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Effect of Simultaneous Water Deficit Stress and *Meloidogyne incognita* Infection on Cotton Yield and Fiber Quality

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Abstract: Both water deficit stress and *Meloidogyne incognita* infection can reduce cotton growth and yield, and drought can affect fiber quality, but the effect of nematodes on fiber quality is not well documented. To determine whether nematode parasitism affects fiber quality and whether the combined effects of nematode and drought stress on yield and quality are additive (independent effects), synergistic, or antagonistic, we conducted a study for 7 yr in a field infested with *M. incognita*. A split-plot design was used with the main plot factor as one of three irrigation treatments (low [nonirrigated], moderate irrigation, and high irrigation [water-replete]) and the subplot factor as 0 or 56 l/ha 1,3-dichloropropene. We prevented water deficit stress in plots designated as water-replete by supplementing rainfall with irrigation. Plots receiving moderate irrigation received half the water applied to the water-replete treatment. The severity of root galling was greater in nonfumigated plots and in plots receiving the least irrigation, but the amount of irrigation did not influence the effect of fumigation on root galling (no irrigation × fumigation interaction). The weights of lint and seed harvested were reduced in nonfumigated plots and also decreased as the level of irrigation decreased, but fumigation did not influence the effect of irrigation. Nematodes affected fiber quality by increasing micronaire readings but typically had little or no effect on percent lint, fiber length (measured by HVI), uniformity, strength, elongation, length (based on weight or number measured by AFIS), upper quartile length, or short fiber content (based on weight or number). Micronaire also was increased by water deficit stress, but the effects from nematodes and water stress were independent. We conclude that the detrimental effects caused to cotton yield and quality by nematode parasitism and water deficit stress are independent and therefore additive.

Key words: drought, *Gossypium hirsutum*, interaction, irrigation, micronaire, southern root-knot nematode.

Adequate water availability is considered the most limiting factor to profitable cotton production in the southeastern United States (Dumka et al., 2004), and plant-parasitic nematodes, especially *Meloidogyne incognita*, are the most damaging pathogens of cotton in the United States (Blasingame and Patel, 2013). Both water deficit stress and nematode parasitism in cotton can result in reduced plant growth and yield, and water stress adversely affects cotton fiber quality (Stiller et al., 2005; Wen et al., 2013; Wiggins, et al., 2013). Infection of cotton by *M. incognita* can cause plants to wilt temporarily, which is the same reaction plants have to water deficit stress (O'Bannon and Reynolds, 1965; Kirkpatrick et al., 1995). Wilting from infection is caused in part by anatomical changes in the root as giant cells and galls are formed following infection by the nematode resulting in disruption of the epidermis, cortical tissue, and xylem (Shepherd and Huck, 1989). When susceptible cotton plants are infected by *M. incognita*, water flow through the plant is reduced (Kirkpatrick et al., 1991; Kirkpatrick et al., 1995). In a greenhouse study, water consumption and plant growth were the same for *M. incognita*-infected and noninfected plants when soil moisture was maintained near field capacity but both were significantly reduced when soil moisture was not always maintained at that level (O'Bannon and Reynolds, 1965). Based largely on anecdotal evidence, many farmers and crop advisors believe that increased irrigation can be used to mitigate the damaging effects of *M. incognita* parasitism of cotton. However, research has not determined whether the effects of irrigation (or water deficit stress) and *M. incognita* infection in field-grown cotton are independent of each other, and therefore additive, or if there is a significant interaction (either synergistic or antagonistic).

The soil environment, especially soil water, can affect nematode movement in the soil (Rebois, 1973). Both plant growth and the population dynamics of plant-parasitic nematodes can be affected by soil moisture levels (Brodie and Quattlebaum, 1970; Pitcher, 1975; Freckman et al., 1987). For example, population densities of *Xiphinema americanum* decline at either high or low soil moisture levels (Griffin and Barker, 1966), as do levels of *Belonolaimus longicaudatus* (Robbins and Barker, 1974) and *Paratrichodorus christiei* (Overman, 1964). The effect of irrigation on the population levels of *M. incognita* in cotton has not been studied.

The goal of this research was to evaluate the relationship between the amount of water received by a cotton crop and the amount of damage caused to the crop by *M. incognita*. The specific objectives of this study were (i) to determine whether supplemental irrigation affects cotton plant response to infection by *M. incognita*, and (ii) to determine whether the amount of water cotton receives affects *M. incognita* population densities.

Materials and Methods

A 7-yr-long study was initiated in 2001 at the University of Georgia Gibbs Farm near Tifton, GA. The soil type was a Tifton Loamy Sand (fine, loamy, siliceous, thermic Plinthic Kandiudults; 85% sand, 11% silt, 4% clay; < 1% organic matter). The field was naturally infested with *M. incognita*. A split-plot design with six

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replications was used with main plots being one of three irrigation treatments: irrigated to current recommendations [high irrigation, water replete], irrigated at half of standard [moderate irrigation], or nonirrigated [low irrigation]. Subplots were 1,3-dichloropropene (1,3-D; Telone II [Dow Agrosciences, Indianapolis, IN] at 56.2 L ha^{-1}) or a nontreated control. The irrigation treatments were not applied until the first flower bud formed (first square). Irrigation was applied through drip tape that was laid at the soil surface on one side of the planting row within a few cm of the plant stems. The target for the high irrigation treatment was 2.5 cm of water (rainfall plus irrigation) per week from the first square growth stage until the first open boll except during a 5-wk period beginning the second week after first bloom when plants received 3.8 cm of water. For the water-replete (high irrigation) standard treatment, rainfall plus irrigation was sufficient to prevent midday wilting from being observed during the growing season. The moderate irrigation treatment was irrigated at the same time as the high irrigation treatment but only received half as much water, and the nonirrigated treatment was not irrigated at all except in June 2002 when severe drought conditions appeared likely to kill the plants and all plots received 5.0 cm of water during the month. The nematicide treatments were used to provide an estimate of nematode-induced yield loss within each irrigation treatment. The fumigant 1,3-D was injected 40-cm deep 7 to 10 d before planting each year. Each subplot consisted of four 15.2-m-long rows. All plots were planted with Deltapine 'DP458BR' cotton (Delta and Pine Land Company, Scott, MS) on 21 May 2001, 14 May 2002, 13 May 2003, 5 May 2004, 11 May 2005, 4 May 2006, and 11 May 2007.

