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Suppression of *Rotylenchulus reniformis* 122-cm Deep Endorses Resistance Introgression in *Gossypium*

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Abstract: Nine sources of resistance to *Rotylenchulus reniformis* in *Gossypium* (cotton) were tested by measuring population density (Pf) and root-length density 0 to 122 cm deep. A Pf in the plow layer less than the autumn sample treatment threshold used by consultants was considered the minimum criterion for acceptable resistance, regardless of population density at planting (Pi). Other criteria were ample roots and a Pf lower than on the susceptible control, as in pot studies. In a Texas field in 2001 and 2002, no resistant accessions had Pf less than the control but all did in microplots into which nematodes from Louisiana were introduced. An environmental chamber experiment ruled out nematode genetic variance and implicated unknown soil factors. Pf in field experiments in Louisiana, Mississippi, and Alabama were below threshold for zero, six and four of the accessions and above threshold in the control. *Gossypium arboreum* A2–87 and *G. barbadense* GB-713 were the most resistant accessions. Results indicate that cultivars developed from these sources will suppress *R. reniformis* populations but less than in pots in a single season.

Key words: cotton, *Gossypium*, nematode, reniform, resistance, *Rotylenchulus reniformis*.

Rotylenchulus reniformis (the reniform nematode) is currently considered to be among the most important plant pest problems in several cotton production regions of the US (Overstreet and McGawley, 1997; Lawrence and McLean, 2001; Blasingame and Patel, 2005). The nematode's greatest impact is in the Mississippi floodplain of Mississippi, Louisiana, and Arkansas, the Tennessee Valley area of northern Alabama, and the Red River Valley of Louisiana. *Rotylenchulus reniformis* also damages cotton in the Lower Rio Grande Valley of Texas and throughout the Coastal Plains production region extending from southern Alabama and the panhandle of Florida across Georgia and South Carolina into North Carolina. It occurs, but is not thought to be an important problem, in eastern Texas and the Texas High Plains and is not found west of Texas.

Rotylenchulus reniformis is notorious for its ability to survive without a host (Heald and Robinson, 1987; Heald and Inserra, 1988; Womersley and Ching, 1989; Caswell et al., 1991; Gaur and Perry, 1991. Because survival over winter in cotton production regions of the US is high (Lawrence and McLean, 2001), end-of-season samples are typically used as the basis for nematode management decisions in the next year's cotton crop. Treatment thresholds in use by consultants and farmers vary with growing conditions from 5,000 to 10,000 nematodes/473 cm^3 (pint) of soil collected at the end of the previous season (Overstreet, 2001; Koenning, 2002; Komar et al., 2003; Sciumbato et al., 2004). These values, respectively, are equal to 8.1 and 16.2 nematodes/g soil at a soil bulk density of 1.3 g/cm^3.

Nematicide application is the most frequently utilized method for controlling *R. reniformis* (Kinloch and Rich, 2001; Lawrence and McLean, 2001) and can provide more than 50% yield increases in some fields or years (Lawrence et al., 1990), but in others is marginally or inconsistently cost-effective (Minton, 1982; Zimet et al., 1999; Overstreet and Erwin, 2003). Sufficiently high rates or deep placement of nematicide, although not economic, can double yields in infested fields (Newman and Stebbins, 2002; Westphal et al., 2004; Robinson et al., 2005b).

Where cotton is grown, *R. reniformis* populations can be greatly reduced by crop rotation with corn, peanut, rice, sorghum (Lawrence and McLean, 2001; Davis et al., 2003), or with resistant soybean cultivars (Robbins et al., 2001, 2002; Davis et al., 2003; Westphal et al., 2004). Rotational crops, however, only suppress populations of *R. reniformis* during the first part of the first year back into cotton (Gazaway et al., 1998, 2000), and yield returns usually do not offset the lower crop market value or additional equipment costs that rotation requires.

No known upland cotton (*G. hirsutum*) cultivars are resistant to *R. reniformis* in pots (Robinson et al., 1999), and none appear to suppress substantially populations of *R. reniformis* in the field. At least 11 tolerant breeding lines have been released (Jones et al., 1988; Cook et al., 1997a; Cook and Robinson, 2005). These lines yield well in infested fields under the growing conditions to which they are adapted and, in contrast to susceptible cultivars, exhibit little or no growth or yield response to

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fumigation in infested fields; however, the highest population suppression reported is only about 62% (Beasley, 1985; Jones, 1987; Cook et al., 1997b; Koenning et al., 2000; Cook and Robinson, 2005) and usually it is less; thus, they cannot be considered resistant when compared with rotational crops, which support virtually no nematode reproduction.

More than 2,000 genotypes of *G. hirsutum* have been evaluated in the search for resistance to *R. reniformis* (Yik and Birchfield, 1984; Robinson and Percival, 1997; Robinson et al., 1999; Robinson, 2001; Robinson et al., 2004). Of these, only 19 were scored as potentially resistant in the first examination. Nine (Yik and Birchfield, 1984) were reclassified as susceptible in a subsequent screen (Robinson and Percival, 1997), and four (TX-110, TX-502, TX-1347, and TX-1348) were reclassified as *G. barbadense*, leaving six primitive *G. hirsutum* accessions (TX-25, TX-748, TX-1586, TX-1828, TX-1860, and TX-2469) as possible resistance sources; all six of the latter were classified moderately resistant, suppressing populations in pots to less than 1/3 but not less than 1/10 of the susceptible control. Stronger levels of resistance have been observed in several other *Gossypium* species (Carter, 1981; Yik and Birchfield, 1984; Robinson et al., 2004).

Levels of resistance to *R. reniformis* higher than those known within *G. hirsutum* might be introgressed from certain primitive accessions of *G. barbadense*, *G. arboreum*, and *G. herbaceum* identified in greenhouse pot studies (Carter, 1981; Yik and Birchfield, 1984; Stewart and Robbins, 1995; Robinson and Percival, 1997; Silvey et al., 2003; Bell and Robinson, 2004; Moresco et al., 2004; Robinson et al., 2004). Some suppress *R. reniformis* populations in pots 90 to 95% compared to susceptible upland cotton. Their ability to suppress *R. reniformis* populations in cotton fields, however, has not been confirmed. Field confirmation of resistance in the sources themselves is critical because interspecific introgression in cotton presents plant breeders with formidable challenges such as linkage block, ploidy manipulation, cytoplast fusion, marker development, and selection for resistance in multiple generations to isolate resistance from unacceptable primitive traits (Calhoun and Bowman, 1999; Percival et al., 1999). Thus, much time and money could be spent to incorporate a trait that does not work in the field.

