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PLANT PATHOLOGY AND NEMATOLOGY

A Comparison of the Damage Functions, Root Galling, and Reproduction of *Meloidogyne incognita* on Resistant and Susceptible Cotton Cultivars

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ABSTRACT

Nematode management decisions should be based, in part, on knowledge of the damage threshold population density, and this value is likely to vary based on the level of resistance of the cotton cultivar. The damage functions of two cotton cultivars resistant to the root-knot nematode (*Meloidogyne incognita*) were compared with that of a susceptible cultivar in field microplots using a 3 x 7 factorial design with three cultivars (susceptible Paymaster HS 260; resistant Acala NemX and Stoneville LA 887) and seven initial nematode population densities (Pi). Final nematode population densities and root gall indices were greater on the susceptible HS 26 than on the resistant cultivars ($P \leq 0.05$). Seed cotton yields of all cultivars decreased with increasing nematode Pi ($r^2 = 0.53$ to 0.81), with relative yield losses being the greatest for HS 26. When yield responses to Pi were fitted to the Seinhorst model [$Y = m + (1\text{-}m)Z^{P-T}$], the damage thresholds for each cultivar were similar (T = 0.1 to 9 nematodes/500cm^3 soil). The minimum yield parameter was lower for the susceptible HS 26 (m = 0.71 to 0.8) than for the resistant cultivars (m = 0.8 to 0.93), but these differences were not significant ($P \geq 0.05$). Based on both the regression and the Seinhorst models, the resistant cultivars have greater tolerance than the susceptible cultivar. The increased tolerance of the resistant cultivars increased the nematode density at which an action threshold for management is acheived.

Cotton yield losses due to nematodes were estimated to be 7.6 x 10^5 bales in 1997 in the United States (Blasingame, 1998). Because of its widespread distribution across all cotton producing areas of the United States, the root-knot nematode (*Meloidogyne incognita* races 3 and 4) is the most important nematode affecting cotton. *Meloidogyne incognita* is especially prevalent in the panhandle of Texas, the coastal plains of the Southeast, and the San Joaquin Valley of California (Starr, 1998). Management of root-knot nematodes has traditionally relied on nematicides and crop rotation. A few cultivars (Stoneville LA887 and Acala NemX) with resistance to *M. incognita* have been released (Garber and Oakley, 1996; Jones et al., 1990), but LA887 is no longer commercially available.

Because resistance to nematodes is usually defined as a plant's ability to inhibit nematode reproduction (Roberts, 2002), resistant cultivars are expected to suppress nematode population densities. The resistance of the cotton genotype Auburn 623 RNR to *M. incognita* was more effective in suppressing nematode population densities than a susceptible genotype grown in soil treated with fumigant nematicides (Shepherd, 1982). Ogallo et al. (1997, 1999) reported that the resistant cultivar NemX suppressed population densities of *M. incognita* relative to a susceptible cultivar.

The relationship between crop yield response and initial nematode population densities is an important property of a crop. The damage threshold is the nematode initial population density above which yield is suppressed. The damage threshold may be estimated from the Seinhorst model, $Y = m + (1\text{-}m)Z^{P-T}$, where Y is the relative yield, m is an estimate of the relative minimum yield, Z is a constant representing the proportion of host unaffected by one nematode, P is the initial nematode density, and T is the damage threshold (Seinhorst, 1965). The minimum yield parameter of the model may be considered an estimate of the tolerance (as defined by Roberts, 2002) of a cultivar. Damage thresholds for *M. incognita* on susceptible cotton cultivars were reported to be in the range of 1 to 10 eggs and juveniles/500 cm^3 soil (Roberts et al., 1985; Starr et al., 1989). No data are available on the damage thresholds for resistant cotton genotypes.

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The primary objective of this research was to compare the damage functions for *M. incognita* on resistant and susceptible cotton genotypes. It was our hypothesis that resistance would result in increased values of T and (or) m from the Seinhorst model. The effects of resistance on population densities of *M. incognita* and on root galling of cotton also were measured.

