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Genetic Resistance and its Residual Effects for Control of the Root-Knot Nematode–Fusarium Wilt Complex in Cotton[1]

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ABSTRACT

Two cotton (*Gossypium hirsutum* L.) cultivars and a breeding stock ('Deltapine 16', 'Auburn 56', and Auburn 623 RNR, respectively), having in order low, intermediate, and high resistance to the root-knot nematode–fusaruim wilt disease complex [caused by *Meloidogyne incognita acrita* (Kofoid & White) Chitwood and *Fusarium oxysporum* Schlecht. f. *vasinfectum* (Atk.) Snyd. & Hans.], were grown in nematicide, DBCP (1,2-dibromo-3-chloropropane), treated vs. untreated plots for 3 years.

Fumigation did not significantly increase lint yield of Auburn 623 RNR compared with 36 and 77% increases for Auburn 56 and Deltapine 16, respectively. Auburn 623 RNR without fumigation was more effective for controlling root-knot nematodes than Auburn 56 and Deltapine 16 with fumigation and was equally effective as those cottons with fumigation for controlling fusarium wilt disease. In unfumigated plots, Auburn 623 RNR vs. Auburn 56 and Deltapine 16 also had lower root-knot nematode numbers (83/500-cm^3 of soil vs. 717 and 1,581, respectively) and lower fusarium wilt percentages (5% vs. 47%, respectively). In the fourth year of the study, susceptible 'Stoneville 213' cotton was grown without fumigation in all plots where the above cottons had been grown. Stoneville 213 following unfumigated Auburn 623 RNR had 147 kg/ha (21%) and 270 kg/ha (47%) higher lint yields than following unfumigated Auburn 56 and Deltapine 16, respectively. Stoneville 213 had smaller root-knot nematode populations following unfumigated Auburn 623 RNR than following fumigated Deltapine 16 and no greater incidence of fusarium wilt disease than when it followed fumigated Auburn 56 and Deltapine 16. If the high level of resistance exhibited by Auburn 623 RNR can be bred into cotton cultivars, it should reduce much of the present root-knot nematode and fusarium wilt damage to cotton and to susceptible crops following resistant cotton in rotations.

Additional index words: Gossypium hirsutum L., *Meloidogyne incognita acrita* (Kofoid & White) Chitwood, *Fusarium oxysporum* Schlecht. f. vacinfectum (Atk.) Snyd. & Hans., Rotation, Nematicide, Cotton breeding, Cotton nematodes.

Atkinson (1) first described the root-knot nematode–fusarium wilt disease complex in cotton (*Gossypium hirsutum* L.) caused by root-knot nematodes [*Meloidogyne incognita acrita* (Kofoid & White) Chitwood] and fusarium wilt [Fusarium oxysporum Schlecht. f. *vasinfectum* (Atk.) Snyd. & Hans.] in Alabama in 1893. Soon thereafter, this complex was recongnized as the major disease problem in cotton of the Southeast. Minton and Minton (13) found no wilt symptoms when the fusarium fungus was present without nematodes, but combining it with root-knot nematodes resulted in 100% wilted plants. However, the nematode in the absence of fusarium is destructive in its own right. For example, it can increase the incidence and severity of several seedling diseases (3). Root-knot nematodes, either alone or associated with fusarium wilt, have increasingly been reported as a serious problem of cotton in many areas of the Cotton Belt (2, 6) and of the world (4, 5, 19).

About 1900, when intensive breeding for resistance to this complex began, primary emphasis was placed on fusarium wilt; however, emphasis shifted to root-knot resistance, as understanding of the nematodes' importance increased (9, 18). Interest in breeding for resistance led to evaluation of the most root-knot-tolerant cottons known (10, 12), but no upland cotton had sufficient resistance to prevent extensive damage by the root-knot nematode–fusarium wilt complex. A program initiated in Alabama in 1965 to breed cottons for higher levels of resistance eventually led to the development of Auburn 623 RNR. This cotton exhibited higher resistance to root galling and fusarium wilting than had any other known *Gossypium* (15). It also exhibited unusually high resistance to root-knot nematode egg production (16).

This study was designed to determine the efficacy of the high resistance in Auburn 623 RNR for control of root-knot nematodes and fusarium wilt disease in cotton and to determine what beneficial residual effects that resistance might have on subsequently grown susceptible cotton.