The data collected included *M. incognita* population levels at planting, early midseason (and late midseason in most years), and following harvest; above-ground dry matter weights, yields; and root galling at harvest. Soil samples were collected on 28 May, 25 June, 31 July, and 26 November 2001; 11 July and 4 December 2002; 28 May, 8 July, and 4 November 2003; 13 May, 24 June, 4 August, and 15 October 2004; 24 May, 8 July, 31 August, and 31 October 2005; 18 May, 7 July, 16 August, and 18 October 2006; and 29 May, 17 July, 7 September, and 1 November 2007. Soil samples consisted of a composite of 10 to 12 cores per plot (2.5-cm diam. and approximately 20-cm deep) collected from the root zone. Nematodes were extracted from 150-cm^3 soil by centrifugal flotation (Jenkins, 1964). Root galling was evaluated each year on a 0 to 10 scale (root gall index, RGI) within 3 wk following harvest by digging and rating 10 root systems per plot. The scale used was as follows: 0 = no galling, 1 = 1% to 10% of the root system galled, 2 = 11% to 20% of the roots system galled, etc., with 10 = 91% to 100% of the root system galled.

Two destructive plant samples were taken from each subplot during each growing season to measure above-ground dry matter. At each dry-matter harvest, plants were severed at the soil line and all above-ground plant material was included in the sample. Samples were collected on 25 July and 6 September 2001, 18 July and 9 September 2002, 31 July and 15 September 2003, 23 July and 9 September 2004, 25 July and 1 September 2005, and 26 July, and 24 August 2006. Dry matter harvests were not collected in 2007. Dry-matter harvests were confined to the center two rows of each subplot, with two meters harvested per row (approximately 25 plants per harvest), and harvest areas were buffered from one another and from row ends by at least 2 m. Fresh weight of the entire sample and also of a subsample (approximately 25% of the entire sample) was determined in the field, and then the subsample was air dried at ambient temperature to a constant weight. Dry weight of the entire sample was then estimated based on the dry weight to fresh weight ratio of the subsample.

A few days before harvesting lint from the plots, whole-plant samples were collected to determine the distribution of cotton bolls on the plants (data not included): those samples removed 3 m of row from each plot. All remaining cotton was harvested from the two center rows of each plot on 13 November 2001, 8 November 2002, 23 October 2003, 6 October 2004, 24 October 2005, 12 October 2006, and 17 October 2007. A subsample of the mechanically harvested cotton was hand ginned to determine the percentages of lint and seed from each plot, and that percentage was used to calculate the kg/ha of lint and of seed for each plot. The lint collected from each plot was submitted to the Fiber and Biopolymer Research Institute at Texas Tech University for fiber quality analysis, which included both High Volume Instrument (HVI; Uster Technologies, Knoxville, TN) analysis and Advanced Fiber Information System (AFIS; Uster Technologies, Knoxville, TN) analyses.

The experiments had a factorial treatment structure with irrigation level and fumigation level as factors. Data were analyzed using the generalized linear mixed models (GLIMMIX) procedure in SAS (SAS Institute, Cary, NC). Data also were evaluated using analysis of covariance (also using the GLIMMIX procedure in SAS) with fumigation as a qualitative variable and nematode population density or root gall ratings (RGI) as a quantitative variable to determine if nematode population density or galling affected measurements of plant growth, yield, or fiber quality. Least squares means were compared by Student's *t*-test using the PDIFF option. For analysis of covariance, fumigation was considered to be a tool that created a range of nematode levels resulting in a range of gall ratings. Data were combined for multiyear analyses, but analyses of individual years also were conducted to give an indication of consistency of results when the combined analysis did not detect differences. In the multiyear analyses, year was considered to be a random variable and differences were considered significant at $P \leq 0.05$.

Results

Monthly rainfall totals and mean soil temperatures at a 10-cm depth from 2001 through 2007 show the monthly and annual variation typical in the southeastern United States (Table 1). Monthly mean soil temperatures were much more consistent among the years than were the monthly rainfall amounts. Plots received irrigation only during the months of June, July, August, and September (Table 1). No irrigation was applied in 2003, so that year was not included in the analyses.

Analyses that combined data from all years indicated that nematode population levels were not affected by irrigation at any point in the growing season (Table 2). Fumigation with 1,3-D reduced population levels for most of the season with only the final sample following harvest showing no difference between fumigated and nonfumigated plots, and irrigation did not influence the effect of fumigation on nematode counts (no irrigation × fumigation interaction) for any sampling date (Table 2). Root galling was significantly reduced by both irrigation and fumigation (Table 2), but the effects were independent (no irrigation × fumigation interaction) when all years were combined for analysis or when years were analyzed independently. The two years in which irrigation had the largest effect on lint yield were 2004 and 2007, and even when only those two years were combined for analysis, there was no irrigation × fumigation interaction affecting root galling.

Differences among treatments were observed in both the first and second dry matter harvests (Table 3). Analyses with data from all years indicated that 1,3-D increased both dry matter harvests but the amount of water applied to plots did not affect dry matter (although irrigation was significant at $P = 0.082$). The level of irrigation did not influence the effect of fumigation (no irrigation × fumigation interaction) for either dry matter harvest when years were combined for analysis or when years were analyzed separately. Covariance analysis (data from all years) found that increased root galling (RGI) was related to reductions in both the first and second dry matter harvest and that the relationship (slope) was the same regardless of the level of irrigation (no RGI × irrigation interaction) (Figs. 1A,B; Table 4). Similarly, there was no RGI × irrigation interaction affecting slope in any year when years were analyzed separately. Increasing nematode counts from the second sampling date were related to decreasing weights of the second dry matter harvest, but not the first dry matter harvest, and the relationship (slope) was the same regardless of the level of irrigation (covariance analysis, data from all years) (Fig. 2A; Table 5). Nematode counts from the first, third, and fourth sampling dates were not significantly related to weights of either the first or second dry matter harvest (covariance analysis, data from all years).

