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# PLANT PATHOLOGY AND NEMATOLOGY

## Delayed Maturity and Associated Yield Loss in Cotton Infected by the Columbia Lance (*Hoplolaimus columbus* Sher) Nematode

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### ABSTRACT

**Traditional agronomic practices are often ineffective in preventing cotton (*Gossypium hirsutum* L.) yield losses due to the Columbia lance (CLN) nematode (*Hoplolaimus columbus* Sher), so control relies heavily on nematicides. Field experiments were conducted at two locations in 1996 and 1997 to document plant parameters affected by CLN and to determine yield losses in fields with low to moderate levels of CLN. Fumigation with 56 L ha$^{-1}$ 1,3-dichloropropene (1,3-D) resulted in a 77% reduction in CLN population densities at planting and a 21% increase in cotton yield across both locations and years. Plant mapping was conducted at first-bloom and at harvest to document the affects of CLN on cotton plant and yield parameters in order to explain yield losses induced by CLN. Yield losses were due to a 22% reduction in the number of harvestable (open) bolls in plants affected by CLN. Whole-plant mapping showed that second position harvestable boll retention of plants affected by CLN was 50% less than non-affected plants. Machine- and hand-picked (sequential dates prior to machine harvest) cotton yields resulted in delayed maturity of infected plants by 32% and 8% in 1996 and 1997, respectively. Understanding which plant parameters are affected by CLN can aid in the development of more productive management schemes that involve either cultivar selection, timing of defoliation, or planting dates and can further aid cotton breeders in the potential development of tolerant cultivars.**

Several different species of nematodes are known to cause yield losses on cotton (*Gossypium hirsutum* L.). Root-knot (*Meloidogyne incognita* Chitwood) nematode has been studied the most extensively, and recently the reniform (*Rotylenchulus reniformis* Linford and Oliveira) nematode has been studied because of its expanding geographic distribution (Koenning et al., 2004). The CLN has been studied less than the root-knot or reniform nematodes, probably because of its limited geographic distribution. The CLN has been reported to cause severe yield losses in cotton when high nematode infestations reduce tap root length resulting in severe moisture stress and nutrient deficiencies (Mueller, 1993). Producers may reduce CLN population densities by use of either crop rotations or nematicides, because cultural practices, such as planting date and relative cultivar maturity date, do not appear to impact nematode densities (Koenning and Bowman, 2005). Subtle delays in the onset of fruiting and the subsequent progress toward maturity have been suggested as the major causes of yield losses by CLN in cotton (Mueller et al., 1996).

The progression of cotton towards maturity may be documented by the position of the first-fruiting branch on the main stem, which marks the onset of fruiting. The number of proceeding nodes may be used to indicate the length of the vegetative growth phase and to assist in the determination of crop maturity (Mauney, 1986). Any stress, including nematode infection, that affects the onset or duration of any of the cotton growth phases can alter crop maturity.

Management of CLN population densities by crop rotation and use of cover or trap crops is limited because of the wide host range of the CLN (Mueller, 1993). In some cases, commonly grown rotational crops (i.e., corn, wheat, and soybean) resulted in substantial increases in populations of CLN in the field (Schmitt and Imbriani, 1987). Although peanut is a non-host, its use as a rotation crop is only important in management of CLN where significant hectares of peanut are commonly grown (Mueller, 1993; Baird et al., 1995). Unfortunately, only 23,877 hectares of peanut are grown in South Carolina, while approximately 106,435 hectares of cotton are produced (USDA-NASS, 2005).

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Since 1968, the CLN has been recognized as a serious pest associated with yield losses in soybean (*Glycine max* L. Merr.) and cotton crops in South Carolina (Fassuliotis, 1975; Martin et al., 1994). Early records of abnormal cotton growth and subsequent yield losses in CLN infested fields were exacerbated by soil compaction and later referred to as the cotton stunt disease complex (Hussey, 1977). To date, the specific affects of CLN on cotton growth and yield parameters remain undocumented.

Cotton lint yield suppression can range from 20 to 30% where CLN densities exceed 50 CLN 100 $cm^3$ $soil^{-1}$ (Lewis et al., 1976; Noe et al., 1991; Mueller and Sullivan, 1988). Since CLN is microscopic and produces no diagnostic root symptoms, such as galls, it is often overlooked as a cause of yield losses. In many cases, the effects of CLN on plant growth may be subtle, but they can result in yield losses exceeding 50% (Mueller, 1993). Where symptoms in the field are less obvious, yield losses of 5 to 10% may be observed (Mueller, 1993); therefore, the affects of CLN on crop performance may be determined by studying cotton growth and yield parameters of CLN affected cotton. More specifically, crop performance can be evaluated by measuring certain yield components, such as total fruiting sites, total bolls, percentage of fruit retention, and number of harvestable or open bolls produced. Crop performance and yield are not only based on these individual components but on the interactions between them.

The objectives of this study were to determine 1) cotton growth and yield components affected by CLN resulting in cotton yield loss, and 2) the severity of CLN-induced yield losses in traditionally high-yielding cotton fields with moderate to low levels of CLN.