The primary objective of this research was to test the hypothesis that representative known sources of resistance to *R. reniformis* within *Gossypium* can suppress final nematode population densities in the field sufficiently, relative to established damage thresholds for fall samples taken the previous year, to merit introgression of resistance into commercial cultivars. Because *R. reniformis* populations often extend deep into the soil in cotton (Robinson et al., 2005a) and because differences in the ability of roots of primitive cottons to proliferate and colonize the soil profile (Quisenberry et al., 1981; McMichael and Quisenberry, 1991; Quisenberry and McMichael, 1996) in different soils could impact the correct assessment of their potential value in resistant cultivar development, the density of roots as well as nematodes 122-cm-deep were compared in four widely separated fields spanning most of the latitude over which cotton is produced in the US, as well as production areas where *R. reniformis* is considered a major problem. A standard agronomic control cultivar in seven field, microplot, and environment chamber experiments allowed comparison of driving factors across a wide range of environments. A preliminary report has been published (Robinson et al., 2002).

Materials and Methods

Inoculum: Inoculum of *R. reniformis* for experiments in pots and microplots came from populations maintained in the greenhouse for 2 or more yr on a mixture of cotton and tomato in silty loam soil. The two populations used were originally from the same fields in Texas and Louisiana where field experiments were conducted in 2002 and are referred to as the TX and LA populations. Inoculum consisted of mixed vermiform stages extracted from soil by Baermann funnel (Robinson and Heald, 1991) the night before plant inoculation and were more than 95% motile when applied.

Soil sample collection and analysis: All soil samples from field experiments were collected on the planting bed with a 3.3-cm-diam., 122-cm-long Environmentalists Subsoil Probe Plus (Clements Associates Inc., Newton, IA 50208) and processed by the same procedures at College Station, TX. Cores were separated into 15.25-cm vertical sections, and each section was thoroughly mixed and divided into 100-g or 40-g subsamples for analysis. Nematodes were extracted from subsamples by Baermann funnel or centrifugal flotation (Jenkins, 1964; Liu et al., 2002). Soil textures were determined by the Bouyoucos method (Piper, 1944). Roots were extracted by suspending a 40-g subsample in 8 liters water and decanting into nested sieves with sequential openings of 425, 180, and 150 µm. Root fragments were transferred with forceps from the 150-µm sieve to 2% formaldehyde solution and stored at room temperature. Total root length per sample was measured with a Win/Mac Rhizo root scanner (Regents Instruments, Ltd., Quebec, Canada) (Box, 1996). Each soil sample from the microplot experiment was a composite of three 2-cm-diam. probes to the bottom of the soil layer.

Experiments: Seven hypothesis-driven experiments were designed and conducted during 2001 and 2002 in a controlled environment chamber and at five field sites that differed significantly in temperature, humidity, rainfall, irrigation availability, soil texture, recommended planting date for cotton, and latitude. The first experiment was a field test planted 20 km north of the southernmost tip of Texas in February of 2001, a nor-

mal planting date for cotton in this area. A parallel microplot experiment was planted in June of the same year, 640 km to the north of the firs site, where the normal planting period extends from mid-April into June. Results of the field and microplot experiments were the basis for a subsequent controlled environment chamber experiment in the fall of 2001, and results of the first three experiments taken together were the basis for the four field experiments conducted in 2002. To facilitate description, the experiments are presented in the same order as conducted: 1) 2001 field experiment; 2) 2001 microplot experiment; 3) 2001 controlled environment chamber experiment; and 4) the four 2002 field experiments.

2001 field experiment: The field was on the USDA North farm, 8 km north of Weslaco, Texas. The field was considered uniformly infested with *R. reniformis* because all 160 samples collected in August 2000 were positive for *R. reniformis*, and mean densities for 40 samples collected 30- to 45-cm deep in each of four equal quadrants along the field differed from the overall mean by less than 5%. The experimental design was a randomized complete block with four blocks and eight treatments on a 102-cm bed, 1 row/plot, and 2.4-m plots. Treatments were *G. hirsutum* cv. Fibermax 832 (susceptible control) and cv. Suregrow 501 (susceptible but putatively tolerant), *G. arboreum* A2–87, *G. herbaceum* A1–17, and the *G. barbadense* accessions GB-13, GB-49, GB-264, and TX-110. Samples for nematode and root measurements were collected at six uniformly spaced points at planting on 8 March and in every plot on 3 July. Plant heights were measured 12 July.

2001 microplot experiment: Microplots at College Station, TX, were bottomless 59-cm-diam. cylinders containing a loamy sand 30-cm deep and countersunk into sand perched on a tile-drained gravel bed. The experimental design was a randomized complete block with six blocks and eight treatments, which consisted of the same genotypes planted in the 2001 field experiment. Cotton was planted in microplots 3 June, and each microplot was inoculated with 10,000 LA population nematodes after seedling emergence. Soil samples were taken on 1 October for nematode analysis only and on 15 November for both root-length density and nematode analysis. Most large roots from the upper central part of microplots were removed with plants just before the 15 November sampling.

Controlled environment chamber experiment: Plants were grown within 500-cm^3 pots in a controlled environment chamber programmed for a 14-hr photoperiod at 383 μmol photons/m^2/sec mixed fluorescent and incandescent light with 26°C night/30°C d and relative humidity above 55%. Pots were filled either with soil collected in August 2001 from the top 30 cm of the field where the 2001 experiment was conducted ("field soil"), or with a 6:1 mixture of fine sand (< 400 μm particle size) and vermiculite supplemented with 5 g/kg pelletized limestone ("sand mix"). Pots were planted on 21 August, inoculated 4 September, and harvested on 23 October 2001. Plants were watered daily and fertilized weekly (15:16:17:1.0:0.2:0.1 of N:P:K:Mg:Fe:Zn).