Analyses with data from all years indicated that both 1,3-D and the amount of water applied affected the weight of both lint and seed harvested (Table 3). Applying 1,3-D increased harvest weights. The highest amount of irrigation increased lint and seed weights compared the lowest level of irrigation. The effects of irrigation and fumigation were independent (no irrigation × fumigation interaction) for both lint and seed yields. However, when years were analyzed separately, there was an irrigation × fumigation interaction for lint yield in 2004 at $P = 0.074$. That interaction was because of a difference in the magnitude of the effect of fumigation among the three irrigation treatments where the difference between fumigated and nonfumigated plots was greatest in plots receiving the most water. There was no irrigation × fumigation interaction affecting lint yield when 2004 and 2007, the two years in which irrigation had the largest effect on lint yield, were analyzed together. The percent lint (weight of lint harvested as a percentage of the total harvest weight of lint plus seed) was not affected by irrigation or fumigation and

Table 1. Mean rainfall, irrigation, and soil temperature at 10-cm depth at the Gibbs Farm, Tifton, GA.

	Year						
	2001	2002	2003	2004	2005	2006	2007
Rainfall[a]							
April	10.9	17.0	22.4	25.7	38.4	10.9	2.8
May	1.3	2.8	4.3	14.5	10.4	17.5	0.0
June	45.0	0.5	41.9	72.6	46.7	26.9	38.1
July	22.1	21.6	47.5	14.7	37.6	18.5	23.1
August	11.9	14.7	52.1	13.7	22.4	18.3	45.0
September	20.1	26.7	25.9	94.0	0.3	13.2	17.0
October	16.0	39.1	29.7	6.6	3.8	7.4	19.6
November	5.1	31.8	7.9	25.9	26.7	18.8	5.8
Irrigation by treatment[a]							
June							
High	0.0	5.0	0.0	0.0	0.0	2.5	2.5
Moderate	0.0	5.0	0.0	0.0	0.0	1.3	1.3
Low	0.0	5.0	0.0	0.0	0.0	0.0	0.0
July							
High	10.0	0.0	0.0	5.0	2.5	7.6	5.0
Moderate	5.0	0.0	0.0	2.5	1.3	3.8	2.5
Low	0.0	0.0	0.0	0.0	0.0	0.0	0.0
August							
High	10.0	7.6	0.0	5.0	2.5	7.6	7.6
Moderate	5.0	3.8	0.0	2.5	1.3	3.8	3.8
Low	0.0	0.0	0.0	0.0	0.0	0.0	0.0
September							
High	0.0	2.5	0.0	0.0	3.8	0.0	0.0
Moderate	0.0	1.3	0.0	0.0	1.9	0.0	0.0
Low	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Temperature, monthly means[b]							
April	19.0	21.1	18.8	19.2	18.0	20.1	19.1
May	23.3	23.9	23.5	25.0	23.0	23.0	23.5
June	27.5	26.0	25.4	25.6	26.4	26.2	26.5
July	30.0	27.9	26.1	26.7	28.0	27.9	28.3
August	30.4	27.6	26.0	26.8	28.4	28.1	29.1
September	27.8	26.3	25.1	24.4	27.4	25.6	26.4
October	22.4	23.2	21.4	22.1	23.4	21.3	23.1
November	19.5	16.6	18.0	17.5	18.6	15.8	17.2

[a] Rainfall and irrigation in cm. No irrigation was applied in months not shown.
[b] Temperature (°C) measured at 10-cm depth.

TABLE 2. *Meloidogyne incognita* numbers (per 150 cm^3) in soil at various sampling times and root galling of cotton plants.

Irrigation level[a]	Fumigation[b]	1st Nema Sample[c]	2nd Nema Sample[d]	3rd Nema Sample[e]	4th Nema Sample[f]	RGI[g]
High	+	14 bc	23 bc	257 a	272 a	2.2 d
High	-	24 ab	51 a	371 a	311 a	3.6 abc
Moderate	+	8 b	16 c	229 a	290 a	2.7 cd
Moderate	-	32 ab	43 ab	323 a	318 a	3.8 ab
Low	+	7 c	15 c	265 a	245 a	3.4 bc
Low	-	37 a	39 abc	352 a	322 a	4.4 a
Irrigation *P* =		0.90	0.26	0.69	0.90	0.05
Fumigation *P* =		0.02	0.04	0.25	0.44	0.01
Irrigation × Fumigation Interaction *P* =		0.33	0.93	0.94	0.66	0.66
High		19 a	37 a	314 a	291 a	2.9 b
Moderate		20 a	29 a	308 a	304 a	3.2 ab
Low		22 a	27 a	276 a	283 a	3.9 a
	+	10 b	18 b	250 b	269 a	2.7 b
	-	31 a	44 a	349 a	317 a	3.9 a

[a] High = water replete; Moderate = one-half the amount applied to High; Low = none.
[b] 1,3-dichloropropene at 56 l/ha (+) or 0 l/ha (-)
[c] First sample collected soon after planting. Analyzed using the GLIMMIX procedure in SAS with year as a random variable. Means within a treatment grouping within a column followed by the same letter are not significantly different according to Student's $t_{(0.05)}$ separation of least squares means.
[d] Second sample collected in early midseason.
[e] Third sample collected in late midseason.
[f] Fourth sample collected soon after harvest.
[g] Root gall indices (RGI) evaluated within 3 wk following harvest on a 0–10 scale based on percentage of the root system with galls.

there were no differences among treatments (Table 3). Covariance analysis found that increased root galling was related to reductions in both lint yield and seed yield and that the relationship (slope) was the same regardless of the level of irrigation (no RGI × irrigation interaction) (Figs. 1C,D; Table 4). Similarly, there was no RGI × irrigation interaction on slope in any year when years were analyzed separately. Increasing nematode counts from both the first and second sampling date also were related to reductions in both lint and seed yield, and the relationship (slope) was the same regardless of the level of irrigation (Figs. 2B-E; Table 5). Nematode counts from the third and fourth sampling date were not significantly related to weights of either lint or seed (covariance analysis, data from all years).