## MATERIAL AND METHODS

A two-year (1996-97) study was conducted in two locations (Edisto and Youngblood) located approximately 5 km apart in Barnwell County, South Carolina, on a Dothan loamy sand (fine-loamy, kaolinitic, thermic Plinthic Kandiudult; 85% sand, 10% silt, 5% clay, and 0.5% organic matter) naturally infested with CLN. Both locations were cropped to cotton in 1995. Plots were arranged in a randomized complete-block design with two treatments established in each block. The first treatment consisted of fumigation with 56 L $ha^{-1}$ of 1,3-dichloropropene (1,3-D) (Telone II; Dow AgroSciences; Indianapolis, IN). The 1,3-D was applied in-furrow at a 30-cm depth when the plot was subsoiled 14 d prior to planting. In the second treatment, plots were subsoiled under the row, but did not receive 1,3-D. Plots consisted of 4 rows with 1-m row spacings. In 1996, plots were 30.5 and 15.2 m long at the Edisto and Youngblood locations, respectively. In 1997, plots were 24.4 m long at both locations. In both years, the Edisto and Youngblood sites included 12 and 8 replications, respectively, and plots were established in the field as in the previous year. Cotton cultivar Stoneville LA887 (Stoneville Pedigreed Seed; Memphis, TN) was planted on 16 May and 30 May 1996 at Edisto and Youngblood, respectively, and at both locations on 7 May 1997. The seeding rate was 20 seeds per meter row (205,095 plants $ha^{-1}$) planted 1.9-cm deep on raised beds. Plots were oversprayed with acephate (Orthene 75; Valent Corp; Walnut Creek, CA) at 0.21 kg a.i. $ha^{-1}$ for thrips control. All plots received fertilizer, herbicide, and insecticide as recommended by the North Carolina State and Clemson University Cooperative Extension Services and were managed identically (Crozier, 2006; Main et al., 2006; Roof and Sullivan, 2004).

**Nematode sampling.** Nematode population densities were determined at planting and at harvest using total soil CLN counts (Davis and Noe, 2000). Twelve, 3.2-cm diameter soil cores were taken at the 20-cm depth from the center two rows of each plot. Soil samples were mixed, and a 400-$cm^3$ subsample was collected. Each 400-$cm^3$ sub-sample was dispersed in 1.9 to 2.8 L of water and wet sieved through 80 mesh (180-µm pore size) and 400 mesh (38-µm pore size) sieves. Material collected on the 400 mesh sieve was further processed for nematode extraction using a centrifugal-flotation procedure (Jenkins, 1964). Numbers of CLN within roots collected from the 80 mesh sieve were determined using a modified mist apparatus for 5 d (Barker et al., 1986). Extracted nematodes were mounted on a grided microscope slide (1 ml in volume) and identified to genus under a dissecting microscope. Nematode counts from both soil and root fractions were adjusted to 100 $cm^3$ of soil. *Hoplolaimus* spp. were assumed to be *H. columbus* if no males were observed in the population (Lewis and Fassuliotis, 1982).

**Plant sampling.** The structural development of plants from fumigated (F) and non-fumigated (NF) plots was characterized by measuring the total number of main stem nodes, monopodial and

sympodial branches, squares, flowers, and bolls, and their location on the plant. Plant parameters were evaluated at first-bloom (240 d after planting) and at harvest. First-bloom sampling was conducted when approximately 50% of the plants within a field had a white flower located at the first position of the first sympodial branch. In 1996, first-bloom dates were 16 July and 1 August, and harvest dates were 5 October and 11 October for the Edisto and Youngblood locations, respectively. In 1997, first-bloom plant sample dates were 14 July and 15 July for the Edisto and Youngblood locations, respectively. Harvest samples were gathered 7 d before machine harvest on 21 October and 20 October for the Edisto and Youngblood locations, respectively.

At each sample date, five plants were randomly selected from rows 1 through 4 (at least one plant selected from each row), excavated from the soil with a spade and removed from the field to be evaluated. Root systems were separated from the plants at the soil line and carefully rinsed with water to remove soil clinging to the roots. The five root systems were weighed together and an estimated mean fresh weight was determined. Taproot lengths were measured individually, and mean length was determined. Where CLN damage to the taproot resulted in a bifurcate root, the length of the longest root of the split taproot was determined.

Individual shoot (entire aboveground plant mass) weights were determined for each of the five plants. Numbers of monopodial and sympodial nodes on the main stem were determined. The uppermost plant node was recognized as containing the youngest, fully expanded leaf near the shoot apex. Positions of monopodial and sympodial branches on the main axis were recorded. Fruit distribution on each sympodium was recorded according to the position of squares, flowers, and bolls retained by the plant (Kerby et al., 1990; Oosterhuis, 1990; Pettigrew, 2004). Fruit retention percentages were calculated for the monopodia and sympodia.

Following fresh weight and plant mapping measurements, plant samples were dried in a forced-air dryer at 45 ºC for at least 48 h to obtain dry root and shoot weights.

**Yield.** Yield was determined by two methods. In the first method, seed cotton was harvested from the center two rows of each plot using a spindle picker. Plots were harvested on 13 November and 14 November in 1996, and on 12 November and 10 November in 1997 at the Edisto and Youngblood locations, respectively. Final yields were adjusted to kg lint $ha^{-1}$. Percentage of lint was determined by ginning a 400-g sub-sample from each plot.

Prior to mechanical picking, yield was also determined by handpicking 3 m of row from one of the center two rows (same two rows that were mechanically harvested) in each plot. Picking was initiated when approximately 50% of the bolls at each location were fully open as estimated by visual observation. Plots were harvested weekly until 100% of the bolls were picked. Handpicking dates at Edisto were 11 October, 18 October, 25 October, and 8 November in 1996 and at Youngblood were 14 October, 21 October, 28 October, and 8 November in 1996. In 1997, plots were handpicked on 3 October and 10 October at both locations. Seed cotton picked at each harvest date was weighed, ginned, and adjusted to kg lint $ha^{-1}$.

**Maturity.** Cotton maturity was approximated by the fumigation affects on the onset of reproductive growth as marked by the node number of the first fruiting branch on the main stem measured at midseason and at harvest. Maturity was also measured by the percentage of harvested lint available at each sequential harvest date as listed above (Meredith et al., 1997; Pettigrew, 2004).

