Cotton Tolerance to *Hoplolaimus columbus* and Impact on Population Densities

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ABSTRACT

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Glyphosate-tolerant transgenic-cotton cultivars were evaluated for tolerance to *Hoplolaimus columbus* in field experiments conducted from 2001 to 2003. The studies were arranged in a split-plot design that included treatment with 1,3-dichloropropene at 42 liter/ha to establish fumigated versus nonfumigated subplots with cultivars as whole plots. Cotton cultivars were divided by relative maturity into two separate but adjacent experiments in order to facilitate cotton defoliation, with 10 early-maturity and 5 late-maturity cultivars. Fumigation was effective in suppressing *H. columbus* population densities and increased cotton lint yield. The cultivar-fumigation interaction was significant for early-season cotton cultivars but not for late-season cultivars. A tolerance index ([yield of nontreated/yield of treated] $\times$ 100) was used to compare cultivar differences. Both groups of cultivars expressed significant levels of tolerance to *H. columbus*, but late-season cultivars tended to yield more than early-season cultivars in infested fields.

Additional keywords: Columbia lance nematode, fumigant nematicide

The Columbia lance nematode *Hoplolaimus columbus* Sher is limited in known distribution to Georgia, North Carolina, South Carolina, and Alabama in the United States (17). This nematode can be a destructive pathogen of cotton (*Gossypium hirsutum* L.), corn (*Zea mays* L.), and soybean (*Glycine max* L.), especially in sandy soils (15-21,25).

Tactics for management of *H. columbus* are limited. Rotation often is not an option in fields infested with this nematode due to its wide host range (10). Peanut (*Arachis hypogaea* L.) and tobacco (*Nicotiana tabacum* L.) can be used in rotation with host crops, but the hectareage of and demand for these two crops are limited. Various cultural practices, including small grain cover crops, planting date, stalk destruction, and relative maturity date, have little impact on population densities of *H. columbus* or cotton yield (8,16). Subsoiling in soils with a hardpan increases cotton

yield when *H. columbus* is present, but many farmers have adopted reduced tillage practices (12,25). The application of poultry litter is effective in suppressing mid-season population densities of Columbia lance nematode and improving cotton lint yield, but rates required for nematode suppression may exceed environmental guidelines (15).

Fumigant and nonfumigant nematicides are effective in preventing soybean and cotton yield suppression by this nematode, and cotton production in nematode-infested fields is highly dependent on nematicides. Additional alternative tactics for nematode management in cotton are needed (3,13,17-19,25,26).

Cotton cultivars vary in their response to parasitism by nematodes. Cultivars resistant to the southern root-knot nematode *Meloidogyne incognita* generally are defined as limiting the reproduction of this species, whereas susceptible cultivars support large numbers of this parasite (9,24). Little variation in reproduction of *H. columbus* has been noted among soybean and cotton cultivars, which may indicate that there is no specific host-plant resistance to this nematode in these plant species (6,13,21). Cultivars that support nematode reproduction but suffer less yield suppression compared with other cultivars are referred to as being tolerant (2,7,24). Soybean tolerance to a number of nematodes, including *H. glycines* and *H. columbus*, is well documented (5,13,14,21,22,24). Cotton tolerance to *H. columbus*, however, is not well documented and much of the research on this subject is contradictory

(6,16,18). Information on cultivar resistance to root-knot nematodes may be obtained through greenhouse experiments, but tolerance must be evaluated in field experimentation (6,9,11,13,14,26).

The widespread use of herbicide-tolerant or insect-resistant cotton cultivars has resulted in numerous cultivars being obsolete. Currently, over 90% of the cotton hectareage in North Carolina is planted to transgenic cultivars tolerant to the herbicide glyphosate (1). Data on field tolerance and resistance of transgenic cultivars to pests and pathogens is generally lacking. Field research conducted from 2001 through 2003 evaluated the relative tolerance to *H. columbus* of glyphosate-tolerant cotton cultivars with or without transgenic insect resistance. The objectives of this research were to evaluate the impact of this nematode species on cotton lint yield of most herbicide-tolerant cotton cultivars being evaluated in the North Carolina official cultivar trials during these years, the reproductive capacity of *H. columbus* on these cultivars, and to determine whether measurable tolerance to this nematode species is available in commonly used cotton cultivars.