Micronaire values were reduced by the application of both irrigation and fumigation resulting in differences among treatments (Table 6), but the effects were independent (no irrigation × fumigation interaction). Similarly, there was no interaction in any year when years were analyzed individually. Covariance analysis found that increased root galling was related to increases in micronaire and that the relationship (slope) was the same regardless of the level of irrigation (no RGI ×

TABLE 3. Cotton plant dry matter weights at midseason; and lint yield, seed yield, and percent lint at harvest.

Irrigation level[a]	Fumigation[b]	1st Dry Matter[c]	2nd Dry Matter	Lint (kg/ha)	Seed (kg/ha)	% Lint
High	+	1.78 a	3.72 a	1583 a	2346 a	40.4 a
High	-	1.37 b	2.97 b	1230 c	1931 cd	39.3 a
Moderate	+	1.69 a	3.70 a	1534 ab	2275 ab	40.2 a
Moderate	-	1.31 b	3.08 b	1245 c	1881 de	40.0 a
Low	+	1.70 a	3.37 ab	1423 b	2117 bc	40.3 a
Low	-	1.35 b	3.00 b	1159 c	1716 e	39.9 a
Irrigation *P* =		0.46	0.40	0.08	0.02	0.84
Fumigation *P* =		0.003	0.01	0.002	0.002	0.21
Irrigation × Fumigation Interaction *P* =		0.95	0.25	0.54	0.95	0.63
High		1.58 a	3.35 a	1407 a	2138 a	39.9 a
Moderate		1.50 a	3.39 a	1390 ab	2078 a	40.1 a
Low		1.53 a	3.19 a	1291 b	1916 b	40.1 a
	+	1.73 a	3.60 a	1513 a	2246 a	40.3 a
	-	1.34 b	3.02 b	1212 b	1843 b	39.7 a

[a] High = water replete; Moderate = one-half the amount applied to High; Low = none.
[b] 1,3-dichloropropene at 56 l/ha (+) or 0 l/ha (-)
[c] Dry matter weights are kg/2 m of row. Analyzed using the GLIMMIX procedure in SAS with year as a random variable. Means within a treatment grouping within a column followed by the same letter are not significantly different according to Student's $t_{(0.05)}$ separation of least squares means.