**Statistics.** Data were evaluated using analysis of variance (PROC ANOVA; ver. 6; SAS Institute; Cary, NC). Means of CLN population densities and growth and yield parameters of cotton in F and NF plots across years and locations were averaged when year by location interactions were not significant. Means were separated using a multiple comparison test of the least significant difference at $P \leq 0.05$.

## RESULTS

**Nematode population densities.** Densities of CLN at planting were significantly greater at the Edisto than the Youngblood location in both years (Table 1). Both soil and total CLN population densities were significantly reduced in fumigated than non-fumigated plots. The magnitude of reduction in population densities caused by fumigation was variable among year and location. Fumigation resulted in significant reductions in CLN population densities not only at planting but also at harvest (Table 1). At Edisto, at-planting CLN populations exceeded 100 CLN per 100 $cm^3$ soil in the NF plots in both years. At Edisto, F plots exhibited a mean reduction in CLN population densities of 87% and 77% compared with

NF plots sampled at planting and at harvest, respectively. In 1996, Youngblood CLN population densities increased more than 6-fold in the NF plots compared with F plots; however, NF populations increased less than 2-fold compared with the F plots in 1997. Populations of CLN recovered from the soil root fraction represented up to 50% of the total at planting (Youngblood in 1996) and 66% at harvest (Edisto in 1996). The total CLN recovered at harvest for F plots was below the established fall damage threshold of 50 in both years at all locations with exception of Edisto (92 CLN 100 cm soil$^{-1}$) in 1996.

**Yield.** Growing conditions in 1996 and 1997 were very different. Total rainfall during the 1996 growing season was 562 and 498 mm at the Edisto and Youngblood locations, respectively. In 1997, 824 mm of rain fell at both locations. From late August through September in 1996, drought conditions oc-

**Table 1. Recovery of *Hoplolaimus columbus* from soil and root fractions of 100 cm$^3$ soil of plots either non- fumigated (NF) or fumigated (F) with 56 L ha$^{-1}$ 1,3-dichloropropene at two location in two years and results of the analysis of variance**

| Year | CLN (count 100 cm soil$^{-1}$) [y] | | | | | |
|---|---|---|---|---|---|---|
| Location | At-planting | | | Harvest | | |
| Treatment | Soil | Root | Total | Soil | Root | Total |
| **1996** | | | | | | |
| Youngblood | | | | | | |
| F | 7 | 7 | 14 | 41 | 8 | 49 |
| NF | 16* | 15* | 31* | 141* | 60* | 201* |
| Edisto | | | | | | |
| F | 7 | 0 | 7 | 44 | 38 | 92 |
| NF | 110* | 6 | 116* | 170* | 199* | 369* |
| **1997** | | | | | | |
| Youngblood | | | | | | |
| F | 5 | 1 | 6 | 9 | 8 | 17 |
| NF | 15* | 2 | 17* | 8 | 20 | 28 |
| Edisto | | | | | | |
| F | 21 | 1 | 22 | 7 | 25 | 32 |
| NF | 111* | 14* | 125* | 49* | 97* | 146* |

| | | Mean squares | | | | | |
|---|---|---|---|---|---|---|---|
| | | At-planting | | | Harvest | | |
| Source of variation[z] | df | Soil | Root | Total | Soil | Root | Total |
| Year (Y) | 1 | 117 | 146 | 2 | 125,200*** | 29,544*** | 276,381*** |
| Location (L) | 1 | 414,128*** | 12 | 50,383*** | 5,761* | 82,411*** | 131,752*** |
| Y*L | 1 | 477226*** | 1,086 | 3,189* | 82 | 7,000 | 5,569 |
| Rep(Y*L) | 36 | 1,244 | 35 | 1,550 | 2,834 | 3,793 | 8,356 |
| Fumigation[z] (F) | 1 | 53,838*** | 941 | 69,014*** | 86,551*** | 105,820*** | 383,774*** |
| F*Y | 1 | 146 | 0 | 153 | 40,673*** | 20,160** | 118,104*** |
| F*L | 1 | 36,727*** | 89 | 40,437*** | 5,578 | 34,184*** | 67,377*** |
| F*Y*L | 1 | 204 | 229 | 1 | 401 | 2,776 | 1,066 |
| Error B | 36 | 841 | 32 | 1,058 | 2,025 | 3,621 | 6,272 |

[y] Total = soil + root. For values within a column for each year and location, *, **, *** indicate significant difference at $P \leq 0.10$, $P \leq 0.05$, and $P \leq 0.01$, respectively.

[z] Y, L, and Y*L were tested using Rep(Y*L) as the error term. F, F*Y, F*L, and F*Y*L were tested using Error B as the error term.

curred at each location. Since locations were only 4.8 km apart, temperatures at the two fields were assumed to be the same.

Yield was significantly ($P \leq 0.05$) less in NF plots than in F plots at both locations and in both years (Table 2). Yield losses across both locations were 17% and 25% in 1996 and 1997, respectively. There was a significant ($P \leq 0.01$) year by location interaction detected for yield. Edisto yields were 216 kg ha$^{-1}$ greater in 1997 than in 1996, whereas yields at Youngblood were 151 kg ha$^{-1}$ less in 1997 than 1996.