The experiment had a completely randomized factorial design with six replications, seven genotypes, and three nematode-soil combinations. Genotypes were Fibermax 832, Suregrow 501, A2–87, GB-264, GB-536, TX-110, and GB-713. Nematode-soil combinations were sand mix inoculated with 4,000 nematodes/pot of the TX population, sand mix inoculated with 4,000 nematodes/pot of the LA population, and naturally infested field soil (6,000 nematodes/pot) with no added nematodes. Nine weeks after planting, plant heights were measured, the root ball from each pot was removed, soil was shaken from roots into a dry bucket, roots were washed and weighed, and nematodes were extracted from a 100-g subsample of soil by Baermann funnel. Nematodes were also extracted from 100-g soil samples of two replications of every treatment by centrifugal flotation.

2002 field experiments: Test sites included the 2001 North farm site at Weslaco, TX (TX), and three additional sites at Baton Rouge, LA (LA), Stoneville, MS (MS), and Huxford, AL (AL). All fields were infested with *R. reniformis* at damaging population densities and had been planted to cotton for 3 yr. Three to six soil samples for texture analysis were collected from eight 15.25-cm layers 0- to 122-cm deep at each site either in 2002 or in previous years.

The same 10 genotypes planted at each site were those planted at Weslaco in 2001, except for deletion of GB-13 and addition of GB-536, GB-713, and TX-1348, with cultivar Fibermax 832 retained as the susceptible control. Due to restricted seed availability, only 60 seeds of each entry were planted per site. Planting dates, which were normal for each site, were 5 March at Weslaco, 30 May at Baton Rouge, and 23 April at both Stoneville and Huxford. Plots of each entry consisted of either a single 3.1-m-long plot (Baton Rouge) or four 1.8-m-long plots in a randomized complete block design (all other sites). Uncertainty in genotype resistance assessment by planting only one block/genotype at Baton Rouge was offset to some extent by the field at Baton Rouge having been planted intensively to experiments on *R. reniformis* on cotton and other crops every year for 40 yr; thus the test area was well characterized and known without question to be uniformly infested based on information from thousands of previously collected samples.

Fields were managed according to standard cotton management practices for each area. Weeds were removed manually when primitive accessions became too tall to cultivate plots with a tractor. Weed management at each site equaled or surpassed that in well maintained cotton fields in the surrounding area, and the

estimated foliar biomass of any weeds present at the end of the season was less than 1% that of the test plants.

Four 122-cm-deep cores for nematode analysis were collected randomly in the plot area at Weslaco on 18 March, 2 wk after planting. Initial population densities (Pi) were not measured at Baton Rouge, Stoneville, or Huxford. One late season soil core for nematode and root analysis was collected from each plot at Weslaco, Stoneville, and Huxford on 23 August, 5 September, and 10 September, respectively; 3 cores/plot were collected at Baton Rouge on 17 September. Several additional late-season cores were taken arbitrarily at each site in clean alleyways between plots.

Site latitudes: College Station, TX (30° 30′N, 96° 4′W); Weslaco, TX (26° 13′N, 97° 58′W); Baton Rouge, LA (30° 23′N, 91° 13′W); Stoneville, MS (33° 35′N, 90° 56′W); and Huxford, AL (31° 32′ N, 87° 35′ W).

Statistical analyses: Nematode counts and root-length measurements were subjected to analysis of variance as appropriate to the experimental design, and treatment means for soil layers were separated by the protected LSD when *F*-values were significant. Nematode counts were transformed to $\log_{10}(X + 1)$ before analysis. All field experiments except Baton Rouge were laid out and analyzed as randomized complete block designs. As noted, the Baton Rouge test was not a randomized, replicated experiment, but rather a trial with one plot per treatment. Plots at Baton Rouge were compared by considering the three subsamples from each plot as replicates and performing a one-way analysis of variance to compare plots, not treatments. Thus, cotton genotype comparisons at Baton Rouge presumed the absence of important plot effects within the field.

Root and nematode population densities and nematodes per cm root in pots, microplots, and field plots were compared to the susceptible control Fibermax 832 by Dunnett's test and afterwards converted to a percentage of the control to facilitate comparisons with pot studies. To evaluate nematode population suppression relative to crop loss potential, final population density (Pf) in field plots was also compared with high and low nematicide application thresholds of 16.2 and 8.1 nematodes/g soil (Overstreet, 2001; Koenning, 2002; Komar et al., 2003; Sciumbato et al., 2004). To estimate the impact of nematode survival on population suppression by resistant accessions, Pf data from field tests also were analyzed after subtracting numbers of nematodes extracted from 122-cm-deep cores taken in clean alleyways.

For each 122-cm-deep soil core collected, the mean depths of nematodes and roots were calculated as: Mean depth = 15.25 cm × $\sum k_i x_i / \sum x_i$ for i = 1 to 8, where k_i = i - 0.5 and x_i is the number of nematodes or centimeters of root per gram soil in the i^{th} 15.25-cm layer downward from the soil surface.

To facilitate comparisons between different experimental systems and different portions of the soil profile, root and nematode population densities were also expressed as nematodes per cm root and as nematodes per cm^2 soil surface area. To compare root densities between pots and field sites, root lengths for root systems from pots, which were weighed but not measured, were calculated from root weights by assuming roots had a specific gravity of 1.0 and the same mean diameter (0.3 mm) as measured for all roots extracted from all field plots. Means of nematode and root densities for soil type and nematode origin treatments in the controlled environment chamber experiment were separated by LSD values.

Results

Soil texture analyses: All sites had deep soils with the A horizon extending below 122 cm. The Weslaco field was a Hidalgo sandy clay loam (56% sand, 23% silt, 21% clay) that transitioned to a sandy loam (58% sand, 24% silt, 18% clay) at 46 cm and to a loam (51% sand, 32% silt, 17% clay) at 92 cm. The Baton Rouge field was a silty loam from 0- to 122-cm deep (mean composition 10% sand, 64% silt, 26% clay) with lowest clay content (18%) between 0 and 15 cm and highest clay content (31%) between 30 and 46 cm. Silt ranged 61 to 69% and sand 8 to 13%. The Stoneville field was a borderline loam/silty loam with a mean composition 0- to 122-cm deep of 30% sand, 51% silt, and 19% clay. The clay content was constant from 0 to 122 cm (± 1%), but the texture transcended from a silty loam in the 0- to 46-cm layer to a loam below that, except in the deepest, 107- to 122-cm layer, where silt content was high enough to be considered a silty loam. The Huxford field had a sandy clay loam soil (47% sand, 25% silt, 28% clay) in the upper 15-cm layer, with a transition in the 15- to 30.5-cm layer to a clay (37% sand, 18% silt, 45% clay) that had a constant clay content (45 ± 1%) from 30.5- to 122-cm deep.