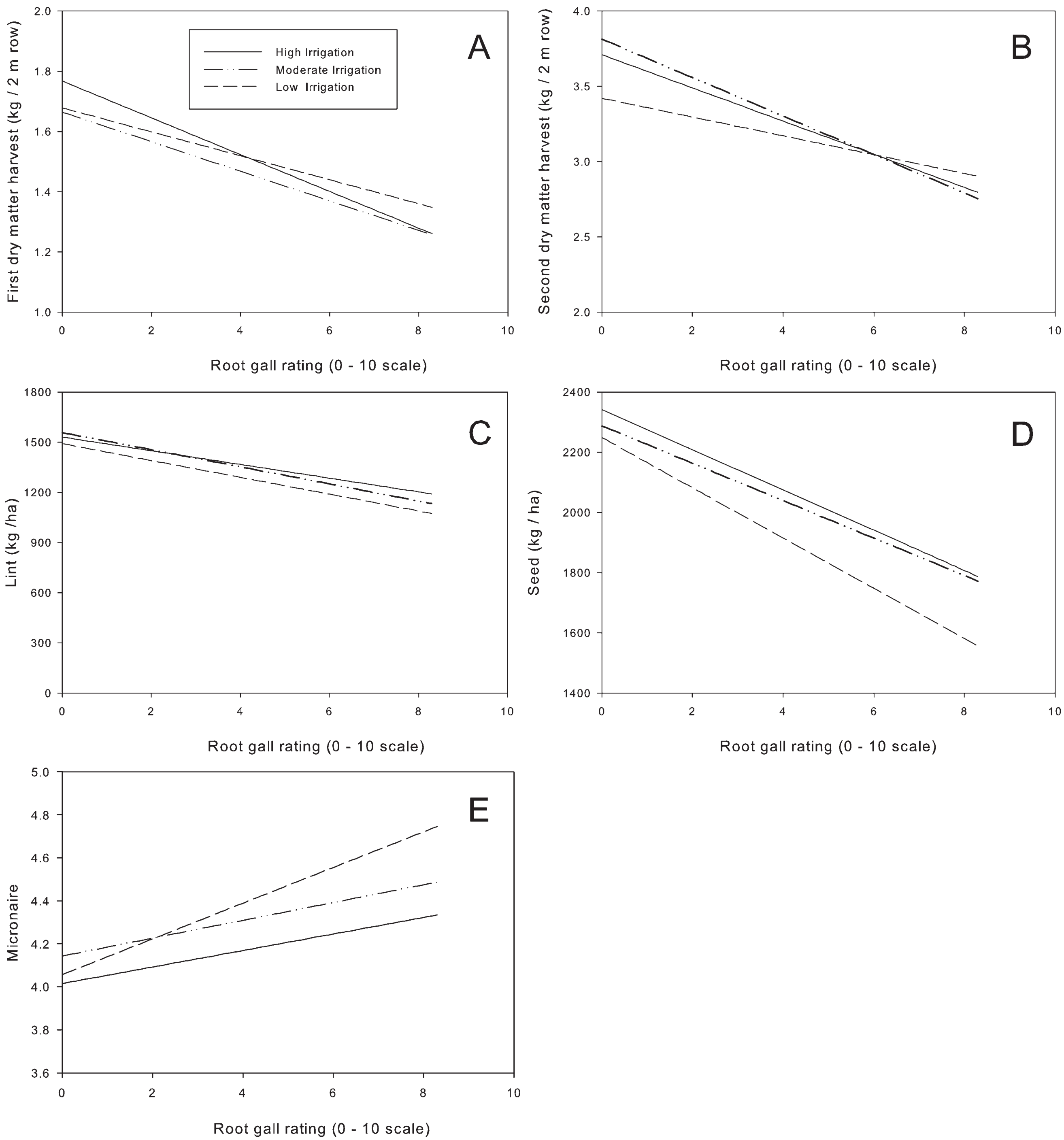

Fig. 1. Relationships between root gall ratings (RGI) and selected cotton growth, yield, and fiber quality characteristics from six years of field testing. Analyses were conducted using the GLIMMIX procedure in SAS with year treated as a random effect. Regression equations are presented in Table 4.

irrigation interaction) (Fig. 1E; Table 4). Similarly, there was no RGI × irrigation interaction on slope in any year when years were analyzed separately. Nematode counts were not significantly related to micronaire on any sampling date (covariance analysis, data from all years) except in 2005 when greater nematode population levels at harvest were related to increased micronaire values. In 2005, increasing nematode population levels were related to the greatest increase in micronaire in plots receiving moderate irrigation.

Fiber length and uniformity as measured by HVI were both increased by irrigation but unaffected by fumigation (Table 6), and fumigation did not influence the effect of irrigation (no irrigation × fumigation interaction) when years were combined for analysis or when years were analyzed separately. Neither fiber

TABLE 4. Regression equations and probabilities for the relationships between root gall indices (RGI) and selected cotton growth, yield, and fiber quality characteristics from six years of field testing.

Variable	Irrigation level	Regression equation[a]
1st dry matter harvest	High	1.767 – (0.061 × RGI)
	Moderate	1.663 – (0.049 × RGI)
	Low	1.677 – (0.040 × RGI)
Irrigation $P = 0.693$		
Root gall index (RGI) $P = 0.050$		
Irrigation × RGI $P = 0.693$		
2nd dry matter harvest	High	3.708 – (0.110 × RGI)
	Moderate	3.812 – (0.128 × RGI)
	Low	3.419 – (0.062 × RGI)
Irrigation $P = 0.430$		
Root gall index (RGI) $P = 0.029$		
Irrigation × RGI $P = 0.642$		
Lint	High	1529.7 – (40.9 × RGI)
	Moderate	1555.7 – (51.1 × RGI)
	Low	1489.2 – (50.3 × RGI)
Irrigation $P = 0.693$		
Root gall index (RGI) $P = 0.050$		
Irrigation × RGI $P = 0.693$		
Seed	High	2341.4 – (66.8 × RGI)
	Moderate	2286.8 – (62.1 × RGI)
	Low	2248.0 – (83.4 × RGI)
Irrigation $P = 0.766$		
Root gall index (RGI) $P = 0.108$		
Irrigation × RGI $P = 0.819$		
Micronaire	High	4.015 – (0.038 × RGI)
	Moderate	4.143 – (0.041 × RGI)
	Low	4.056 – (0.083 × RGI)
Irrigation $P = 0.554$		
Root gall index (RGI) $P = 0.008$		
Irrigation × RGI $P = 0.309$		

[a] Reported probabilities are from covariance analyses using the GLIMMIX procedure in SAS with year as a random effect.

strength nor elongation was affected by irrigation or fumigation (Table 6).

Advanced fiber information system (AFIS) measurements of fiber length, based either on weight (length-w) or number (length-n), indicated no differences among treatments (Table 7). Measurements of short fiber content based on either weight (SFC-w) or number (SFC-n) were not affected by irrigation or by fumigation; however, although there was no irrigation × fumigation interaction, there was a difference in SFC-w between fumigated and nonfumigated plots when the least amount of irrigation was applied (Table 7). Neither the upper quartile length based on weight (UQL-w) nor the immature fiber content (IFC) was affected by irrigation or by fumigation (Table 7). UQL-w differed between the highest and lowest irrigation level in fumigated plots, and IFC differed between the highest and lowest irrigation level in nonfumigated plots, although neither UQL-w nor IFC had an irrigation × fumigation interaction when all years were included in the analysis.

DISCUSSION

In the multiyear analyses presented in this study, year was treated as a random effect instead of a fixed effect, which influences the interpretation of the results. If year is a fixed effect, we can only draw inferences about treatment effects during the set of years in which the experiment was conducted. In contrast, treating year as a random effect allows us to draw inferences about treatment effects in all years rather than just during the years in our study. The more robust analysis with year as a random effect allows greater confidence in the likelihood that treatment effects, differences, and interactions observed during the study also will be observed in future years.

Damage to the cotton crop from nematode parasitism included reducing the first and second dry matter harvests, reducing the weights of both lint and seed harvested, and increasing fiber micronaire readings. In contrast, nematodes typically had little or no effect on percent lint, length, uniformity, strength, elongation, length (based on weight or number), upper quartile length, or short fiber content (based on weight or number). It appears that the damage caused to cotton from *M. incognita* is primarily through reductions in quantity (weights) rather than from reducing fiber quality, although increased micronaire readings in *M. incognita*-damaged plants are a clear exception to that generalization. Micronaire values are a measurement based on the air permeability of a specified plug of cotton fibers, in which low values indicate fine or immature fibers and high values indicate coarse fibers. The price paid for cotton is reduced if micronaire values fall outside the desirable range of 3.5 to 4.9, so micronaire is an important component of fiber quality.