**Table 2. Lint yield of LA887 cotton either nonfumigated (NF) or fumigated (F) with 56 L ha$^{-1}$ 1,3-dichloropropene for suppression of *Hoplolaimus columbus* at two locations in two years and results of the analysis of variance**

| Year | Yield (kg ha $^{-1}$) [y] | |
|---|---|---|
| Location | F | NF |
| 1996 | | |
| Youngblood | 1038** | 864 |
| Edisto | 1051** | 875 |
| 1997 | | |
| Youngblood | 887** | 666 |
| Edisto | 1267** | 967 |

| Source of variation[z] | df | Mean squares |
|---|---|---|
| Year (Y) | 1 | 9,461 |
| Location (L) | 1 | 414,128*** |
| Y*L | 1 | 477,226*** |
| Rep(Y*L) | 36 | 24355 |
| Fumigation (F) | 1 | 779,730*** |
| F*Y | 1 | 34778 |
| F*L | 1 | 5610 |
| F*Y*L | 1 | 6171 |
| Error B | 36 | 16164 |

[y] For values within a year and location , *,**,*** indicates significance at $P \leq 0.10$, $P \leq 0.05$, and $P \leq 0.01$, respectively.

[z] Y, L, and Y*L were tested using Rep(Y*L) as the error term. F, F*Y, F*L, and F*Y*L were tested using Error B as the error term.

**Cotton maturity as determined by percentage of harvested lint.** The harvested lint picked at four weekly harvests in 1996 and two weekly harvests in 1997 illustrate the affects of CLN on cotton maturity. The mean harvested lint at first pick ranged from 46 to 85% across years, locations, and treatments (Table 3). In three of the four locations, over both years, yields were greater at first pick in the F plots than in the NF plots. In 1996, the F and NF plots at the Edisto location were 74 and 57% of the lint harvested at first pick, respectively. Lint harvested in the F plots at the second, third, and final pickings represented 14, 10, and 2% of the total lint. In comparison, lint harvested from the NF plots at the second, third, and final pickings were 17%, 25%, and 1%, respectively, of the total lint harvested from the F plots. At the third picking, the F and NF plots harvested contained 10 and 25%, respectively, of the total lint for the season at Edisto in 1996.

**Cotton maturity as determined by plant mapping at mid-season.** In general, mid-season mean plant height, and dry shoot and root weights were greater in the F than the NF plots (Table 4). Fumigated plots had taller ($P \leq 0.01$) plants than NF plots. The 20% increase in plant height recorded at Edisto in 1997 versus the 10% increase at Edisto in 1996 resulted in a significant ($P \leq 0.01$) year by location interaction. Although the average number of total plant nodes (16.1 and 15.5 for F and NF plots, respectively) across both years and locations were not different, there was a significant ($P \leq 0.10$) fumigation effect. In 1997, the F plots at the Edisto location contained plants with more nodes. Fumigation resulted in greater height-to-node ratios than in NF plots. Significantly greater mid-season height-to-node ratios in the F plots were caused by longer internode lengths of cotton plants grown in the F versus NF plots.

In three out of four locations across years, fumigation resulted in significantly ($P \leq 0.05$) greater dry shoot weights compared with cotton cropped in NF plots. A significant ($P \leq 0.01$) fumigation affect was recorded for root length at Youngblood in 1996 and Edisto in 1997, wherein root length was increased by as much as 11% and 30%, respectively. In all cases, cotton dry root weight was increased in F plots, albeit at varying amounts dependent on year and location. The percentage increase in dry root weight as a result of fumigation at Youngblood was 43% in 1996 and 35% in 1997, while at Edisto it was 53% in 1996 and 56% in 1997, resulting in a significant ($P \leq 0.01$) year by location interaction.

At each location within each year, the number of monopodial branches was significantly ($P \leq 0.01$) less in the F versus the NF plots. Fumigation resulted in a significantly ($P \leq 0.01$) lower number of monopodia (5.7) on the main-stem compared with cotton grown in nonfumigated plots (6.7 monopodia) at Edisto in

1996. The position of the first-fruiting branch was significantly ($P \leq 0.01$) higher on plants grown in the NF plots than in the F plots, thereby marking a delay in the onset of the first fruiting or sympodial branch on CLN infested plants. In addition, the plants grown in the F (10.1 sympodia) plots contained significantly ($P \leq 0.05$) more mean sympodial branches than plants grown in NF (8.8 sympodia) plots.

**Cotton maturity as determined by plant mapping at harvest.** Mean plant heights at-harvest were significantly greater ($P \leq 0.05$) for plants grown in F rather than NF plots across locations and years (Table 5). Mean total nodes across both years and locations were not significantly different between treatments. Fumigation resulted in greater height-to-node ratios than in NF plots. Significantly greater

**Table 3. Grams of lint available per three meter of row at four bi-weekly harvests in 1996 or two weekly harvests in 1997 of LA887 cotton grown in plots either nonfumigated (NF) or fumigated (F) with 56 L ha$^{-1}$ 1,3-dichloropropene for suppression of *Hoplolaimus columbus* Sher at two locations and results of the analysis of variance**

| Year | Lint harvested (g) [y] | | | |
|---|---|---|---|---|
| Location | | | | |
| Treatment | First picking | Second picking | Third picking | Final picking |
| 1996 | | | | |
| Youngblood | | | | |
| F | 177*** | 57 | 52 | 3.6** |
| NF | 99 | 46 | 69 | 3 |
| Edisto | | | | |
| F | 271*** | 50 | 38*** | 5.6** |
| NF | 154 | 47 | 68 | 3 |
| 1997 | | | | |
| Youngblood | | | | |
| F | 238* | 52** | 0 | 0 |
| NF | 180 | 31 | 0 | 0 |
| Edisto | | | | |
| F | 213 | 67 | 0 | 0 |
| NF | 171 | 64 | 0 | 0 |

| | | Mean squares | | | |
|---|---|---|---|---|---|
| Source of variation[z] | df | First picking | Second picking | Third picking | Final picking |
| Year (Y) | 1 | 11,792* | 285 | - | - |
| Location (L) | 1 | 15,882** | 2,042** | 528 | 127 |
| Y*L | 1 | 39,151*** | 3,586*** | NS | NS |
| Rep(Y*L) | 36 | 3,619 | 882*** | 528 | 1,244** |
| Fumigation (F) | 1 | 104,519*** | 1,786** | 5,245*** | 6,232*** |
| F*Y | 1 | 10,992* | 97 | - | - |
| F*L | 1 | 574 | 935 | 360 | 561 |
| F*Y*L | 1 | 3,625 | 145 | n/a | n/a |
| Error B | 36 | 3,715 | 345 | 407 | 587 |

[y] For values within a column for each year and location, *, **, *** indicates significance at $P \leq 0.10$, $P \leq 0.05$, and $P \leq 0.01$, respectively.