MATERIALS AND METHODS

Field experiments were conducted over the years 2001 to 2003 in growers fields infested with *H. columbus*. The cotton cultivars to be evaluated were divided by relative maturity into two separate but adjacent experiments. The experiments in 2001 and 2002 were located in different areas of the same field in Scotland County, NC. The soil type at this location was a Wagram loamy sand (84% sand, 11% silt, 5% clay, <1% organic matter). The mean initial population density (Pi) per 500 cm³ of soil in 2001 was 412 $\pm$ 21 and 515 $\pm$ 31 for early- and late-maturing cultivars, respectively, and the mean Pi for 2002 was 278 $\pm$ 25 and 302 $\pm$ 11 for early- and late-maturing cultivars, respectively. Experiments in 2003 were located in Robeson County, NC in a grower's field with a Goldsboro sandy loam (82% sand, 14% silt, 4% clay; <1% organic matter) and mean Pi of 332 $\pm$ 18 and 234 $\pm$ 20 *H. columbus* per 500 cm³ of soil for early- and late-maturing cultivars, respectively.

The experimental design was a split-plot with six replicates. Subplots were treated with 1,3-dichloropropene (Telone II; Dow AgroSciences, Indianapolis, IN) at 42 liter/ha versus nontreated. Whole plots

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were planted to transgenic glyphosate-tolerant cotton cultivars with or without transgenic insect resistance (Table 1). Standard management practices for cotton production were used throughout this research and plots were not irrigated (1).

Selected plots were fumigated in early April and all plots planted in mid-May. All plots received an in-furrow application of aldicarb (Temik 15G; Bayer Crop Science Inc., Research Triangle Park, NC) at 0.5 kg

a.i./ha at planting for early-season insect control. Plots were two rows, 12.2 m long with 1.01-m row spacing and 3.6-m alleys. Cotton was defoliated the last week in September and harvested approximately 2 weeks later. Lint yield was determined by ginning subsamples of seed cotton taken from the first two replicates after picking with a commercial cotton picker.

Samples for nematode assays for each plot were collected prior to fumigation

(Pi), mid-season (Pm), and at cotton harvest (Pf). Each soil sample consisted of 8 to 10 cores (2.5 cm in diameter) taken to a depth of 15 cm and composited. A 500-cm³ subsample was processed by elutriation and centrifugation to extract adult and juvenile nematodes from soil (4).

Analysis of variance (ANOVA) was used for a split-plot design with log (Pi + 1) as a covariate using PC/SAS software (SAS Institute, Cary, NC). Early- and late-maturing cultivars were analyzed separately. Nematode numbers were transformed log ($x + 1$) prior to analysis to standardize the variance. Nontransformed numbers are presented in tables for clarity. Years for the field experiments were considered to be random effects; therefore, the cultivar-year interaction was used to test differences for cultivar, fumigation, and cultivar-fumigation effects for combined analysis over years. Years differed ($P \leq 0.01$), and first-order interactions for year and cultivar were not observed ($P \leq 0.10$) for population data, but were observed for yield data. Second-order interactions were not significant.

Tolerance indices (TI) were calculated where $TI = (\text{yield of nontreated} / \text{yield of treated}) \times 100$ and analyzed as a randomized complete block design (RCBD). The Waller Duncan k -ratio t test (k -ratio = 50) was used for mean separation and regression analysis was used to evaluate the influence of Pi and the tolerance index on Pf and Pm on data from nontreated plots as an RCBD. Data on nematodes from nontreated plots were subjected to regression analysis and used to determine whether a relationship between nematode reproduction and cotton lint yield was present. Comparison of transgenic insect-resistant cultivars with susceptible cultivars was by orthogonal contrasts.