The significant differences identified through factorial analysis also were found in the relationships identified through covariance analysis with increases in root galling leading to decreases in dry matter harvests, lint yield, and seed yield, but increases in micronaire. Root galling had more associations with measurable damage than did nematode counts. Neither mid- nor late-season nematode counts (the third and fourth nematode samples) provided significant regressions (slopes $\neq 0$) with any of the measured variables. However, several relationships similar to those found with root galling were found with nematode levels earlier in the growing season: nematode levels from the second sample date (early midseason) were related to lint yield, seed yield, and both dry matter harvests, but nematode levels on the first sampling date (early season) were only related to lint and seed yield. Greater variability associated with nematode counts from field plots may be partly why

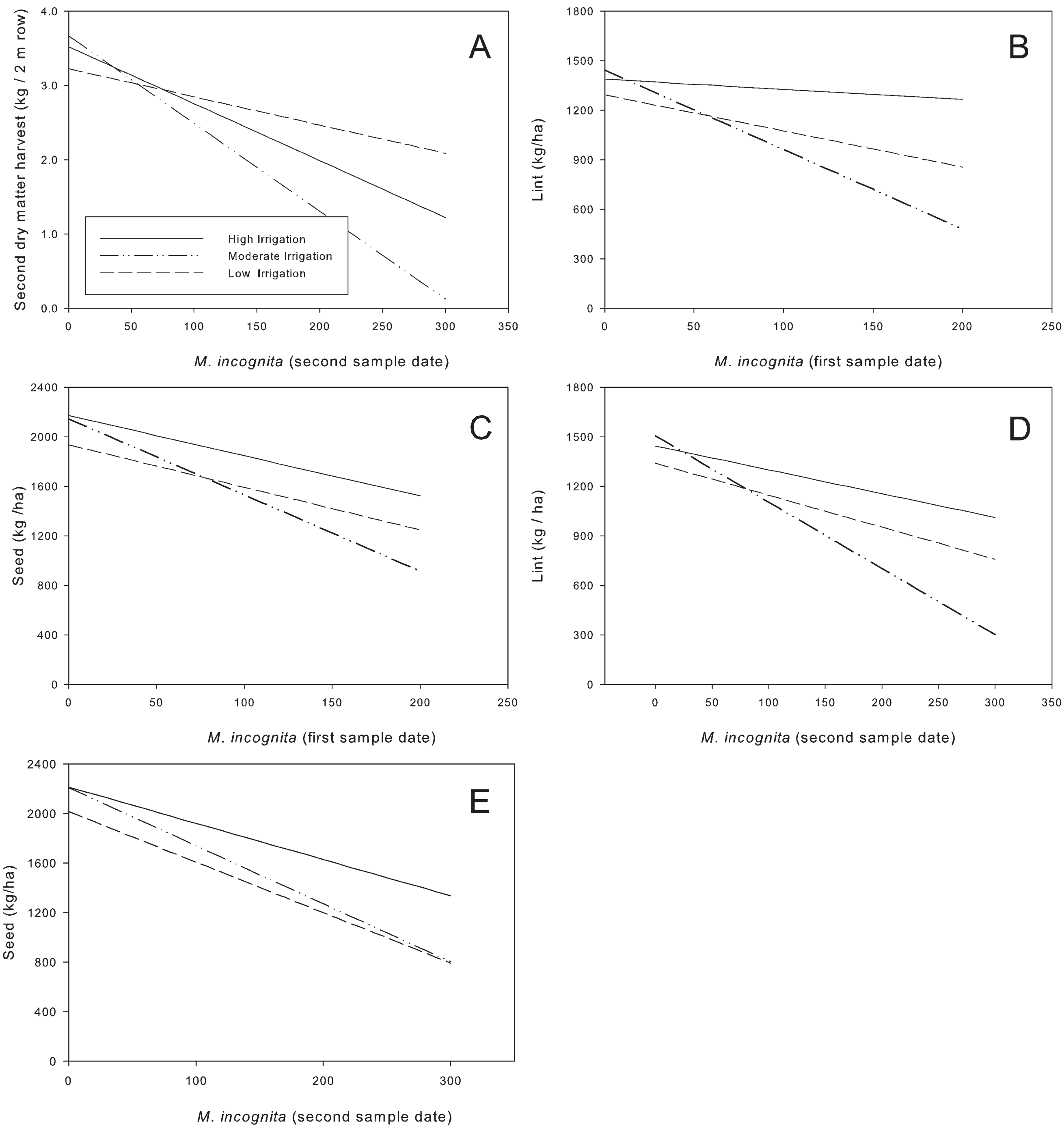

FIG. 2. Relationships between *Meloidogyne incognita* population levels at selected dates and selected cotton growth and yield from six years of field testing. Analyses were conducted using the GLIMMIX procedure in SAS with year treated as a random effect. Regression equations are presented in Table 5.

we found fewer significant regressions with nematode levels than with root galling in this study. Additionally, root galling provides a cumulative record of the damage caused by *M. incognita* through the growing season, whereas nematode counts provide an estimate of population levels at only one point in time and many nematodes would be inside the roots where they would not be included in soil counts. The use of root galling instead of nematode counts may be preferable because the relationships between nematode levels and plant weights were dependent on when the nematode samples were collected (sample date) and because root galling was related to micronaire but nematode levels were not. Although we find root galling is easier, faster, and more consistent to evaluate than nematode population levels, end-of-season root galling has the disadvantage that it is evaluated after the crop has been produced and the damage has already been done. By

TABLE 5. Regression equations and probabilities for the relationships between nematode population levels at selected dates and selected cotton growth and yield characteristics from six years of field testing.

