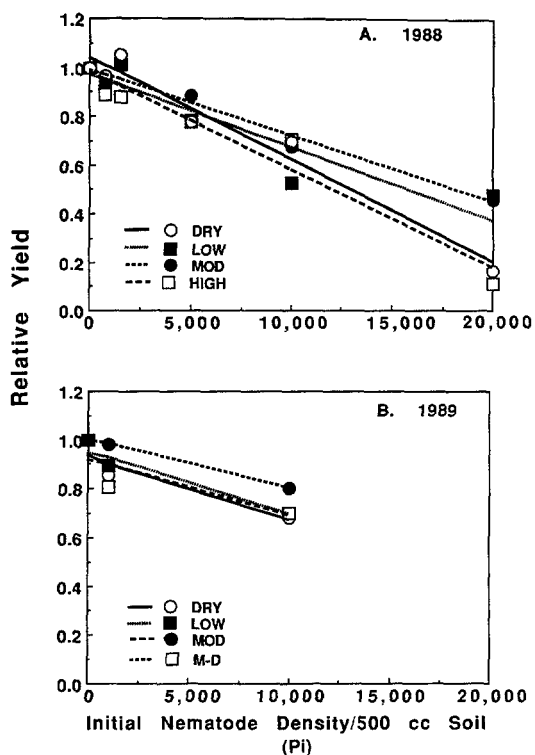
FIG. 2. The effect of *Meloidogyne incognita* and irrigation regime on relative yield of tobacco. A) 1988: DRY = $1.04 - 0.000042(\text{Pi})$, $R^2 = 0.83$; LOW = $0.97 - 0.000030(\text{Pi})$, $R^2 = 0.53$; MOD = $0.99 - 0.000027(\text{Pi})$, $R^2 = 0.52$; HIGH = $0.98 - 0.000040(\text{Pi})$, $R^2 = 0.52$. B) 1989: DRY = $1/[1.07 + 0.000042(\text{Pi})]$, $R^2 = 0.63$; LOW = $\text{Log}[2.58 - 0.000057(\text{Pi})]$, $R^2 = 0.59$; MOD = $\text{Log}[2.72 - 0.000049(\text{Pi})]$, $R^2 = 0.75$; M-D = $\text{Log}[2.50 - 0.000050(\text{Pi})]$, $R^2 = 0.72$. MOD = moderate irrigation regime; M-D = alternating moderate and dry irrigation.

function of environment and competition for resources (5), the root-knot nematode represents the competition factor. The nematode is competing for metabolic products of the plant. The giant cell initiated by the nematode is a "sink" for plant products (7). Where nutrients are the only limiting factor, the rate of growth will be proportionate to the most limiting element (3). If the giant cell is capable of disproportionately diverting photosynthate from other necessary plant-growth processes and nitrogen is a limiting factor, then it is possible to visualize why the combination of the root-knot nematode and nutrient deficiency would combine to increase yield loss and cause a synergistic loss in the intrinsic rate of plant growth (r).

Seinhorst (12) observed differences in water uptake and hypothesized three mechanisms by which patterns of water uptake would explain yield differences. In our studies a reduced water uptake pattern was observed as Pi increased. There was no additional water provided in plots for the 1988 and 1989 DRY treatments, so CSMP comparisons between Pi reflect the strong influence of *M. incognita* on water uptake. It is not possible to compare water uptake between the water treatments, because different amounts of water were added to the plots.

For predictive yield modeling, the relationship between soil moisture stress and root-knot nematode mostly resulted in additive stresses. A predictive model is most useful in the range of yield loss where alternative management tactics are available. Predicted yield losses at low (Pi = 1,000) and high (Pi = 10,000) levels of the nematode were compared for the eight models generated. The range of predicted yield from optimal irrigation to no irrigation ranged from a 10% difference at low nematode levels to a 22% difference at high nematode levels. Given the lack of accuracy in estimating the initial nematode population in commercial fields, the error in yield-loss prediction due to different soil moisture conditions may be insignificant.

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