2001 field experiment: On 3 July, the Fibermax 832 control in the plots and other commercial cotton cultivars in surrounding fields had open bolls and were within 2 wk of defoliation and harvest. On 12 July, Fibermax 832 was 0.8 m and Suregrow 501 was 0.7 m tall. All primitive accessions were taller than the control ($P < 0.001$), with heights ranging from 1.3 m for A2–87 to 1.6 m for GB-264. All *G. hirsutum*, *G. arboreum*, and *G. herbaceum* entries flowered and set fruit; the *G. barbadense* accessions did not flower.

Roots of Fibermax 832 decreased logarithmically with depth ($P < 0.01$), with 65% of all root length in the top 30.5 cm, 24% in the next 30.5 cm, and 12% below 61 cm (Fig. 1). However, roots were recovered consistently in the lowest, 107- to 122-cm layer. Mean root length density 0- to 122-cm deep for primitive accessions did not differ from the control (Table 1), and

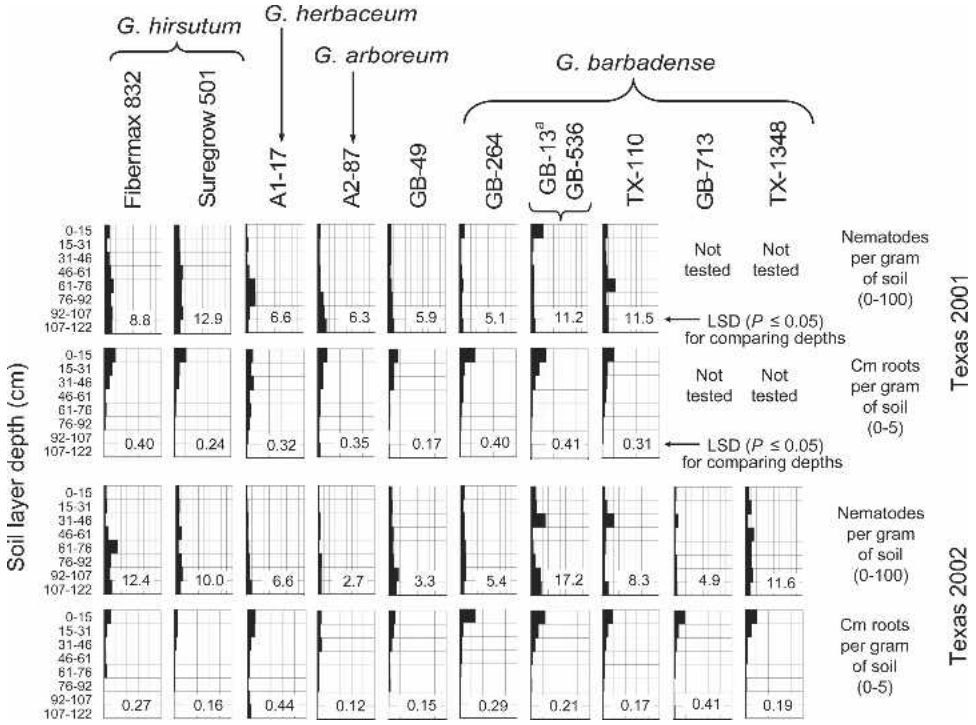

FIG. 1. Nematodes and roots collected in July of 2001 and August of 2002 from eight 15.25-cm layers of soil 0- to 122-cm deep in a field at Weslaco, TX, that was infested with *Rotylenchulus reniformis* and planted to selected resistant and susceptible genotypes of cotton and related species. All graphs for each parameter (nematodes and roots) are to the same scale, and the number above the x-axis in each graph is the LSD for comparisons between depths within that graph. Each graph is the mean of four replications, except for Surgrow 501 and A1–17 in 2002, which had three replications. [a]The GB-13/GB-536 column gives 2001 data for plots planted to GB-13 and 2002 data for plots planted to GB-536, as those accessions were only planted in those years.

means ranged from 77% of the control for GB-49 to 108% for A2–87 (Fig. 1).

The Pi of *R. reniformis* at planting 0- to 122-cm deep was 6.0 nematodes/g soil. The Pf for Fibermax 832 in the plow layer (0–30.5 cm) and subsequent 30.5-cm increments downward were 6.2, 8.8, 12.8, and 13.0 nematodes/g soil (Fig. 1), with a mean nematode depth of 67 cm (Table 1). For every genotype, the mean nematode depth was between 24- and 40-cm deeper than the mean root depth (Table 1). Roots of A1–17 and A2–87 were deeper ($P < 0.01$ and $P < 0.05$, respectively) than those of the Fibermax 832 control, but root depths of other primitive accessions did not differ. No entry suppressed the overall Pf of *R. reniformis* in the soil 0- to 30.5- or 0- to 122-cm deep when compared by Dunnett's test to Fibermax 832 ($P < 0.05$) (Tables 2,3). Pf of *R. reniformis* from 0 to 122 cm under primitive accessions ranged from 52% of the control for GB-264 to 90% of the control for TX-110 (Table 3). Pf in all plots was below the high economic threshold (16.2 nematodes/g soil) (Tables 2,3).

2001 microplot experiment: Plants were 0.7 to 2 m tall by 1 November. The *G. hirsutum*, *G. arboreum*, and *G. herbaceum* entries flowered and set fruit; the *G. barbadense* accessions did not flower. The *R. reniformis* Pf in microplots planted to the control, Fibermax 832, was 148 nematodes/g soil, a 1,600-fold increase over the Pi, assuming 83-liter microplot volume and 1.3 soil bulk density. All primitive accessions suppressed nematode populations relative to the control ($P < 0.01$ or $P < 0.05$), with greatest suppression (98%) under A2–87 and least (70%) under GB-49 (Table 4).