RESULTS

Fumigation with 1,3-dichloropropene was effective in suppressing the population density of *H. columbus* ($P \leq 0.01$) at mid-season all years (Tables 1 and 2; Fig. 1). Nematode numbers were suppressed ($P \leq 0.10$) by fumigation at cotton harvest in 2001 and 2002, but not in 2003 as indicated by the year-fumigation interaction ($P \leq 0.10$). Early-season cotton cultivars had lower ($P = 0.0026$) nematode numbers in fumigated plots at midseason in all years and lower ($P \leq 0.10$) Pf numbers in fumigated plots in 2001 and 2002, but not in 2003 (Fig. 1A). Late cotton cultivars had lower ($P = 0.0015$) nematode numbers in fumigated plots at midseason in all years and lower ($P \leq 0.10$) Pf nematode levels in fumigated plots in 2001 and 2002, but not in 2003 (Fig. 1B). Cotton cultivars did not differ ($P \leq 0.10$) in their ability to support reproduction of *H. columbus*, and there was no year-cultivar interaction ($P \leq 0.10$) for either early-season or late-season cultivars. Covariate analysis demonstrated

Table 1. Cotton lint yield as influenced by cultivar and application of 1,3-dichloropropene (1,3-D) at 42 l/ha and tolerance index for 10 early to midseason cotton cultivars and for five mid- to late-maturity cotton cultivars in experiments in fields infested with *Hoplotaimus columbus* conducted from 2001 to 2003 in Scotland and Robeson Counties, NC^w

Cultivar ^y	Lint yield (kg/ha) ^x		TI
	Fumigated 1,3-D	Nontreated	
Early-season cultivars			
DP 425RR	698 ed	722 bcd	106 a
DP 436RR	753 ed	752 bc	101 ab
DP 422B/RR	671 e	532 e	83 d
ST 4892BR	878 ab	792 a	92 abcd
ST 4793R	727 ed	688 cd	93 abcd
SG 215BG/RR	844 bc	761 b	92 abcd
SG 501BR	907 a	747 bc	82 d
SG 521R	740 ed	749 bc	100 abc
PM 1218BG/RR	705 ed	671 d	100 abc
PM 1199 RR	778 cd	672 d	88 bcd
Mean ^z	770 A	709 B	...
Late-season cultivars			
DP451B/RR	963 a	932 a	95 ab
DP458BRR	882 ab	792 b	88 ab
DP655BRR	902 ab	856 b	101 a
DP5415RR	902 ab	781 b	91 ab
DP5690RR	838 b	678 c	80 b
Mean ^z	898 A	806 B	...

^w Tolerance indices (TI) were calculated where $TI = (\text{yield of nontreated} / \text{yield of treated}) \times 100$.

^x Means followed by the same lowercase letter in a column do not differ according to Waller Duncan k ratio t test (k -ratio = 50). The cultivar-fumigation interaction was significant for cotton lint yield for early-season cultivars ($P = 0.02$), but not for late-season cultivars ($P \leq 0.10$). Mean for each cultivar is based on 18 observations, six replicates per year.

^y Cultivar designation containing "B" indicates transgenic insect resistance.

^z Means for relative maturity (fumigated with 1,3-D versus nontreated) followed by the same uppercase letter do not differ according to analysis of variance ($P \leq 0.05$).

Table 2. Partial analysis of variance and analysis of covariance for main effects and first-order interactions using log (Pi + 1) as a covariate for midseason (Pm) and harvest (Pf) population density of *Hoplotaimus columbus* per 500 cm³ of soil, and cotton lint yield for 15 cotton cultivars in a split-plot design and tolerance index analyzed as a randomized complete block design

Source, maturity	df	F value ^x			
		Pm	Pf ^y	Yield	TI ^z
Early-season cultivars					
Year	2	203**	478**	1,120**	5.43**
Cultivar	9	1.21	1.36	7.75**	2.06*
Fumigant	1	56.7**	43.9**	20.70**	...
Cultivar–fumigant	9	0.71	0.41	2.31*	...
Year–cultivar	18	1.55	1.00	4.55**	1.01
Fumigant–year	2	30.40**	29.2**	3.75*	...
Log (Pi + 1)	1	12.40**	10.34**	8.55**	13.63**
Late-season cultivars					
Year	2	99.10**	38.48**	535**	6.29**
Cultivar	4	1.11	0.61	5.58**	1.43
Fumigant	1	41.60**	6.51*	23.1**	...
Cultivar–fumigant	4	0.28	0.89	1.44	...
Year–cultivar	8	0.45	0.95	14.98**	0.96
Fumigant–year	2	8.62**	7.01**	0.87	...
Pi	1	1.59	0.16	3.63*	1.42

^x Values followed by * and ** are significant at $P \leq 0.10$ and 0.01, respectively.