MATERIALS AND METHODS

Experiments were conducted in 1997 and 1998 in field microplots containing a Lufkin loamy sand (91% sand, 2% silt, and 7% clay, <1% organic matter, pH 7.7; Utisol). Each microplot was 81 cm x 61 cm x 46 cm deep. Plots were fumigated with 1,3-dichloropropene to eliminate existing nematodes prior to planting each year. The experimental design was 3 x 7 factorial arranged in a randomized complete block with five replications for each treatment. Treatments were seven different initial population densities (Pi) of *M. incognita* and three cotton cultivars. The cultivars were the nematode-resistant cultivars Acala NemX and Stoneville LA 887, and the susceptible cultivar Paymaster HS 26. In 1997, the initial population densities (Pi) of *M. incognita* were 0, 0.5, 1, 10, 50, 100, and 500 eggs and second-stage juveniles (J2)/500 cm^3 soil. In 1998, the Pi's were 0, 1, 5, 10, 50, 100, and 325 eggs and J2/500 cm^3 soil.

Meloidogyne incognita (race 3, isolate 82-2) was cultured on tomato (*Lycopersicon esculentum* Mill). Nematode inoculum was prepared by combining infected tomato root fragments and infested soil from greenhouse cultures with pasteurized sand. The inoculum concentration was then determined by enumerating the eggs and J2 extracted from the infested soil by elutriation (Byrd et al., 1976) and centrifugation (Jenkins, 1964). Eggs of *M. incognita* were extracted from egg masses adhering to the root fragments recovered during elutriation with NaOCl (Hussey and Barker, 1973) and counted. Sufficient infested soil was incorporated into each plot to achieve the desired Pi to a depth of 30 cm. Immediately following infestation of the soil, 10 cotton seeds were planted in each plot in a single row. Plots were thinned to four plants after emergence. Each plot was fertilized according to Texas Cooperative Extension recommendations based on soil test analysis. Irrigation was applied as needed and foliar insects were managed with appropriate pesticide applications.

Population densities of *M. incognita* were estimated 8 wk after planting (Pm) and at crop maturity (Pf). At each sampling date, eight cores 2.5-cm-dia x 30-cm-deep were collected from each plot and combined to form one composite sample per plot. Second-stage juveniles and eggs were extracted from each sample as described above for inoculum preparation and counted using a stereo microscope. Each plot was hand-harvested at crop maturity and seed cotton yield per plot was determined. After the plants were harvested, each plant was dug and severity of root galling was determined based on a 0 to 5 scale, with 0 representing no galling and 5 representing >75% of roots galled (Barker et al., 1986).

Analysis of variance using the SAS (SAS Institute, Cary, NC 27511) general linear model was performed to determine the main treatment effects on nematode population densities, root gall indices, and seed cotton yields. Mean separation for significant treatments was by least significant differences. Regression analysis was performed to determine the relationships between Pi, Pm, Pf, and seed cotton yield for each cotton genotype. Yield responses to Pi were fitted to the Seinhorst model using the computer program SeinFit (Viaene et al., 1997) to estimate the effect of host resistance on the damage threshold (T) and the minimum yield (m) values. *T*-tests were used to compare slopes of regression equations, and estimated values of T and m from the Seinhorst models.

RESULTS

Analysis of variance indicated that in each year both Pm and Pf values were affected by cultivar. HS 26 had greater ($P \leq 0.05$) values of Pm than NemX or LA887 at the three highest Pi levels, but not at the lower Pi levels (Table 1 and 2). HS 26 had greater ($P \leq 0.05$) Pf values than did NemX and LA 887 at all Pi levels (Table 1 and 2). The Pf for NemX ranged from 1 to 27% of that of HS26, whereas the Pf for LA 887 ranged from 2% to 52% of that of HS 26. The two resistant cultivars had similar nematode population densities. In both years, Pm increased linearly ($P \leq 0.05$) with Pi for five of the six data sets with r^2 values ranging from 0.66 to 0.99. Similarly, in 1997 Pf increased linearly ($P \leq 0.05$) with Pi ($r^2 = 0.35$ to 0.74). However, the Pf values were not related to Pi in 1998.

The effects of Pi, cultivar, and the interaction of Pi and cultivar were all significant ($P \leq 0.05$) with

Table 1. Effect of initial population densities (Pi) of *Meloidogyne incognita* on population densities at midseason (Pm) and crop maturity (Pf) for the susceptible cultivar HS 26 and the resistant cultivars NemX and LA 887 in 1997 [z]

Pi	Pm				Pf			
	HS 26	NemX	LA887	LSD[y]	HS 26	NemX	LA887	LSD[y]
0.5	58	0	95	NS	1029	32	261	377
1.0	30	0	6	NS	945	146	39	544
10	1744	30	22	443	4804	40	110	1120
50	4340	33	148	2605	2482	171	564	1492
100	1862	99	102	451	3454	55	338	2647
500	6735	237	152	3961	3127	348	505	2156
LSD[x]	3386	NS	NS		NS	NS	NS	NS

[z] Mean population density of *M. incognita* measured as number of eggs and J2 per 500 cm^3 of soil.