Growth chamber experiment: Plants were short and roots were dense. The mean plant height of genotypes at harvest ranged from 22 to 31 cm in field soil and from 35 to 52 cm in sand mix. The calculated mean root-length densities of genotypes ranged from 2.0 to 4.4 cm root/g of field soil and from 10.3 to 30.2 cm root/g of sand (Table 5), compared to 0.5 to 1.4 cm root/g soil in the upper soil layers at the 2001 field site at Weslaco (Fig. 1).

The Pf per plant on Fibermax 832 was 315,600, a 68-fold increase over the Pi. On the susceptible control, values for nematodes per g soil, cm roots per g soil, and nematodes per cm root for the LA and TX populations in sand did not differ from each other, but in all cases exceeded the corresponding value for the TX population in the sandy clay loam field soil. The Pf of the TX population on Fibermax 832 in field soil (25 nematodes/g soil) was 2.5-fold its Pi (10 nematodes/g soil), but only 4% of its Pf (654 nematodes/g soil) in sand mix (Table 5).

All five primitive accessions suppressed densities of both populations of *R. reniformis* 69 to 97% below the control in sand mix ($P < 0.01$), but in the sandy clay loam field soil none suppressed populations (Tables

TABLE 1. Mean depth of *Rotylenchulus reniformis* and roots of upland cotton (*Gossypium hirsutum*) and resistant primitive accessions of *Gossypium* spp. in cotton fields at Weslaco, TX (TX) in 2001 and 2002, and at Baton Rouge, LA (LA), Stoneville, MS (MS), and Huxford, AL (AL) in 2002. Each number is the mean for four replicate plots per entry, except at Baton Rouge (LA), where there were three cores per plot. Standard deviations are in parentheses. Asterisks and circumflex (***, **, *, ^) indicate root depth differences that differ from zero and genotypes that differ from the susceptible control Fibermax 832, at $P < 0.001$, 0.001, 0.05, and 0.10, respectively. Depth differences are compared with zero by paired t-tests on replicated core samples for each genotype × site combination. Root and nematode densities in soil are compared with the susceptible control Fibermax 832 by Dunnett's test.

Site/yr	FM 832 *G. hi.*[a]	SG 501 *G. hi.*	A1-17 *G. he.*	A2-87 *G. ar.*	GB-49 *G. ba.*	GB-264 *G. ba.*	GB-13/536 *G. ba.*[b]	TX-110 *G. ba.*	GB-713 *G. ba.*	TX-1348 *G. ba.*	Mean[c]
					Nematode average depth (cm)[d]						
TX/2001	67 (9)	62 (13)	71 (1)	78 (8)	68 (10)	59 (6)	50 (9)	68 (7)	—	—	67a
TX/2002	72 (15)	68 (7)	75 (13)	76 (8)	73 (13)	65 (4)	68 (9)	58 (13)	65 (16)	65 (10)	69a
LA/2002	35 (9)	29 (4)	32 (16)	19 (2)	21 (3)	37 (5)	40 (5)	34 (9)	29 (4)	23 (4)	30c
MS/2002	21 (10)	21 (6)	38 (6)	33 (9)	22 (4)	28 (25)	32 (14)	21 (2)	27 (5)	24 (6)	27c
AL/2002	33 (3)	46 (7)	51 (7)**	48 (6)*	37 (9)	43 (6)	37 (12)	38 (5)	38 (6)	44 (4)	41b
Mean	46	45	53	51	44	46	50	44	45	43	
					Root average depth (cm)						
TX/2001	27 (5)	28 (12)	47 (5)**	42 (1)*	29 (3)	28 (7)	26 (2)	30 (8)	—	—	33a
TX/2002	30 (8)	28 (9)	35 (12)	38 (7)	33 (5)	25 (13)	23 (5)	31 (4)	29 (9)	28 (5)	30ab
LA/2002	18 (4)	17 (2)	20 (3)	18 (0)	16 (1)	22 (7)	21 (2)	20 (2)	17 (6)	19 (5)	19c
MS/2002	27 (3)	27 (7)	32 (5)	37 (10)	28 (3)	28 (9)	37 (9)	26 (7)	27 (4)	35 (7)	30ab
AL/2002	30 (9)	29 (7)	29 (7)	29 (10)	25 (2)	27 (11)	30 (16)	33 (3)	30 (9)	30 (6)	29b
Mean	26	26	32	33*	26	26	29	28	27	30	
					Root depth minus nematode depth (cm)[e]						
TX/2001	−40***	−34**	−25**	−36**	−39**	−31***	−24**	−38**	—	—	−34c
TX/2002	−43**	−40*	−41***	−38*	−41*	−40**	−45***	−26*	−36*	−37**	−39c
LA/2002	−17*	−11^	−12	0^	−5^	−15	−19*	−15^	−12^	−4^	−11b
MS/2002	6	5*	−6	4*	6*	0	5	5	0	12***	4a
AL/2002	−4	−17*	−23^	−18^	−12^	−16**	−7	−5*	−8	−14*	−12b
Mean	−20	−20	−21	−18	−18	−20	−21	−16	−18	−14	
					Mean root length density (cm roots extracted per cm^2 soil surface area 0–122-cm deep)						
TX/2001	52.4	44.4	53.7	55.9	40.2	53.2	55.4	50.7	—	—	50.8cd
TX/2002	27.9	16.7	45.2	26.6	32.7	45.0	48.6	41.1	35.7	42.8	36.2d
LA/2002	113.5	92.7	115.7	95.8	120.3	163.4**	92.7	126.8**	92.1	106.7	112.0a
MS/2002	86.6	77.6	75.0	71.4	65.7	61.0	65.1	68.1	69.6	90.1	73.0b
AL/2002	40.8	51.9	47.6	56.6	57.5	38.9	110.1**	81.6*	38.9	46.7	57.1c
Mean	64.2	56.6	67.4	61.2	63.3	72.3	74.4	73.7	59.1	71.6	
					Nematodes/cm root extracted						
TX/2001	33.1	42.0	24.4	23.9	25.8	16.6	24.5	29.0	—	—	27.5c
TX/2002	95.8	80.1	20.9*	21.5*	43.5	26.5*	35.7	32.8*	23.1*	36.8	41.7b
LA/2002	35.0	39.8	20.7	12.8*	19.4	22.8	21.3	16.9	13.0*	29.3	23.1c
MS/2002	32.1	22.9	5.4**	4.1**	14.8	15.1	9.0	8.5*	3.9**	9.6*	12.5d
AL/2002	93.6	88.5	76.3	32.5**	41.6*	60.0	5.6**	27.2**	39.0*	49.8	51.4a
Mean	57.9	54.7	29.5*	19.0**	29.0*	28.2**	19.2**	22.9**	21.3**	32.0*	

[a] *G. hi.* = *Gossypium hirsutum*; *G. he.* = *G. herbaceum*; *G. ar.* = *G. arboreum*; *G. ba.* = *G. barbadense*.