^y Analysis performed on transformed values (log $X + 1$).

^z Tolerance indices (TI) were calculated where $TI = (\text{yield of nontreated} / \text{yield of treated}) \times 100$.

that Pi was an important factor influencing nematode Pm and Pf for early cotton cultivars, but not for late cotton cultivars. Analysis of nematode population data from nonfumigated plots showed that Pm was positively related to preplant population density (Fig. 2). There was no apparent difference associated with insect resistance according to orthogonal comparison of means of insect-resistant cultivars versus cultivars without the Bt resistance transgene (*data not included*). Similarly, there was no relationship between insect resistance and the tolerance index, in that both groups contained *H. columbus*-tolerant and -sensitive cultivars.

Fumigation increased ($P \leq 0.01$) the yield of both early-season and late-season cotton compared with nonfumigated plots (Tables 1 and 2). The first-order cultivar–fumigation interaction was significant ($P = 0.041$) for early cultivars, but not ($P = 0.17$) for late-maturing cultivars in the combined analysis over all years (Table 2). Analysis of covariance provides some evidence that Pi was a more important factor for yield of early compared with late cotton cultivars because Pi was a significant covariate ($P = 0.0003$) for nonfumigated early cultivars, whereas Pi was not a significant covariate ($P = 0.24$) for the late cultivars. Although a valid statistical comparison of early- versus late-maturing cultivars cannot be performed, late-maturing cultivars yielded considerably more than early cultivars.

Mean tolerance indices for early-season cultivars ranged from 82 to 106 for early-season cultivars, and from 80 to 101 for late cultivars demonstrating considerable variation in cultivar tolerance (Table 1). Year had an impact ($P \leq 0.01$) on cultivar tolerance for both groups, but the year–cultivar interaction was not significant ($P \leq 0.10$), showing a high level of consistency in tolerance rankings over years. Tolerance index was not correlated with yield for either late or early cultivars ($P \leq 0.10$). Nonetheless, the highest-yielding early cultivars in fumigated plots tended to be the least tolerant; whereas, among the late cultivars, the highest-yielding cultivars in fumigated plots were those most tolerant to Columbia lance nematode. Midseason numbers of *H. columbus* were negatively related ($P \leq 0.0026$) to the tolerance index, but final nematode densities were not (Fig. 3).

DISCUSSION

In 2 of the 3 years of this study, fumigation with 1,3-dichloropropene suppressed *H. columbus* numbers at cotton harvest compared with nonfumigated plots. Because of its relatively low rate of reproduction on cotton compared with other plant-parasitic nematodes such as root-knot and reniform nematodes, *H. columbus* cannot compensate for the initial kill by relatively high rates of 1,3-dichloropropene. The positive relationship between preplant

nematode population density and Pm confirms the relatively low reproductive rate for this nematode, but also may be related to between-plot variation in soil texture or other edaphic factors that favor reproduction and are reflected in variation in Pi between plots. The use of analysis of covariance with Pi as a covariate serves the same purpose, but the use of a quantifiable edaphic factor as a covariate might provide greater insight into the biology and ecology of this nematode. These data also suggest that techniques used in precision agriculture may be useful for management of Columbia lance nematode. The primary constraint on site-specific management of plant-parasitic nematodes is the need for large numbers of nematode assays to accurately quantify potential yield loss (17). Soil texture and other edaphic factors are relatively easy to measure and not subject to temporal variation as are nematode population densities, and a single measure may be sufficient for years. Thus, a map of field soil characteristics could be substituted for nematode density and management tactics applied accordingly.

Population densities of *H. columbus* at midseason and cotton harvest were not influenced by cultivar according to ANOVA, as has been reported in other research (16,18). The negative relationship

between *H. columbus* midseason density and TI, however, may indicate a small difference in reproduction of this nematode related to cultivar. Root-knot-resistant cotton cultivars generally were more tolerant than susceptible cultivars in other research, but tolerant cultivars may actually support greater levels of nematode reproduction (7,9). Soybean cultivars tolerant to *Heterodera glycines* supported more reproduction by this nematode and, in theory, tolerant cultivars may support more nematode reproduction (7,14).