[z] Y, L, and Y*L were tested using Rep(Y*L) as the error term. F, F*Y, F*L, and F*Y*L were tested using Error B as the error term.

at harvest height-to-node ratios in the F plots (0.3 to 0.6) reflected longer (as much as 13% greater) internode lengths of cotton plants grown in the F versus NF plots.

A significant ($P \leq 0.01$) fumigation by year interaction occurred for dry shoot weight. Fumigation increased shoot weight by a greater percentage in 1997 (37%) than in 1996 (7%). More specifically, percentage increase in dry shoot weights were 31% at Youngblood and 23% at Edisto in the F versus NF plots. Mean dry root weights were significantly ($P \leq 0.01$) greater in F (13 g) versus NF (11 g) plots only in 1997, resulting in a fumigation by year interaction. More specifically, fumigation in 1997 resulted in dry

**Table 4. Mid-season plant height, total nodes, height-to-node ratio (HNR), dry shoot (DS) weight, root length, dry root (DR) weight, and number of both sympodial and monopodial branches of LA 887 cotton grown in plots either nonfumigated (NF) or fumigated (F) with 56 L ha$^{-1}$ 1,3-dichloropropene for suppression of *Hoplolaimus columbus* Sher at two locations in each of two years and results of the analysis of variance**

| Year / Location / Treatment | Plant characteristic[x] | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Height (cm) | Total nodes (no.) | HNR | DS weight (g) | Root length (cm) | DR weight (g) | Sympodial branches (no.) | Monopodial branches (no.) |
| **1996** | | | | | | | | |
| **Youngblood** | | | | | | | | |
| **F** | 78* | 16.0 | 4.9*** | 39** | 35*** | 5.0*** | 9.3** | 6.7** |
| **NF** | 69 | 15.6 | 4.4 | 26 | 27 | 3.5 | 8.1 | 7.5 |
| **Edisto** | | | | | | | | |
| **F** | 65*** | 16.0 | 4.1*** | 18 | 22 | 2.9*** | 10.3*** | 5.7*** |
| **NF** | 59 | 15.8 | 3.7 | 12 | 21 | 1.9 | 9.1 | 6.7 |
| **1997** | | | | | | | | |
| **Youngblood** | | | | | | | | |
| **F** | 77*** | 15.5 | 5.0*** | 45** | 30 | 5.2*** | 10.1* | 6.4*** |
| **NF** | 68 | 15.3 | 4.5 | 36 | 29 | 3.9 | 8.7 | 6.6 |
| **Edisto** | | | | | | | | |
| **F** | 80*** | 16.1* | 5.0** | 56** | 30** | 5.0*** | 10.8*** | 5.3*** |
| **NF** | 67 | 15.4 | 4.4 | 35 | 27 | 3.2 | 9.4 | 6.0 |

| Source of variation[z] | df | Mean squares | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Height | Total nodes | HNR | DS weight | Root length | DR weight | Sympodial branches | Monopodial branches |
| **Year (Y)** | 1 | 611*** | 2.0 | 4.000*** | 7,197*** | 112*** | 19*** | 7.0*** | 14.000*** |
| **Location (L)** | 1 | 573*** | 0.4 | 3.000*** | 733*** | 563*** | 26*** | 11.0*** | 7.000*** |
| **Y*L** | 1 | 569*** | 0.4 | 2.000*** | 2,202*** | 394*** | 10*** | 0.5 | 2.000** |
| **Rep(Y*L)** | 36 | 83** | 1.0 | 0.300 | 73 | 12 | 1 | 1.0 | 1.000 |
| **Fumigation (F)** | 1 | 1,530*** | 2.0* | 4.000*** | 2,671*** | 200*** | 37*** | 29.0*** | 15.000*** |
| **F*Y** | 1 | 29 | 0.1 | 0.100 | 189* | 20 | 1 | 0.1 | 0.001 |
| **F*L** | 1 | 6 | 0.3 | 0.002 | 56 | 21 | 1 | 0.1 | 0.100 |
| **F*Y*L** | 1 | 79 | 1.0 | 0.140 | 385** | 75** | 0 | 0.1 | 0.400 |
| **Error B** | 36 | 42 | 0.7 | 0.200 | 60 | 13 | 1 | 0.9 | 0.400 |

**[y] For values within a column for each year and location, *,**,*** indicates significant difference at $P \leq 0.10$, $P \leq 0.05$, and $P \leq 0.01$, respectively.**

**[z] Y, L, and Y*L were tested using Rep(Y*L) as the error term. F, F*Y, F*L, and F*Y*L were tested using Error B as the error term.**

root weights approximately 20% greater than that of plants grown in the NF plots.

At harvest, a mean total of six monopodia were measured for both treated and nontreated plots. The total of at-harvest sympodial branches also was not different between treatments, as mean total sympodia were 14 for plants either grown in F or NF plots.