MATERIALS AND METHODS

Experiment A

Two cotton cultivars and a breeding stock, Deltapine 16 (DPL 16), Auburn 56 (Aub 56), and Auburn 623 RNR (Aub 623), respectively, were planted for 3 years in the same plots at the Plant Breeding Unit, Tallassee, Ala. Each cotton was planted in nematicide-treated and untreated plots highly infested with root-knot nematodes (RKN) and fusarium wilt (FW). Soil in the test area was Wickham sandy loam, a member of the fine-loamy, mixed, thermic Typic Hapludults. The experimental design was a randomized, complete block with six replications. Plots were six rows wide (1 m between rows) and 15 m long. Prior to harvest, 50 bolls were hand picked from the middle two rows/plot in the first, third, and fifth replications; then, all cotton was harvested from the middle two rows/plot in all replications with a spindle-type picker and weighed. Boll samples were ginned. Seed and lint weights were used for calculating percent lint. Total seed cotton harvested/plot × percent lint was used to calculate lint yield/plot. All other data were taken from these same two rows of each plot, except FW data were taken from 10-m lengths of rows two and five. The nematicide DBCP (1,2-dibromo-3-chloropropane) was applied at a 1.25× rate (23.4 liters/ha) 15 cm deep over the entire plot with tractor-mounted chisels spaced 30 cm apart. Nonfumigated plots were also chiseled.

To estimate nematode numbers, 20 cores of soil, 2.5 cm × 15 cm deep, were collected in the plant root zone from each plot, composited, and thoroughly mixed in October when nematode numbers normally peak. A 500-cm^3 sample was processed by the centrifugal-flotation technique (8). Along with high levels of RKN, fields in and around the test area have previously been found to contain *Trichodorus christiei* (Allen) Siddiqi (stubby root); *Tylenchorchynchus claytoni* Steiner (stunt); *Hoplolaimus galeatus* (Cobb) Sher. (lance); *Pratylenchus brachyurus* (Godfrey) Goody (lesion); *Criconemoides* spp. Taylor (ring); *Helicotylenchus* spp., Steiner; and *Rotylenchus* spp., Filipjev. Both of the latter nema-

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tode species were spiral and were counted together.

Plant counts/row were made in late June after thinning and again in early September. Differences in those counts were considered as plants lost due to wilt. In September, plants showing foliar and vascular symptoms of FW were also counted and added to the earlier differences to determine total and then percentage wilted plants.

Cottons chosen for this study have shown widely contrasting levels of resistance to the RKN-FW disease complex in greenhouse and field tests. Aub 623 is an F_{10} selection from a cross between upland cotton and a primitive *G. hirsutum* from Mexico (15). Aub 623 has high RKN-FW resistance while Aub 56 is intermediate in resistance to RKN-FW and represents the highest resistance presently available in commercially grown cottons. DPL 16 is susceptible to both RKN and FW. In preliminary greenhouse tests, 450, 45,000 and 96,000 RKN eggs/plant were produced in 40 days on Aub 623, Aub 56, and DPL 16 seedlings, respectively.

Experiment B

In the fourth year, 'Stoneville 213' (ST 213) cotton without fumigation was planted on the same plots utilized in Exp. A. ST 213 is highly susceptible to both RKN and FW.

In addition to the data taken in Exp. A, plant height (cm), boll weight (g), and fiber data were taken in this experiment; and data were taken from the same rows of each plot as in Exp. A. Twelve grams of fiber from each boll sample was analyzed for span length (50) and 2.5%), strength (T_1), elongation (%), and micronaire by the USDA Fiber Testing Laboratory which is presently located in New Orleans, La. An attempt was made to repeat this experiment in the fifth year, but extensive hail damage in the pinhead-square stage of growth effectively destroyed the test.

RESULTS

Experiment A

Yield comparisons were not made between Aub 623, a breeding stock, and the two commercial cultivars of cotton, because Aub 623 is a segregant from a cross of upland with wild cotton and is not yet comparable with commercial cottons in productivity. For this reason, the analysis of variance of yield was based on yield differences within each cotton in fumigated vs. unfumigated plots in each replication over years. The interaction of differences in yield within cotton × year was nearly significant ($P < 0.15$). Cottons differed in their yield response to fumigation (Table 1); but the magnitude of this response for each cotton (fumigated vs. unfumigated) was relatively consistent from year to year, except for DPL 16. In that cultivar, there was a slight trend of decreasing yields from year to year in unfumigated plots. Aub 623 had a nonsignificant yield increase of 42 kg/ha (7%) in response to fumigation compared with highly significant increases of 243 kg/ha (36%) and 395 kg/ha (77%) for Aub 56 and DPL 16, respectively.