[b] GB-13 was planted in 2001 but replaced by GB-536 at all sites in 2002. GB-13 is omitted from calculation of means.

[c] Site means with the same letter do not differ by the LSD at $P < 0.05$; site means are potentially impacted by off-site effects, such as sample storage and processing dates.

[d] Depths were obtained by dividing 122-cm-deep core samples into 15.25-cm-long sections, splitting each section in half, extracting roots or nematodes from each half, determining the number of nematodes and cm of roots per gram soil, then calculating the depth at which 50% of the total nematodes or roots were accumulated when moving from the surface downward.

[e] Negative values indicate nematodes are deeper than roots.

4,5). A similar result was obtained for nematodes per cm root (Table 5) and for two replications extracted by both centrifugal flotation and Baermann funnel (Table 4). Calculated extraction efficiency of the Baermann funnel relative to centrifugal flotation was 54% for sand mix and 108% for field soil.

Generally poorer root growth in field soil than in sand in itself did not account for low Pf in field soil on the susceptible control because nematodes per cm root averaged for the five resistant accessions in field soil (6.7 nematodes/cm root, mean of 30 pots) were greater than nematodes per cm root averaged across the 10 combinations of resistant accessions and nematode populations in sand (6.2 nematodes/cm root, mean of 60 pots) (Table 5).

The most resistant accession in sand mix was GB-713, with 5% of the nematodes per g soil and 3% of the nematodes per cm root of Fibermax 832 (values are means of TX and LA populations).

2002 field experiments: Estimated height and foliar biomass of primitive accessions were 150 to 200% that of agronomic cotton in all fields. GB-713 and TX-110 were tallest and were more than 2 m tall in all fields. All *G. hirsutum*, *G. arboreum*, and *G. herbaceum* entries flowered and set fruit at all sites; the *G. barbadense* accessions did not flower at any site.

TABLE 2. Final population densities (Pf) of *Rotylenchulus reniformis* 0- to 30.5-cm deep in soil under susceptible cultivars of Upland cotton (*Gossypium hirsutum*) and resistant primitive accessions of *Gossypium* spp. in cotton fields at Weslaco, TX (TX), Baton Rouge, LA (LA), Stoneville, MS (MS), and Huxford, AL (AL). Each number is the mean of nematodes separately extracted from the top two 15.25-cm layers of soil within 122-cm-deep cores taken in four replicate plots per entry, except at Baton Rouge (LA), where there were three cores per plot and one plot per entry. Expression of data as percentages of the control does not affect differences detected by this analysis.

	Pf in soil in plow layer (0- to 30.5-cm deep)													
	Relative density compared to susceptible control (% Fibermax 832)							Absolute density compared to economic threshold (nematodes/g soil)						
	2001	2002				Mean[a]		2001	2002				Mean	
	TX	TX	LA	MS	AL	A	B	TX	TX	LA	MS	AL	A	B
Susceptible cultivars														
Fibermax 832 (*G. hi.*)	100	100	100	100	100	100	100	6.1τ[b]	4.0 τ	69.7	59.2	53.8	46.7	35.6
Suregrow 501 (*G. hi.*)	143	135	86	58	58*	84	79	8.8ττ	5.4 τ	60.0	34.5	31.4	39.4	28.1
Primitive accessions														
A1-17 (*G. he.*)	52	39	61*	6**[c]	21**	32*	12	3.2τ	1.6 τ	42.4	3.5τ	11.3ττ	14.8ττ	4.4τ
A2-87 (*G. ar.*)	67	31	35**	9**	12**	22*	0**	4.1τ	1.3 τ	24.4	5.6τ	6.5τ	10.3ττ	–0.1τ
GB-13 (*G. ba.*)	212	—	—	—	—	—	—	13.0ττ	—	—	—	—	—	—
GB-49 (*G. ba.*)	88	136	68	33*	51*	72	62	5.4τ	5.5 τ	47.1	19.4	27.3	33.6	22.1
GB-264 (*G. ba.*)	101	136	84	29*	34**	71	62	6.2τ	5.5 τ	58.3	17.3	18.4	33.1	21.9
GB-536 (*G. ba.*)	—	213	41**	12**	54*	80	70	—	8.6ττ	28.7	7.0τ	28.9	37.3	24.8
TX-110 (*G. ba.*)	103	163	54*	17*	48**	70	59	6.3τ	6.6 τ	37.5	10.1ττ	25.8	32.9	21.0
GB-713 (*G. ba.*)	—	72	39**	8**	25**	36	17	—	2.9 τ	27.5	4.7τ	13.6ττ	16.9	6.0τ
TX-1348 (*G. ba.*)	—	204	97	32*	29**	90	86	—	8.2ττ	67.8	18.7	15.4ττ	42.2	30.6
Mean for primitives	104	124	60	18	32	59	46	6.4τ	5.0 τ	41.8	10.7ττ	17.2	27.6	16.3
Mean suppression	—	—	40	72	68	39	—	—	—	27.9	42.6	36.6	19.0	—
Additional samples														
At planting	15.8	58	—	—	—	—	—	0.97	2.3	—	—	—	—	—
Pf in clean alleyways	—	17	28	28	14.4	24	—	—	0.7	19.5	16.5	7.73	11	—

[a] Mean A is the mean value for 2002 across all four locations; mean B is A calculated after subtracting from the mean for each entry at each location, the number of nematodes in similar core samples taken from clean alleyways between plots.

[b] Single and double Greek letter tau (τ, ττ) indicate nematode population densities at or below end-of-season treatment thresholds of 5,000 and 10,000 nematodes/ "pint" soil, as recommended to farmers by the Cooperative State Agricultural Extension Service in various southern states, and equivalent to 8.1 (for τ) and 16.2 (for ττ) nematodes/g soil at 1.3 bulk soil density.