**Location of harvestable bolls as determined by plant mapping.** Averaged across both years and locations, there were significantly ($P \leq 0.01$) more (36%) open bolls in the F plots than in the NF plots (Table 6). There were significantly ($P \leq 0.01$) more open bolls in F than NF plots on sympodial branches. Fumigation also resulted in more ($P \leq 0.10$) monopo-

**Table 5. At-harvest plant height, total nodes, height-to-node ratio (HNR), dry shoot (DS) weight, root length, dry root (DR) weight, and number of both sympodial and monopodial branches of LA 887 cotton grown in plots either non-fumigated (NF) or fumigated (F) with 56 L ha$^{-1}$ 1,3-dichloropropene for suppression of *Hoplolaimus columbus* Sher at two locations in each of two years and results of the analysis of variance**

| Year / Location / Treatment | Plant characteristic[y] | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Height (cm) | Total nodes (no.) | HNR | DS weight (g) | Root length (cm) | DR weight (g) | Monopodial branches (no.) | Sympodial branches (no.) |
| **1996** | | | | | | | | |
| **Youngblood** | | | | | | | | |
| **F** | 92* | 18.0 | 5.1** | 85 | 42 | 13 | 11 | 7 |
| **NF** | 80 | 18.0 | 4.5 | 92 | 41 | 13 | 11 | 7 |
| **Edisto** | | | | | | | | |
| **F** | 114* | 21.0 | 5.4*** | 149 | 42 | 20 | 15 | 6 |
| **NF** | 105 | 21.0 | 5.1 | 133 | 41 | 21 | 15 | 6 |
| **1997** | | | | | | | | |
| **Youngblood** | | | | | | | | |
| **F** | 101*** | 20** | 5.2*** | 101*** | 37 | 10*** | 14 | 6 |
| **NF** | 85 | 18.0 | 4.7 | 70 | 36 | 8 | 13 | 5 |
| **Edisto** | | | | | | | | |
| **F** | 135*** | 21.0 | 6.3** | 170** | 37 | 16*** | 16 | 5 |
| **NF** | 121 | 21.0 | 5.7 | 131 | 37 | 13 | 16 | 5 |

| Source of variation[z] | df | Mean squares | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Height | Total nodes | HNR | DS weight | Root length | DR weight | Sympodial branches | Monopodial branches |
| **Year (Y)** | 1 | 3,160*** | 7*** | 4*** | 242 | 425*** | 507*** | 50*** | 19*** |
| **Location (L)** | 1 | 16,262*** | 122*** | 12*** | 66,249*** | 3 | 932*** | 166*** | 4*** |
| **Y*L** | 1 | 574 | 2.0 | 2*** | 741 | 1 | 10 | 5*** | 1.00 |
| **Rep(Y*L)** | 36 | 116 | 2** | 0.2 | 758 | 29 | 7 | 1.0 | 1.00 |
| **Fumigation (F)** | 1 | 2,860*** | 2** | 6*** | 7,332*** | 11 | 10 | 2.0 | 0.10 |
| **F*Y** | 1 | 104 | 0.3 | 0.4 | 4,363** | 1 | 69*** | 0.2 | 0.01 |
| **F*L** | 1 | 36 | 3** | 0.1 | 1,085 | 1 | 0.2 | 0.2 | 2* |
| **F*Y*L** | 1 | 3 | 0.6 | 0.4 | 307 | 0.5 | 5 | 0.3 | 0.04 |
| **Error B** | 36 | 92 | 0.8 | 0.2 | 662 | 23 | 7 | 0.9 | 0.50 |

[y] **For values within a column for each year and location, *,**,** indicates significant difference at $P \leq 0.10$, $P \leq 0.05$, and $P \leq 0.01$, respectively.**

[z] **Y, L, and Y*L were tested using Rep(Y*L) as the error term. F, F*Y, F*L, and F*Y*L were tested using Error B as the error term.**

dial bolls open at harvest only at Edisto in 1996 and Youngblood in 1997, resulting in a significant ($P < 0.01$) year by location interaction. NF plots had 24% fewer total open bolls per plant averaged across years and locations compared with F plots.

Open bolls increased on sympodial branches 1-5 and 6-10 in the F versus NF plots (Table 6). The percentage increase ($P \leq 0.05$) in open bolls on branches 1-5 at harvest as a result of fumigation ranged from 32% to 65%, except for Edisto (2%, not significant) in 1997 resulting in a year by location interaction ($P \leq 0.05$). On branches 6-10, fumigation resulted in a 82% and 28% increase in open bolls only at Edisto in 1996 and 1997, respectively, resulting in a fumigation by location interaction ($P \leq 0.10$).

**Table 6. At-harvest total number of sympodial and monopodial open bolls located on sympodial branches 1-5, 6-10, 11-15, and 1-15 of LA887 cotton grown in plots either nonfumigated (NF) or fumigated (F) with 56 L ha$^{-1}$ 1,3-dichloropropene for suppression of *Hoplolaimus columbus* Sher at two locations in each of two years and results of the analysis of variance**

| Year / Location / Treatment | No. of harvestable bolls at each location | | | | | | No. bolls | | |
|---|---|---|---|---|---|---|---|---|---|
| | Sympodial bolls | Monopodial bolls | Total bolls | Branches 1-5 | Branches 6-10 | Branches 1-15 | Position 1 | Position 2 | Positions 1+2 |
| **1996** | | | | | | | | | |
| **Youngblood** | | | | | | | | | |
| **F** | 5.0*** | 1.0 | 6.0*** | 3.6** | 0.5 | 4.1 | 3.0 | 1.0 | 4.0* |
| **NF** | 3.0 | 1.0 | 4.0 | 2.8 | 0.5 | 3.3 | 3.0 | 0.5 | 3.5 |
| **Edisto** | | | | | | | | | |
| **F** | 7.0*** | 2.0* | 9.0*** | 5.6** | 2.0*** | 7.6** | 5.0*** | 3.0*** | 8.0*** |
| **NF** | 4.0 | 1.0 | 5.0 | 3.4 | 1.1 | 4.5 | 3.0 | 1.0 | 4.0 |
| **1997** | | | | | | | | | |
| **Youngblood** | | | | | | | | | |
| **F** | 8.0*** | 2.0* | 9.0*** | 5.0*** | 2.7 | 7.8** | 6.0 | 2.0** | 8.0*** |
| **NF** | 6.0 | 1.0 | 7.0 | 3.8 | 2.2 | 6.3 | 5.0 | 1.0 | 6.0 |
| **Edisto** | | | | | | | | | |
| **F** | 10.0 | 1.0 | 11.0 | 4.6 | 4.6** | 10.4 | 8.0 | 2.0 | 10* |
| **NF** | 9.0 | 1.0 | 10.0 | 4.5 | 3.6 | 8.8 | 6.0 | 2.0 | 8.0 |