The consistent positive yield response of some cultivars to fumigation and minimal response of other cultivars across years in the presence of *Hoplolaimus columbus* demonstrates the existence of useable tolerance to *H. columbus* in certain cotton cultivars. Earlier research on this nematode species on cotton indicated that tolerance may exist, but conclusive evidence for tolerance, such as a cultivar–fumigant, interaction was lacking (16). Three cultivars with tolerance indices less than 85 (SG 501BR, DP 422B/RR, and DP 5690RR) all had yield losses of more than 100 kg/ha, whereas there was little or no loss in yield of cultivars with a TI greater than 90. Both the early and late cotton maturity groups contained cultivars that displayed distinct and repeatable levels of

Fig. 1. Influence of in-furrow injection of 1,3-dichloropropene (1,3-D) on midseason (Pm) and final (Pf) population densities of *Hoplolaimus columbus* per 500 cm³ of soil in field plots from 2001 to 2003. Means are least squared means and error bars are the standard error. A, Early-season and B, mid- to late-season cotton cultivars.

tolerance ($TI \geq 95$: DP 451B/RR, DP 655BRR, DP 425RR, DP 436RR, SG 521BG/RR, and PM1218 BG/RR), but late-season cultivars generally yielded more than early-season cultivars in fields

infested with *H. columbus*. Also, late-season cultivars were less sensitive to *H. columbus* Pi than early-season cultivars as evidenced by covariate analysis. The trend for higher yield in infested fields and

greater tolerance to Columbia lance nematode of late-maturing cultivars compared with early cultivars may not be related to tolerance, but to the following: (i) late-maturing cultivars are less determinant than early cultivars and (ii) the less determinate growth habit gives these cultivars a better ability to recover from drought or other stress which is common in the sandy fields where this nematode occurs. Unfortunately, the mechanisms by which tolerance acts are poorly understood, although they may be related to rooting pattern or root growth dynamics, as is the case with soybean cyst nematode (22). Potentially, late-maturing cotton cultivars may prove to be more tolerant to nematode parasites than early cultivars because of their less determinant growth pattern.

The use of cultivars tolerant to *H. columbus* is a viable option for growers when this nematode is present at damaging levels. Tolerance to nematodes, however, is density dependent, and additional tactics may be required to manage *H. columbus* if population densities greatly exceed the damage threshold (5,7,14). Still, a grower should be able to use less nematicide or a nonfumigant nematicide rather than a fumigant nematicide with a tolerant cotton cultivar to optimize economic return. Tolerance, however, is not the only criterion for cultivar selection, because yield potential may be of more importance. With late-maturing cultivars, cultivar selection is straightforward because the two highest-yielding cultivars in fumigated or nonfumigated plots were DP 451B/RR and DP 655BRR, which also had the highest tolerance indices ($TI = 95$ and 101 , respectively). The situation is problematic with the early-maturing cultivars because the highest-yielding early maturity cultivar in nonfumigated plots was SG 501BR, which was also the least tolerant ($TI = 82$), and the four most tolerant cultivars ($TI \geq 100$) had an average yield of 723 kg/ha in nonfumigated plots compared with 747 kg/ha for SG 501BR. The optimal compromise for a cotton grower would be selection of the early cultivar ST 4892BR (TI of 92) because it was the highest-yielding cultivar in nontreated plots (792 kg/ha) and did not differ significantly from SG 501BR in treated plots. The data indicate that breeding goals should include selection for both high yield and tolerance.

Research comparing cultivar response to *H. columbus* at varying population densities is needed but difficult to achieve in practice. Evaluation of tolerance at different population levels requires extensive land and material for testing (14,23). Comparison of fumigated versus nonfumigated plots appears to be the most cost-effective means for evaluating tolerance (6,13,14,23). Expanded screening of soybean, cotton, and corn germ plasm may identify resistance or greater levels of tolerance to this nematode. The impact of

Fig. 2. Impact of preplant ($\log [P_i + 1]$) *Hoplotaimus columbus* population density per 500 cm³ of soil on **A**, midseason (P_m) and **B**, harvest (P_f) *H. columbus* numbers. Dashed lines are 99% confidence limits.

Fig. 3. Relationship between tolerance index (TI) and midseason (P_m) population densities of *Hoplotaimus columbus* per 500 cm³ of soil. Dashed lines are 99% confidence limits.

cropping systems, cover crops, and potential changes in cultural practices on *H. columbus* also require investigation.

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