The differences in RKN numbers and percent FW among cottons were relatively consistent in magnitude from year to year, except for DPL 16. In that cultivar, there was a slight trend for increasing RKN numbers and percent FW in nonfumigated compared with fumigated plots from year to year. This trend may largely account for

Table 1. Mean lint yield, percent fusarium wilt, and numbers of root-knot nematodes of three cottons produced with (+) and without (−) fumigation over 3 years.

Plot treatment				
Cotton	Fumigation	Lint yield	Fusarium wilt‡	Root-knot nematodes‡
		kg/ha	%	no.
Auburn 623 RNR	+	656	4 a*	49 a
	−	614	5 a	83 a
Auburn 56	+	910†	6 a	385 b
	−	667	24 b	717 c
Deltapine 16	+	911†	9 a	462 bc
	−	516	47 c	1,581 d

* Means within a column followed by the same letter were not significantly different at the 0.05 probability level, according to Duncan's Multiple Range Test.
† Within a cotton, + and − fumigation differed significantly at the 0.05 probability level.
‡ Fusarium wilt and nematode data were taken in September and October of each year, respectively.

Table 2. Mean numbers of plant parasitic nematodes, except root-knot, of three cottons produced with (+) and without (−) fumigation over 3 years.

Plot treatment		Nematodes†					
Cotton	Fumigation	Stubby root	Stunt	Lance	Lesion	Ring	Spiral
		no.					
Auburn 623 RNR	+	274 a*	259 ab	166 a	86 a	8 a	3 a
	−	234 a	542 c	318 a	29 a	5 a	1 a
Auburn 56	+	171 a	324 abc	364 a	54 a	21 a	5 a
	−	221 a	370 abc	374 a	21 a	7 a	4 a
Deltapine 16	+	218 a	160 a	238 a	141 a	3 a	3 a
	−	232 a	436 bc	292 a	48 a	11 a	5 a

* Means within a column followed by the same letter were not significantly different at the 0.05 probability level, according to Duncan's Multiple Range Test.
† Nematode data were taken in October of each year.

the near significance of the interaction of difference in yield within cotton × year reported above. It may also largely account for the near significance of the interactions: numbers of RKN on cotton × year ($P < 0.11$), numbers of RKN on cotton × fumigation × year ($P < 0.18$), percent wilted cotton × year ($P < 0.15$), and percent wilted cotton × fumigation × year ($P < 0.16$). In unfumigated plots, Aub 56 and DPL 16 displayed 9× and 19× greater RKN numbers, respectively, than Aub 623, which had only 83 larvae/500-cm^3 of soil (Table 1). With 4 and 5% wilt in fumigated and unfumigated plots, respectively, Aub 623 showed essentially no response for FW. In contrast, Aub 56 and DPL 16 with 6 and 9% wilting, respectively, in fumigated plots and 24 and 47%, respectively, in unfumigated plots showed significant responses.

Numbers of stubby root, stunt, lance, lesion, ring, and spiral nematodes are given by treatment in Table 2. Differences in numbers of those nematodes among cottons were not significant. Except for lesion, ring, and spiral nematodes, higher numbers were generally present in unfumigated than in fumigated cottons. However, because of large error variances, the differences were not significant, except for the stunt nematode, which had sig-

Table 3. Mean lint yield, percent fusarium wilt, numbers of root-knot nematodes, and plant height of 'Stoneville 213' cotton grown following three cottons produced with (+) and without (−) fumigation over 3 years.*

Prior 3-year plot treatment					
Cotton	Fumigation	Lint yield	Fusarium wilt†	Root-knot nematodes†	Plant height
		kg/ha	%	no.	cm
Auburn 623 RNR	+	919 a*	8 a	140 a	32.1 a
	−	844 a	9 a	260 ab	29.5 abc
Auburn 56	+	914 a	13 a	490 bc	32.9 a
	−	697 b	39 b	1,100 d	27.8 bc
Deltapine 16	+	874 a	14 a	640 c	30.8 ab
	−	574 c	74 c	1,660 e	26.2 c

* Means within a column followed by the same letter were not significantly different at the 0.05 probability level, according to Duncan's Multiple Range Test.
† Fusarium wilt and nematode data were taken in September and October, respectively.

Table 4. Mean numbers of plant parasitic nematodes, except root-knot, of 'Stoneville 213' cotton grown following three cottons produced with (+) and without (−) fumigation over 3 year.