| Source of variation[z] | df | Mean squares | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Sympodial bolls | Monopodial bolls | Total bolls | Branches 1-5 | Branches 6-10 | Branches 1-15 | Position 1 | Position 2 | Positions 1+2 |
| **Year (Y)** | 1 | 186*** | 0.10 | 179.0*** | 5* | 86.0** | 186.00*** | 115.000*** | 3.0* | 157.00*** |
| **Location (L)** | 1 | 65*** | 0.20 | 70.0*** | 6* | 30.0** | 90.00*** | 26.000*** | 8.0* | 62.00*** |
| **Y*L** | 1 | 2 | 4.00*** | 0.2 | 8** | 1.0 | 0.01 | 4.000 | 1.0 | 1.0 |
| **Rep(Y*L)** | 36 | 2 | 1.00 | 4.0 | 2 | 0.4 | 3.00 | 1.000 | 1.0 | 3.0 |
| **Fumigation (F)** | 1 | 35*** | 3.00*** | 58.0*** | 18*** | 4.0*** | 52.00*** | 16.000*** | 10.0*** | 52.00*** |
| **F*Y** | 1 | 1 | 0.02 | 1.0 | 2 | 0.3 | 0.03 | 0.002 | 0.3 | 0.3 |
| **F*L** | 1 | 2 | 0.10 | 2.0 | 1 | 2.0* | 11.00* | 0.300 | 0.3 | 1.0 |
| **F*Y*L** | 1 | 4 | 0.30 | 7.0 | 3 | 0.4 | 2.00 | 0.400 | 1.0 | 0.0 |
| **Error B** | 36 | 3 | 0.40 | 4.0 | 2 | 0.6 | 3.20 | 1.600 | 0.7 | 3.0 |

[y] For values within a column for each year and location, *,**,*** indicates significant difference at $P \leq 0.10$, $P \leq 0.05$, and $P \leq 0.01$, respectively.

[z] Y, L, and Y*L were tested using Rep(Y*L) as the error term. F, F*Y, F*L, and F*Y*L were tested using Error B as the error term.

There was a significant main effect of year on the number of open bolls at first- and second-positions. In 1997, more total sympodial open bolls were at first- and second-position than in 1996 (Table 6). Fumigated plots had more first- and second-position bolls than NF plots over both years and locations. Fumigation increased first-position bolls by 33% compared with NF plots. Plants grown in F plots had 78% more second-position bolls than plants grown in NF plots.

**Boll retention as determined by position on sympodial branches.** Mean total (representing both monopodial and sympodial bolls) open boll retention (46%) was not significantly affected by fumigation (Table 7). Position 1 boll retention (64%) averaged over years, locations, and treatments was not differ-

**Table 7. Total retention of harvestable sympodial bolls located at positions 1, 2, and 1+2 of LA887 cotton grown in plots either nonfumigated (NF) or fumigated (F) with 56 L ha$^{-1}$ 1,3-dichloropropene for suppression of *Hoplolaimus columbus* Sher at two locations in each of two years and results of the analysis of variance**

| Year | Boll retention (%)[y] | | | |
|---|---|---|---|---|
| Location | | | | |
| Treatment | Position 1 | Position 2 | Positions 1+2 | Total per plant |
| **1996** | | | | |
| Youngblood | | | | |
| F | 67 | 35* | 51*** | 41 |
| NF | 61 | 28 | 45 | 39 |
| Edisto | | | | |
| F | 63 | 51*** | 57** | 46 |
| NF | 64 | 41 | 53 | 44 |
| **1997** | | | | |
| Youngblood | | | | |
| F | 66 | 34 | 52 | 49 |
| NF | 62 | 31 | 45 | 47 |
| Edisto | | | | |
| F | 65 | 49*** | 57** | 52 |
| NF | 64 | 30 | 47 | 49 |

| | | Mean squares | | | |
|---|---|---|---|---|---|
| Source of variation[z] | df | Position 1 | Position 2 | Positions 1+2 | Total per plant |
| Year (Y) | 1 | 3 | 1,825*** | 1,155*** | 207* |
| Location (L) | 1 | 31 | 215* | 6 | 777*** |
| Y*L | 1 | 2 | 22 | 29 | 43 |
| Rep(Y*L) | 36 | 110 | 317*** | 93 | 48 |
| Fumigation (F) | 1 | 118 | 487** | 454*** | 1 |
| F*Y | 1 | 117 | 145 | 23 | 43 |
| F*L | 1 | 1 | 4 | 5 | 65 |
| F*Y*L | 1 | 66 | 46 | 3 | 71 |
| Error B | 36 | 156 | 75 | 60 | 52 |

[y] For values within a column for each year and location, *,**,*** indicates significance at $P \leq 0.10$, $P \leq 0.05$, and $P \leq 0.01$, respectively.