[y] LSD values (P=0.05) for comparison of means for cultivars within a Pi for Pm and Pf (across rows).

[x] LSD values (P=0.05) for comparison of mean differences for Pi within each cultivar (down columns).

Table 2. Effect of initial population densities (Pi) of *Meloidogyne incognita* on population densities at midseason (Pm) and crop maturity (Pf) for the susceptible cultivar HS 26 and the resistant cultivars NemX and LA 887 in 1998 [z]

Pi	Pm				Pf			
	HS 26	NemX	LA887	LSD[y]	HS 26	NemX	LA887	LSD[y]
1	11	8	14	NS	1042	139	277	641
5	95	17	5	60	2354	632	325	1410
10	37	46	12	NS	3034	460	971	2127
50	280	45	13	149	2668	316	1391	1790
100	793	58	11	452	6673	253	2114	3215
325	2144	134	140	1804	1583	140	788	1126
LSD[x]	3386	NS	NS		NS	NS	NS	NS

[z] Mean population density of *M. incognita* measured as number of eggs and J2 per 500 cm^3 of soil.

[y] LSD values (P=0.05) for comparison of means for cultivars with in a Pi for Pm and Pf (across rows).

[x] LSD values (P=0.05) for comparison of mean differences for Pi within each cultivar (down columns).

respect to the gall index. HS 26 had greater ($P \leq 0.05$) gall indices than the resistant cultivars, which were not different from each other (Fig. 1). The gall index for each cultivar increased with increasing Pi (r^2 = 0.61 to 0.85, $P \leq 0.05$).

Cultivar and Pi each affected seed cotton yield ($P \leq 0.05$), and the Pi x cultivar interaction was significant ($P \leq 0.05$). Seed cotton yield of NemX was lower than that of LA 887 or HS 26 ($P \leq 0.05$) in the non-infested plots (Pi = 0), whereas the yields of the latter two cultivars were similar (Fig.2 A, B) in both years in the non-infested plots. A negative relationship was observed between seed cotton yield and the natural log of Pi for all three cultivars in both years, with modest fit of the data to the model (r^2 values ranged from 0.52 to 0.81, $P \leq 0.05$) (Table 3). When *t*-tests were used to compare the rate of yield decease due to increasing Pi of each resistant cultivar

Table 3. Comparison of regression models for the relationship between of initial population density (Pi) of *Meloidogyne incognita* and seed cotton yield for the root-knot susceptible cotton cultivar HS 26 and the resistant cultivars NemX and LA 887

Cultivar	Model – 1997[z]	r^2	Model - 1998[z]	r^2
HS 26	Yield = 210.8 - 11.9 Ln (Pi)	0.81	Yield = 428.9 - 24.4 Ln (Pi)	0.53
NemX	Yield = 185.4 - 5.11 Ln (Pi)*	0.62	Yield = 278.6 - 8.1 Ln (Pi)*	0.56
LA 887	Yield = 221.4 - 5.3 Ln (Pi)*	0.53	Yield = 391.3 - 5.8 Ln (Pi)*	0.53

[z] * indicates that the rate of decrease in seed cotton yield was different ($P \leq 0.05$) from the rate of decrease for the susceptible cultivar HS 26.

with that of the susceptible cultivar, the rate was greater ($P \leq 0.05$) for the susceptible cultivar than for either resistant cultivars. The rate of yield decrease for HS 26 ranged from 224 to 421% of that of the resistant cultivars, which were not different from each other.

Using the Seinhorst model to analyze the yield responses of the three cultivars to increasing Pi revealed a modest fit of the data to the model (r^2 = 0.51 to 0.89, $P \leq 0.05$). The estimated values for minimum yield (m) ranged from 0.8 to 0.93 for the two resistant cultivars, whereas the estimates for the susceptible cultivar were 0.71 to 0.8 (Table 4), but these differences in m were not significant ($P > 0.05$). With the exception of NemX in 1997, the damage threshold (T) was not affected by cultivar and was very low, ranging from a Pi of 0.1 to1.5 nematodes/ 500 cm^3 soil (Table 4).