[c] Asterisks (*, **) indicate difference from the susceptible control cv. Fibermax 832 at each site at $P < 0.05$ and $P < 0.01$, respectively, based on Dunnett's test for differences between treatments and a standard control.

Mean root-length density in all fields was greatest in the upper 30.5-cm layer, decreasing with depth (Figs. 1,2). For Fibermax 832, the percentages of total roots in the four 30.5-cm layers from the surface to 122 cm were 59, 20, 19, and 1% at Weslaco, 88, 8, 3, and 1% at Baton Rouge, 65, 27, 6, and 2% at Stoneville, and 65, 24, 11, and < 0.5% at Huxford. Roots were deepest at Weslaco and shallowest at Baton Rouge (Figs. 1,2; Table 1). The total root length (cm root per cm^2 soil surface area) of primitive accessions usually did not differ from the Fibermax 832 control, but was greater than the control for TX-110 at Baton Rouge and Huxford, for GB-264 at Baton Rouge, and GB-536 at Huxford (Table 1). Total root length averaged across all locations differed little among genotypes, ranging from 92% of Fibermax 832 for GB-713 to 116% of Fibermax 832 for GB-536. Total root length differed three-fold across locations ($P < 0.001$), however, with 36 cm root/cm^2 soil surface area at Weslaco and 112 cm/cm^2 at Baton Rouge (Table 1).

The mean Pi of *R. reniformis* at the test site at Weslaco at planting in 2002 (6.5 nematodes/g soil) was comparable to the mean Pi in 2001 (6.0 nematodes/g soil), and Pf on the Fibermax 832 control in 2002 (9.5 nematodes/g soil) was comparable to that in 2001 (10.2 nematodes/g soil) (Table 3). As in 2001, no primitive accession in 2002 significantly suppressed *R. reniformis* populations at Weslaco in the top 30.5 cm (Table 2) or top 122 cm of soil (Table 3) compared to Fibermax 832 ($P < 0.05$). In both 2001 and 2002, mean population densities under A2–87 and A1–17 were less than under the control 0- to 30.5-cm as well as 0- to 122-cm deep (significant across years) (Tables 2,3). GB-713 (not tested in 2001) had lower population densities than any other *G. barbadense* accession ($P < 0.01$).

Rotylenchulus reniformis vermiform stages were found at all depths at all sites. Nematode population densities 0- to 122-cm deep for Fibermax were greatest at Baton Rouge (25 nematodes/g soil) and lowest at Weslaco (9.5 nematodes/g soil) (Table 3). However, population densities 30.5- to 122-cm deep under the susceptible cultivars Fibermax 832 and Suregrow 501 at Weslaco were similar to those at Baton Rouge (Fig. 3). The lower average Pf 0- to 122-cm deep at Weslaco was attributable to the relative absence of nematodes in the top 30.5 cm (4.0 nematodes/g soil) at Weslaco, compared with the other sites, which had 53.8 to 69.7 nematodes/g soil in the top 30.5 cm (Figs. 1,2; Table 2).

The ability of resistant accessions to suppress soil populations of *R. reniformis* relative to the control varied

TABLE 3. Final population densities (Pf) of *Rotylenchulus reniformis* 0- to 122-cm deep in soil under susceptible cultivars of Upland cotton (*Gossypium hirsutum*) and resistant primitive accessions of *Gossypium* spp. in cotton fields at Weslaco, TX (TX), Baton Rouge, LA (LA), Stoneville, MS (MS), and Huxford, AL (AL). Each number is the mean of nematodes separately extracted from eight 15.25-cm layers of soil within 122-cm-deep cores taken in four replicate plots per entry, except at Baton Rouge (LA), where there were three cores per plot and one plot per entry. Expression of data as percentages of the control does not affect differences detected by this analysis.

	Pf in soil profile (0- to 122-cm deep)													
	Relative density compared to susceptible control (% Fibermax 832)							Absolute density compared to economic threshold (nematodes/g soil)						
	2001	2002				Mean[a]		2001	2002				Mean	
	TX	TX	LA	MS	AL	A	B	TX	TX	LA	MS	AL	A	B
Susceptible cultivars														
Fibermax 832 (*G. hi.*)	100	100	100	100	100	100	100	10.2τ[b]	9.5τ	25.0	18.3	23.7	19.1	13.6
Suregrow 501 (*G. hi.*)	113	79	92	61	113	86	80	11.5ττ	7.5τ	22.9	11.1	26.8	16.5	11.0
Primitive accessions														
A1-17 (*G. he.*)	72	43	61	13**[c]	62	45**	24*	7.4τ	4.1τ	15.2ττ	2.4τ	14.7ττ	8.6ττ	3.1τ
A2-87 (*G. ar.*)	73	37	29*	11**	28**	26*	−3**	7.5τ	3.5τ	7.3τ	1.9τ	6.8τ	5.0τ	−0.5τ
GB-13 (*G. ba.*)	64	—	—	—	—	—	—	6.6ττ	—	—	—	—	—	—
GB-49 (*G. ba.*)	64	91	58	34*	63	62*	45	6.5τ	8.7ττ	14.5ττ	6.3τ	14.9ττ	11.8ττ	6.3τ
GB-264 (*G. ba.*)	52	75	92	32*	61	65*	54	5.3τ	7.2τ	23.1	5.8τ	14.5ττ	12.4ττ	7.0τ
GB-536 (*G. ba.*)	—	118	52	20**	52	61*	43	—	11.3ττ	13.1ττ	3.6τ	12.3ττ	11.6ττ	6.1τ
TX-110 (*G. ba.*)	90	85	53	19**	55	53**	33	9.1ττ	8.1τ	13.3ττ	3.4τ	13.2ττ	10.1τ	4.7τ
GB-713 (*G. ba.*)	—	40	34*	10**	39*	31**	3**	—	3.8τ	8.4ττ	1.8τ	9.3ττ	5.9τ	0.4τ
TX-1348 (*G. ba.*)	—	103	78	33*	62	69	57	—	9.8ττ	19.4	6.0τ	14.6ττ	13.2ττ	7.7τ
Mean for primitives	69	74	57	22	53	51	33	7.0τ	7.0τ	14.2ττ	4.0τ	12.6ττ	9.8ττ	4.3τ
Mean suppression	31	26	43	78	47	49	—	3.2	2.5	10.7	14.3	11.2	9.3	—
Additional samples														
At planting	59	69	—	—	—	—	—	6.0	6.5	—	—	—	—	—
Pf in clean alleyways	—	20	44	27	18	27	—	—	1.9	10.9	4.9	4.2	5.5	—

[a] Mean A is the mean value for 2002 across all four locations; mean B is A calculated after subtracting from the mean for each entry at each location, the number of nematodes in similar core samples taken from clean alleyways between plots.