Prior 3-year plot treatment		Nematodes†					
Cotton	Fumigation	Stubby root	Stunt	Lance	Lesion	Ring	Spiral
		no.					
Auburn 623 RNR	+	198 a*	2 a	18 a	54 a	3 a	7 a
	−	288 a	144 a	750 c	36 a	1 a	3 a
Auburn 56	+	216 a	18 a	36 a	4 a	72 a	5 a
	−	198 a	108 a	468 bc	72 a	18 a	2 a
Deltapine 16	+	108 a	1 a	3 a	36 a	2 a	17 a
	−	270 a	18 a	216 ab	54 a	72 a	3 a

* Means within a column followed by the same letter were not significantly different at the 0.05 probability level, according to Duncan's Multiple Range Test.
† Nematode data were taken in October.

nificantly higher numbers in the unfumigated plots of Aub 623 and DPL 16.

Experiment B

ST 213 following unfumigated Aub 623 yielded 147 kg/ha (21%) and 270 kg/ha (47%) more lint than following unfumigated Aub 56 and DPL 16, respectively (Table 3). Where ST 213 followed fumigated and unfumigated Aub 623, it had 140 and 260 RKN/500-cm^3 of soil, respectively. In comparison, ST 213 following fumigated Aub 56 and DPL 16 had 490 and 640 RKN, respectively, which was significantly more than following fumigated Aub 623. RKN numbers in ST 213 following fumigated Aub 56 and DPL 16 were significantly lower than in ST 213 following the same cottons without fumigation.

Where fumigated and unfumigated Aub 623 preceded ST 213, only 8 and 9%, respectively, of ST 213 plants wilted compared with 39 and 74% wilting where ST 213 followed unfumigated Aub 56 and DPL 16, respectively. Wilting was lower in ST 213 preceded by either unfumigated or fumigated Aub 623 where it was preceded by fumigated Aub 56 and DPL 16, but differences among those treatments were not significant.

The tallest ST 213 plants in the experiment succeeded the three cottons with fumigation, but ST 213 plants following unfumigated Aub 623 were not significantly shorter. The Aub 56 unfumigated treatment caused significantly shorter plants than did the Aub 56 fumigated ones. The same trend was significant following the DPL 16 treatments.

Mean numbers of stubby root, stunt, lance, lesion, ring, and spiral nematodes in plots of ST 213 following the three cottons are given in Table 4. Differences in numbers of those nematodes among prior cotton treatments were not significant. Although numbers of those nematodes were higher in previously unfumigated plots vs. those in previously fumigated plots, the differences were not significant, except for the lance nematode, which had higher numbers in unfumigated plots.

Differences in boll weight, lint percent, 50 and 2.5% span length, stelometer (T_1), percent elongation, and micronaire were not significant between ST 213 plants succeeding each of the three cottons, either with or without fumigation.

DISCUSSION

Aub 623 in both fumigated and unfumigated plots (Exp. A) showed exceptionally high resistance to RKN and FW. Resistance of Aub 623, compared with that of the other cottons, was further indicated by its small, nonsignificant response to fumigation in lint yield, RKN, and FW. This study adds confirmation to reports of resistance in Aub 623 from previous experiments (15, 16, 20).

Aub 623, Aub 56, and DPL 16 had low, intermediate, and high responses to fumigation, respectively, in lint yield, RKN numbers, and FW percentages. The magnitude of response in these cottons to fumigation was negatively related to their levels of resistance.

Aub 623 probably has a significant amount of its wild parents' germplasm, which has not been subjected to long term selection on soils containing parasitic nematodes indigenous to the United States as has that of currently grown cultivars. Consequently, prior to this study, there was concern that Aub 623 might be more susceptible than adapted cultivars to some of the parasitic nematodes other than RKN. This study reduced those concerns related to the stubby root, stunt, lance, lesion, ring, and spiral nematodes studied, by indicating that numbers of these nematodes on Aub 623 and the other two cottons in unfumigated plots (Exp. A) were similar and that they did not reduce yield of Aub 623 to any greater extent than that of the other cottons. The latter conclusion was drawn from the evidence in Exp. A that response of Aub 623 to fumigation was negligible.

Average numbers of stubby root and lance nematodes tended to be higher and numbers of stunt nematodes were significantly higher in unfumigated plots of Exp. A. Although together these nematodes probably contributed to the response of all three cottons to fumigation, their individual and combined effects must have been small, considering the negligible response of Aub 623 to fumigation. This observation is further supported by a report (11) that when pure cultures of stubby root, stunt, lesion, and spiral nematodes were combined with FW propagules, wilt caused by fusarium was not significantly increased.