Table 4. Estimates of the damage threshold (T) and minimum yield (m) parameters from the Seinhorst model[z] for the relationship between initial population densities of *Meloidogyne incognita* on yield of the root-knot susceptible cotton cultivar HS 26 and the resistant cultivars NemX and LA 887

Cultivar	1997			1998		
	T	M	r^2	T	M	r^2
HS 26	0.1	0.71	0.85	1.5	0.8	0.70
NemX	9.0	0.80	0.80	1.0	0.89	0.69
La 887	0.1	0.86	0.54	1.0	0.93	0.51

[z] The Seinhorst model is $Y = m + (1- m) Z^{P-T}$; where Y = relative yield, m = relative minimum yield, Z = a constant, P = initial nematode density, and T = the damage threshold. Nematode densities are in nematodes per 500 cm^3 soil.

DISCUSSION

Based on previous reports (Koenning et al., 2001; Ogallo et al., 1997 and 1999; Shepherd, 1982) and since resistance to nematodes is defined as an inhibition of nematode reproduction (Roberts, 2002), it was expected that the *M. incognita*-resistant cotton cultivars NemX and LA 887 would have lower final population densities of *M. incognita* and lower root gall indices than the susceptible HS 26. In most instances, nematode densities at midseason (Pm) were linearly related to the initial density for both the resistant and susceptible cultivars. Final nematode densities at crop maturity (Pf) were not consistently related to Pi. This lack of apparent relationship is due in part to all populations reaching the carrying capacity of the host before crop maturity, regardless of Pi or level of host resistance. Additionally, for the intolerant susceptible HS 26, the damage to the host resulting from nematode parasitism would limit the carrying capacity of the host. These relationships between initial and final nematode population densities have been reported previously (McSorley and Phillips, 1993; Seinhorst, 1967).

Comparison of damage functions in this study was complicated by including NemX, which is a cultivar developed for the environment and production practices of California and is not grown in central Texas or in eastern cotton production areas. Yields of NemX, which were low in this study, were similar to those of the high yielding, susceptible cotton cultivars commonly grown in California (Ogallo et al., 1999). Despite the overall low yield of NemX in these experiments, the resistant cultivars had less yield suppression relative to the susceptible cultivar in response to nematode infection. Even though there were substantial differences in overall yield between the 2 yr of this study (due primarily to a heavy infestation of the boll weevil in 1997), the estimated damage thresholds (T) for the Seinhorst model for each cultivar were similar in each year. Additionally, the very low estimated damage thresholds observed were similar to those reported previously (Roberts et al.,1985; Starr et al., 1989). These low damage threshold densities confirm that cotton is intolerant of infection by *M. incognita*. It was surprising, however, that estimated values of T were not affected by host resistance and that the major effect of resistance on the damage function was to increase the minimum yield parameter (m) of the Seinhorst model. Our hypothesis that resistance would result in an increase in the damage threshold density was not supported by the data from these experiments.

Even though these observed differences in m were not significant in the present study, our observations were similar to previous reports that resistance to *M. incognita* in pepper (*Capsicum annuum* L.) (Di Vito et al., 1992) or in tomato (Di Vito et al., 1991) did not affect T, but resulted in greater estimated values of m. Further, the rate of decrease in seed cotton yield with increasing nematode densities for the susceptible cultivar was two-fold the rate observed for the resistant cultivars. This is consistent with the resistant cultivars having higher estimated values of m and being more tolerant of infection by root-knot nematodes than the susceptible cultivar. The apparent greater tolerance of the resistant cultivars in the this study was different from the reports of Colyer et al. (1997) and Koenning et al. (2001), where resistant cultivars were not observed to be more tolerant of root-knot nematodes than susceptible cultivars. These differences with respect to apparent tolerance may be related to differences in experimental design among these studies. Measuring the yield response to a wide range of nematode population densities in this study allowed a more precise measurement of tolerance than would be possible in field tests where there was less precise control of nematode population densities.

Since these nematode-resistant cotton cultivars are not immune to nematode damage, a positive yield response to nematicide treatment would be expected when initial nematode densities exceed the damage threshold, as has been demonstrated previously (Colyer et al. 1997; Koenning et al., 2001). By being more tolerant than susceptible cultivars, the relative yield loss will be less for the resistant cultivars than for susceptible cultivars across a wide range of nematode population densities. The economic threshold is that population density at which economic loss exceeds the cost of control (Norris et al., 2003). Because the resistant cultivars in this study had less yield loss across a range of nematode population densities than did the susceptible cultivar, it will take a greater nematode population density to cause economic loss. Thus, the economic threshold for the resistant cultivars is greater than for susceptible cultivars. The estimation of the precise economic threshold will be affected by the genetic yield potential of a cultivar, expected cotton prices, and other production factors that influence the economics of production.