Variables	Irrigation level	Regression equation[a]
2nd sampling date vs. 2nd dry matter harvest	High	3.520 – (0.008 × Nem2)
	Moderate	3.666 – (0.012 × Nem2)
	Low	3.222 – (0.004 × Nem2)
Irrigation $P = 0.072$		
2nd nematode sample (Nem2) $P = 0.058$		
Irrigation × Nem2 $P = 0.074$		
1st sampling date vs. lint	High	1387.1 – (0.62 × Nem1)
	Moderate	1441.7 – (4.82 × Nem1)
	Low	1291.7 – (2.19 × Nem1)
Irrigation $P = 0.179$		
1st nematode sample (Nem1) $P = 0.044$		
Irrigation × Nem1 $P = 0.196$		
1st sampling date vs. seed	High	2170.8 – (3.25 × Nem1)
	Moderate	2143.4 – (6.15 × Nem1)
	Low	1932.9 – (3.43 × Nem1)
Irrigation $P = 0.040$		
1st nematode sample (Nem1) $P = 0.020$		
Irrigation × Nem1 $P = 0.600$		
2nd sampling date vs. lint	High	1443.3 – (1.44 × Nem2)
	Moderate	1503.7 – (4.01 × Nem2)
	Low	1338.4 – (1.94 × Nem2)
Irrigation $P = 0.041$		
2nd nematode sample (Nem2) $P = 0.016$		
Irrigation × Nem2 $P = 0.120$		
2nd sampling date vs. seed	High	2212.1 – (2.93 × Nem2)
	Moderate	2206.8 – (4.69 × Nem2)
	Low	2013.1 – (4.08 × Nem2)
Irrigation $P = 0.037$		
2nd nematode sample (Nem2) $P = 0.014$		
Irrigation × Nem2 $P = 0.492$		

[a] Reported probabilities are from covariance analyses using the GLIMMIX procedure in SAS with year as a random effect. Nem1 = early midseason sample; Nem2 = late midseason sample.

the time early or early-midseason nematode counts could be obtained by a farmer, it may also be too late to benefit from implementing any additional nematode management actions. Root galling during the growing season was not evaluated but may provide a useful alternative to estimating nematode levels.

Fumigation and irrigation in our study are assumed to have had the greatest effect on the cotton crop through reducing *M. incognita* parasitism and water deficit stress, respectively, but either factor could potentially also affect other soilborne organisms that might be capable of influencing the variables we measured. In the factorial analyses, there were some differences between the group of variables affected by fumigation (presumed reduction in parasitism by *M. incognita*) and those affected by the lack of irrigation (presumed water deficit stress). Although both reduced lint and seed harvest and increased micronaire, lack of irrigation did not significantly reduce the dry matter harvests. At the levels and frequency of water deficit stress encountered in this study, *M. incognita* caused numerically greater reductions in plant growth and yield than did lack of irrigation. However, during years of severe drought, we would expect water deficit stress to have the greater effect. Lack of irrigation reduced fiber length and uniformity as measured by HVI, whereas fumigation and accompanying reductions in nematode parasitism did not affect either variable. Although infection of cotton by *M. incognita* reduces water flow in the plant, which can result in temporary wilting similar to water deficit stress, the qualitative and quantitative differences in the variables affected and the magnitude of effects show that the two sources of stress are not having identical effects on the plant. That is likely attributable in part to the timing and duration of the stress each causes: the stress caused by nematode infection is probably more chronic even though it may sometimes be less severe than the stress from lack of rainfall and irrigation. Additionally, the stresses differed in that nematode infection and subsequent stress would have begun soon after plants began to grow, a time when nematode infection is likely to cause the greatest damage to plants, whereas water deficit stress was not applied until approximately one month after emergence when the plants were about to initiate flowering. Another factor causing different reactions to the two stresses is probably that *M. incognita*-induced galls act as a nutrient sink that redirects some of the energy in the plant in addition to impeding root function (Hussey, 1985).

The relationship between nematode density and yield can be influenced greatly by environmental factors (Meon et al., 1978). Our primary objective was to determine whether the damaging effects of *M. incognita* and water deficit stress from insufficient rainfall and irrigation are independent or if the effect of one influences the effect of the other. The effects on a crop of concurrent low water availability and nematode infection may not always be additive (Fasan and Haverkort, 1991), and both additive and nonadditive effects have been documented. High-moisture conditions were able to compensate for *Heterodera rostochiensis* damage in potato (Klar and Franco, 1979) and for *Pratylenchus thornei* on wheat (Nicol and Ortiz-Monasterio, 2004). But in tobacco, soil moisture stress and *M. incognita* stress resulted in mostly additive stresses (Wheeler et al., 1991), as did moisture stress and *Globodera pallida* infection in potato (Haverkort et al., 1992). Similarly, the effects of moisture and *M. hapla* were mostly additive in snap bean (Wilcox-Lee and Loria, 1987). The response of corn to irrigation was not affected by *Pratylenchus* spp. (McDonald and van den Berg, 1993), nor was the damage caused by *Heterodera avenae* to oats influenced by irrigation (Seinhorst, 1981). *Heterodera glycines* on

TABLE 6. Cotton fiber properties as measured by High Volume Instrument (HVI).

Irrigation level[a]	Fumigation[b]	Micronaire[c]	Length (mm)[d]	Uniformity (%)	Strength (g/tex)	Elongation (%)
High	+	4.07 c	27.5 a	82.1 ab	29.3 a	6.13 a
High	-	4.17 bc	27.5 a	82.2 a	29.1 a	6.08 a
Moderate	+	4.25 ab	27.3 ab	81.9 ab	29.1 a	6.05 a
Moderate	-	4.30 ab	27.2 b	82.0 ab	29.2 a	6.01 a
Low	+	4.30 ab	27.1 bc	81.7 ab	28.9 a	6.09 a
Low	-	4.44 a	26.9 c	81.5 b	28.9 a	6.03 a
Irrigation P =		0.04	0.01	0.12	0.52	0.46
Fumigation P =		0.04	0.38	0.99	0.80	0.49
Irrigation × Fumigation Interaction P =		0.52	0.65	0.56	0.90	0.99
High		4.12 b	27.5 a	82.1 a	29.2 a	6.107 a
Moderate		4.28 ab	27.3 ab	81.9 ab	29.1 a	6.029 a
Low		4.37 a	27.0 b	81.6 b	28.9 a	6.060 a
	+	4.21 b	27.3 a	81.9 a	29.1 a	6.09 a
	-	4.30 a	27.2 a	81.9 a	29.1 a	6.04 a