[z] Y, L, and Y*L were tested using Rep(Y*L) as the error term. F, F*Y, F*L, and F*Y*L were tested using Error B as the error term.

ent among variables. Position 2 boll retention was significantly ($P \leq 0.01$) greater in the F (42%) plots than in the NF (33%) plots. Cumulative boll retention at Positions 1 and 2 for plants grown in F plots were on average 10% greater ($P \leq 0.05$) than those grown in NF plots.

## DISCUSSION

Fumigation significantly reduced CLN population densities at planting by an average of 86% in 1996 and 80% in 1997. These reductions in nematode densities were expected since use of lower rates of 1,3-D have been demonstrated to cause similar reductions (Mueller and Sullivan, 1988; Koenning and Bowman, 2005). In this study, season-long suppression of CLN was observed. In a similar study, a substantially lower rate of 1,3-D rate (46 L $ha^{-1}$) than that applied in this study (56 L $ha^{-1}$) also resulted in season-long suppression of CLN population growth (Koenning and Bowman, 2005). Densities of CLN at harvest in three of the four fields were an average of 75% lower in F plots than NF plots.

The population densities of CLN at planting varied among locations and years. An increase in population densities was observed in all plots both years. The percentage increase was greater in F than NF plots as measured at harvest. This was especially true for Edisto in 1996 where the difference in at harvest and at planting CLN population densities in F plots was four-times that in the NF plots. Other researchers have reported similar results where nematicides were applied (Schmitt and Bailey, 1990; Mueller and Sullivan, 1988; Schmitt and Imbriani, 1987). With fewer CLN in the F plots, there was less intra-specific competition for feeding sites. This is consistent with data published on root-knot nematode and the soybean cyst (*Heterodera glycines* Ichinohe) nematode (Mueller and Sullivan, 1988).

The CLN damage threshold at planting in cotton is approximately 50 CLN per 100 $cm^3$ of soil (Koenning et al., 1990; Noe, 1993). In both years, the CLN-population densities in NF plots at Edisto were approximately double the CLN damage threshold. These plots sustained yield losses of 17 and 25% in 1996 and 1997, respectively. Koenning and Bowman (2005) reported a maximum mean cotton yield loss of 21.4% in CLN-infested plots. At Youngblood, population densities at planting were one-half to one-third of the damage threshold, but yield losses of 17 and 25% were still observed. This indicates that the CLN damage threshold may be lower than previously reported.

Fumigation reduced but did not eliminate CLN from the soil. Therefore, CLN infection levels of cotton were assumed to be very low in F versus NF plots. Therefore, it was reasonably to compare growth, yield, and maturity of non-infected versus infected plants by comparing F with NF plots. Chlorosis or severe stunting was not observed in NF plots. Within NF plots, growth was uniform. The effects of CLN on plant growth were not evident in the field unless cotton grown in NF plots was compared directly with cotton grown in F plots.

Yield is a function of boll number and boll size per unit area, both of which can be adversely affected by many factors. One factor that is poorly understood is the effect of nematodes, especially CLN, on plant growth. Obviously, CLN feed only on roots, and therefore their effects on cotton growth parameters are indirect. Indirect affects, such as decreased internode length and plant height, of cotton because of root restriction have been documented, whereas others have simply correlated stunted cotton growth as a result of the combined effects of soil compaction and parasitism of CLN on root growth (Smith et al., 1991; Hussey, 1977).

Plant height reductions in CLN-infected cotton illustrate the suppression of the crop growth rate throughout the growing season. Reductions in internode length and the number of main-stem nodes contributed to reductions in plant height. The number of main-stem nodes and height-to-node ratio offer a means to monitor early season crop growth (Bourland et al., 1992). With good fruit retention at midseason, reductions in internode lengths and therefore plant height can be assumed to be influenced by physiological factors outside the scope of this research.

With each additional main-stem node, the number of potential fruiting sites increases and therefore yield potential increases. Yield reductions in the NF plots were caused by a reduction in the total number of open bolls at harvest. Since more than 80% of the open bolls were located at the first- and second-positions on the sympodial branches in the F plots, a greater number of main-stem nodes in the F versus NF plots resulted in a significant increase in first-position bolls in the F versus NF plots. In the NF plots, a greater percentage of yield was reduced in the NF plots because of a significant reduction in boll retention at the second-position on sympodial branches.

Previous researchers reported a delay in the shift from vegetative to reproductive growth in CLN-infected cotton (Mueller et al., 1996). Prolonged vegetative growth is evident by greater number of monopodial branches in the NF than F plots at midseason. Therefore, CLN-infected cotton at midseason is physiologically younger than non-infected cotton and subsequently has a different sink (vegetative versus reproductive growth) than non-infected cotton.

The delay in the transition from vegetative to reproductive growth may be because of the prolonged period of root development. Reductions in both root and shoot weights in NF versus F plots at midseason illustrate effects of CLN on growth of the whole plant. There was no significant difference in root weights at harvest in F versus NF plots; however, shoot weights were significantly greater in the F than the NF plots. The period of root development (vegetative growth) appears to have been maintained longer in the NF than in the F plots, thereby delaying the shift in cotton growth as measured by plant mapping to the reproductive growth phase.

Sequential harvests indicated that crop maturity was delayed in the NF plots. More lint was available by the first-picking date in the F than in the NF plots. Since cotton maintained vegetative growth longer in NF than F plots, a lack of fumigation appears to delay the onset of the boll period in plots where population densities of CLN are dense and remain unmanaged.

The effects of CLN on cotton previously described in refereed journals are not well documented; therefore, additional work is needed to define the effects of CLN on growth, development, and performance of cotton. By understanding which plant growth and yield components are affected by CLN, we can further aid in the development of more productive management schemes involving either cultivar selection, timing of defoliation, or planting dates and can further aid the cotton breeder in the potential development of tolerant cultivars.

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