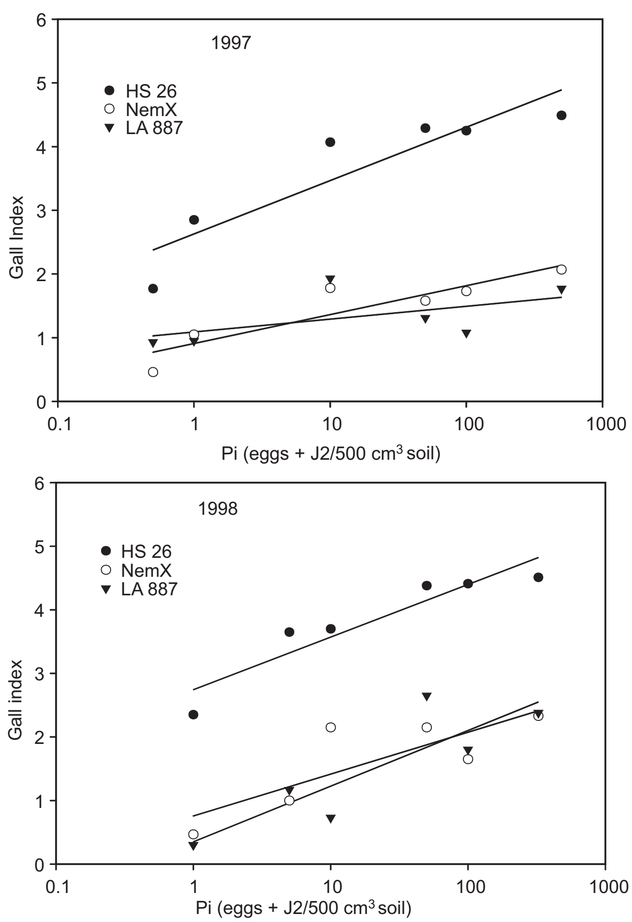

Figure 1. Effect of initial population densities (Pi) of *Meloidogyne incognita* on root-gall index (0 = no galls and 5 >75 % of the roots galled) of the susceptible cotton cultivar Paymaster HS 26 and the root-knot resistant cultivars Acala NemX and Stoneville LA 887.

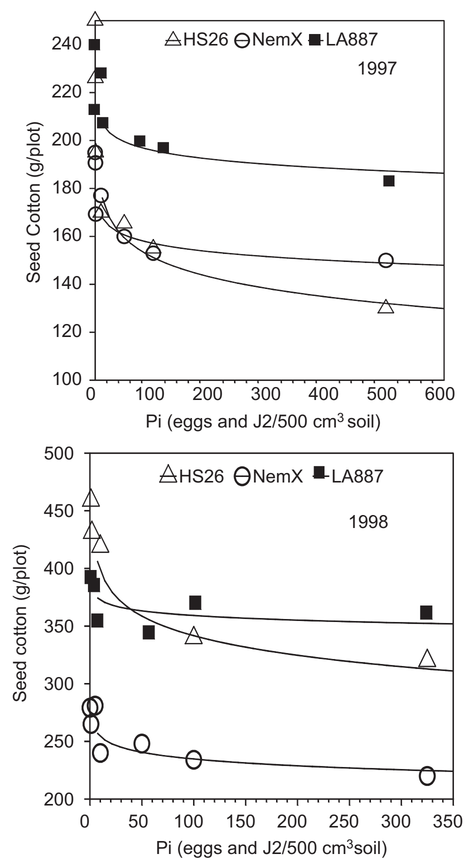

Figure 2. Effect of initial population densities (Pi) of *Meloidogyne incognita* on seed cotton yield of the susceptible cultivar Paymaster HS 26 and the root-knot resistant cultivars Acala NemX and Stoneville LA 887.

In addition to the direct benefit of resistance on cotton yields, incorporation of resistant cotton genotypes into cropping systems that include other susceptible crops such as soybean, will be of benefit by suppressing nematode population densities. Because resistance results in lower nematode densities at the end of a growing season, susceptible crops following resistant cotton genotypes will be exposed to a lower nematode population density than if a susceptible cotton cultivar had been grown. Such susceptible crops should have greater yields in nematode-infested fields following cotton cultivars with resistance to *M. incognita* than following a susceptible cultivar as has been reported by Ogallo et al. (1999) for a resistant cotton, susceptible lima bean cropping system.

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