[a] High = water replete; Moderate = ½ the amount applied to High; Low = none.
[b] 1,3-dichloropropene at 56 l/ha (+) or 0 l/ha (-).
[c] Analyzed using the GLIMMIX procedure in SAS with year as a random variable. Means within a treatment grouping within a column followed by the same letter are not significantly different according to Student's $t_{(0.05)}$ separation of least squares means.
[d] Length was reported by the fiber analysis lab in inches and converted to mm.

soybean was shown to have a synergistic interaction with dry soil (Heatherly and Young, 1991), and plant compensation for nematode damage at high moisture has been reported with *H. glycines* in soybean (Johnson et al., 1994). Conflictingly, the effects of *H. glycines* and low soil moisture in soybean also have been shown to be additive so that supplemental irrigation cannot be used to compensate for damage from the nematode (Young and Heatherly, 1988; Heatherly et al., 1992; Koenning and Barker, 1995). Similarly, irrigation did not compensate for *Pratylenchus penetrans* damage in apple (Jaffee and Mai, 1979) or *Pratylenchus* spp. in maize (McDonald and van den Berg, 1993). Such research strongly suggests that the independence of moisture stress and nematode stress on crops is fairly common, although not universal.

Previous studies in cotton reached contradictory conclusions regarding the effect of irrigation on nematode damage: a nematicide efficacy study claimed that unusually heavy rainfall masked the detrimental effects of *M. incognita* (Kinloch and Rich, 1998), but a study evaluating the effects of irrigation on susceptible and moderately resistant cultivars in *M. incognita*-infested fields concluded that irrigation could not be used to

TABLE 7. Cotton fiber properties as measured by Advanced Fiber Information System (AFIS).

Irrigation level[a]	Fumigation[b]	Length-w (mm)[c]	Length-n (mm)[c]	SFC-w (%)[d]	SFC-n (%)[d]	UQL-w (mm)[e]	IFC (%)[f]
High	+	24.3 a	19.7 a	8.31 ab	24.5 a	25.25 a	7.08 ab
High	-	24.2 a	19.7 a	8.43 ab	24.8 a	25.20 ab	7.13 a
Moderate	+	24.2 a	19.7 a	8.28 ab	24.2 a	25.09 ab	6.97 ab
Moderate	-	24.1 a	19.7 a	8.24 ab	24.3 a	25.03 ab	6.73 ab
Low	+	23.8 a	19.3 a	8.88 a	25.5 a	24.80 b	7.03 ab
Low	-	24.0 a	19.6 a	8.08 b	23.8 a	24.82 ab	6.59 b
Irrigation P =		0.23	0.56	0.84	0.82	0.07	0.23
Fumigation P =		0.91	0.69	0.34	0.37	0.86	
Irrigation × Fumigation Interaction P =		0.63	0.32	0.18	0.17	0.84	0.13
High		24.2 a	19.7 a	8.37 a	24.6 a	25.14 a	7.1 a
Moderate		24.1 a	19.7 a	8.26 a	24.2 a	25.14 a	6.9 a
Low		23.9 a	19.5 a	8.48 a	24.7 a	24.26 a	6.8 a
	+	24.1 a	19.6 a	8.49 a	24.7 a	25.14 a	7.0 a
	-	24.1 a	19.7 a	8.25 a	24.3 a	24.26 a	6.8 a

[a] High = water replete; Moderate = ½ the amount applied to High; Low = none.
[b] 1,3-dichloropropene at 56 l/ha (+) or 0 l/ha (-).
[c] Length-w (based on weight), Length-n (based on number), and Upper Quartile Length (based on weight) were reported by the fiber analysis lab in inches and converted to mm. Data were analyzed using the GLIMMIX procedure in SAS with year as a random variable. Means within a treatment grouping within a column followed by the same letter are not significantly different according to Student's $t_{(0.05)}$ separation of least squares means.
[d] Short fiber content based on weight (SFC-w) or number (SFC-n).
[e] Upper quartile weight based on weight.
[f] Immature fiber content.

minimize nematode damage to the crop (Wheeler et al., 2009). Infection of cotton by *M. incognita* reduces the flow of water through the plant (Kirkpatrick et al., 1991; Kirkpatrick et al., 1995), which is why we believed there was the potential for an interaction with a lack of irrigation, but for the six years included in our analyses, the overall effects on the variables measured were independent and therefore additive. Our study shows that ameliorating the losses caused by either of these two independent sources of damage will not significantly affect the losses caused by the other. Based on the range of conditions encountered in our study, we conclude that reducing the levels of *M. incognita* will not reduce damage from lack of rainfall or irrigation and that increasing irrigation will not reduce the damage caused by *M. incognita*.

A secondary objective of our study was to determine whether population levels of *M. incognita* were affected by supplemental irrigation. At the extremes, too little moisture can interfere with nematode mobility and excessive moisture can diminish nematode survival (Sultan and Ferris, 1991; Johnson et al., 1993). We conclude that nematode levels were not affected by irrigation; however, it is possible that supplemental irrigation could affect population levels of *M. incognita* under greater extremes of soil moisture or extremes that persist for longer periods of time than those encountered during our study. Although nematode levels were seemingly unaffected by irrigation, root galling was reduced by the highest level of irrigation. We speculate that these seemingly contradictory results may be attributable in part to the previously discussed cumulative nature of root galling versus the single point in time of a nematode count as well as the endoparasitic nature of *M. incognita* and the greater variability in nematode counts than in galling estimates. If irrigation somehow reduced the size of galls, then that potentially could have influenced our estimates of root galling even though RGI data is based on estimates of incidence. Additionally, because our assessments of galling were based on the percentage of the root system covered with galls, if irrigation resulted in larger root systems without changing the number of galls, then our gall ratings could have been reduced. We hypothesize that if such a reduction in the number of galls per gram of root in highly irrigated plots occurs and is large enough compared with nonirrigated plots, it could result in reduced damage to the plant (nematode tolerance) thereby resulting in a significant irrigation × fumigation interaction, however, we did not document such an interaction.

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