Correlations of lint yield with RKN numbers and with FW and correlations of FW and RKN numbers were calculated from individual plot values for unfumigated cottons over the 3 years in Exp. A and from all individual plot values in Exp. B. Lint yield of the three cottons was negatively correlated with RKN numbers ($r = -0.86$, $P = < 0.01$; and $r = -0.88$, $P = < 0.01$; in Exp. A and B, respectively). It was also negatively correlated with FW percentages ($r = -0.85$, $P = < 0.01$; and $r = 0.86$, $P = < 0.01$; in Exp. A and B, respectively). FW was therefore highly positively correlated with RKN numbers ($r = 0.93$, $P = < 0.01$; and $r = 0.91$, $P = < 0.01$; in Exp. A and B, respectively). The following is cited as evidence that the RKN was the most important factor affecting response of the three cottons to fumigation: (a) the negative correlation between lint yield and RKN in Exp. A and B, (b) the positive correlation between FW percentages and RKN in Exp. A and B, and (C) the positive response of Aub 56 and DPL 16 (Exp. A) to fumigation and ST 213 (Exp. B) to reduction of RKN numbers by fumigation and by resistance of Aub 623. This conclusion is supported by the following indications of FW dependency on RKN as an inoculating or predisposing agent in the RKN-FW disease complex: (a) the failure of Aub 623, whose resistance controlled RKN, to respond significantly to fumigation; (b) the significantly reduced FW in Aub 56 and DPL 16 (Exp. A) following fumigation; (c) the significantly reduced FW in ST 213 (Exp. B) following unfumigated Aub 623; (d) the significantly reduced FW in ST 213 (Exp. B) following Aub 56 and DPL 16 with fumigation; and (e) the numerous reports by others (7, 13, 14, 17) that FW was significantly reduced or prevented by controlling RKN with fumigation, by rotation with a resistant crop, or in plants exposed to FW without RKN. Although possible direct effects of fumigation on the fusarium fungus were not studied, our long term experience suggests that the fumigant DBCP has little effect on it, if any.

Unfumigated Aub 623 was as effective as fumigated Aub 56 and more effective than fumigated DPL 16 for controlling RKN in subsequently grown ST 213 (Exp. B). These three treatments were equally effective in controlling symptoms of FW in ST 213. Also, lint yield response of ST 213 to residual effects of unfumigated Aub 623 was not significantly different from its yield response to residual effects of fumigated Aub 623, Aub 56, and DPL 16. Application of a 1.25× rate of DBCP as used in Exp. A, was an uneconomical method for control of RKN in commercial cotton production. Thus, performance (Exp. A) and residual effects (Exp. B) for Aub 56 and DPL 16 in plots fumigated by this method were unusually high standards for measuring the performance and residual effects of unfumigated Aub 623.

While the major residual effect of unfumigated Aub 623 in controlling RKN and FW was most likely Aub 623's high RKN resistance, unfumigated Aub 623, which had extremely low wilting, possibly could have reduced FW in ST 213 by being a poor host and thus by not increasing FW propagules. Also, Aub 623 root exudate may have had antibiotic effects on FW propagules. Further research would be required to investigate these possible mechanisms of FW control.

FW and RKN numbers were as low in unfumigated Aub 623 plots in September and October, respectively, of the first year as in the later years of Exp. A. Consequently, residual effects of Aub 623 on RKN after only one year probably would be sufficient to be beneficial to a RKN-susceptible cotton or possibly other crop following it in rotation. This assumption, of course, would require further testing.

Aub 623 apparently acts as a trap crop in depressing RKN numbers. Larvae of the RKN enter its roots in about the same numbers as enter susceptible cotton roots; however, most do not reach egg-laying maturity (R. L. Shepherd, unpublished). Because cotton is normally susceptible only to this one species of RKN, a cotton resistant to this species could possibly control other RKN species, thereby enhancing its value in rotations.

If the exceptionally high level of resistance exhibited by Aub 623 can be bred into cotton cultivars, it should reduce most of the economic loss in cotton to RKN and to FW, when RKN is the predisposing agent, and help prevent RKN damage to susceptible cotton or possibly other crops following resistant cotton in rotations. These conclusions are similar to those of Hyer et al. (7) who reported more effective control of the RKN-FW complex with high resistance to RKN in his breeding line N6072 than with the tolerance to wilt and moderate resistance to nematodes in Aub 56. Resistant cottons should greatly reduce the need for costly and potentially soil-polluting nematicides and also reduce the energy requirements associated with application of agricultural chemicals.

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