[b] Single and double Greek letter tau (τ, ττ) indicate nematode population densities at or below end-of-season treatment thresholds of 5,000 and 10,000 nematodes/"pint" soil, as recommended to farmers by the Cooperative State Agricultural Extension Service in various southern states, and equivalent to 8.1 (for τ) and 16.2 (for ττ) nematodes/g soil at 1.3 bulk soil density.

[c] Asterisks (*, **) indicate difference from the susceptible control cv. Fibermax 832 at each site at $P < 0.05$ and $P < 0.01$, respectively, based on Dunnett's test for differences between treatments and a standard control.

with depth and across sites. All accessions had a lower Pf than the control 0- to 122-cm deep at Stoneville, but only A2–87 and GB-713 had Pf lower than the control at Baton Rouge and Huxford ($P < 0.05$ or $P < 0.01$) and none did at Weslaco (Figs. 1,2; Table 3). Population suppression 0- to 122-cm deep by GB-713 ranged from 90% ($P < 0.01$) of the control population at Stoneville to 61% ($P < 0.05$) at Huxford, and suppression 0- to 122-cm deep by A2–87 ranged from 89% ($P < 0.01$) at Stoneville to 71% ($P < 0.05$) at Baton Rouge (Table 3). When compared to the control at each location, populations at Baton Rouge, Stoneville, and Huxford, but not at Weslaco, were suppressed more in the top 30.5 cm of soil than when averaged 0- to 122-cm deep (Tables 2,3). At Huxford, for example, all accessions suppressed the relative population density in the top 30.5 cm of soil, but only two did 0- to 122-cm deep.

A greater mean depth for nematodes than for roots as observed at Weslaco in 2001 was seen in 2002 again at Weslaco and also at Baton Rouge and Huxford, but not at Stoneville (Table 1). A corresponding increase with depth was observed in the ratio of nematodes to roots, e.g., in 30.5-cm layers from the surface downward within Fibermax 832 plots, there were 12, 33, 245, and 1,170 nematodes/cm root at Weslaco, 38, 55, 110, and 266 nematodes/cm root at Baton Rouge, and 82, 111, 154, and 163 nematodes/cm root at Huxford, compared with 143, 84, 51, and 16 nematodes/cm root at Stoneville, (calculated from data in Fig. 1). It was noted that the site with the least population suppression by resistant accessions, Weslaco (Tables 2,3), had the greatest mean difference (-39 cm) between nematode and root depth (Table 1), and the site with the greatest population suppression by resistant accessions, Stoneville, had the least difference (+ 4 cm) (Table 1).

Suppression of nematode population densities 0- to 30.5-cm deep relative to the control was correlated with suppression 30.5- to 122-cm deep at Weslaco ($P = 0.004$), Stoneville ($P = 0.001$), and Baton Rouge ($P = 0.096$), but not at Huxford ($P = 0.48$) (Fig. 3). Suppression relative to the control 0- to 122-cm deep averaged across all primitive accessions was 78% at Stoneville, 47% at Huxford, and 43% at Baton Rouge; corresponding suppression values for 0- to 30.5-cm deep were 72%, 68%, and 40%.

With two exceptions (GB-264 and TX-1348 at Baton Rouge), mean Pf 0- to 122-cm deep under all resistant accessions at all locations was below the high economic threshold of 16.2 nematodes/g soil, whereas Pf under both susceptible cultivars was above the 16.2 nema-

TABLE 4. Relative final population density (Pf) of *Rotylenchulus reniformis* in Texas in 2001 in three experiments conducted under field, environment chamber, and microplot conditions to elucidate factors influencing suppression of *R. renifomis* by primitive cotton accessions that are known to be resistant to the nematode in pots. Each number not in parentheses is the mean of four replicates in the field, six replicates in the growth chamber, and six replicates averaged across two dates per replicate in the microplot experiment, with nematodes in each case extracted by Baermann funnel; the numbers in parentheses are additional means for two extra replicates of samples extracted by centrifugal flotation in the growth chamber experiment.

	Relative Pf of vermiform *R. reniformis* in soil (% of Fibermax 832 susceptible control)				
	Field	Controlled environment chamber			Microplot
	Nematodes already in soil		Nematodes injected into soil		
	Texas *R. renifomis* population			Louisiana *R. renifomis* population	
Plant genotype[a]	Sandy clay loam		Sand		Sandy loam
Fibermax 832 (*G. hi.*)	100	100 (100)	100 (100)	100 (100)	100
Suregrow 501 (*G. hi.*)	113	86 (97)	76 (203)	103 (61)	71
A1-17 (*G. he.*)	72	—[b]	—	—	18**[c]
A2-87 (*G. ar.*)	73	64 (30)	16 (27)**	10 (10)**	2**
GB-13 (*G. ba.*)	64	—	—	—	28*
GB-49 (*G. ba.*)	64	—	—	—	30**
GB-264 (*G. ba.*)	52	74 (157)	31 (21)*	10 (6)**	17**
GB-536 (*G. ba.*)	—	54 (67)	19 (15)**	8 (5)**	—
TX-110 (*G. ba.*)	90	74 (87)	29 (33)**	4 (4)**	20**
GB-713 (*G. ba.*)	—	74 (60)	7 (21)**	3 (3)**	—

[a] *G. hi.* = *Gossypium hirsutum*; *G. he.* = *G. herbaceum*; *G. ar.* = *G. arboreum*; *G. ba.* = *G. barbadense*.
[b] Dashes indicate entries not included in a given experiment. Note TX-1348 not included in 2001 experiments.
[c] Asterisks (*, **) indicate significantly different from 100% at $P < 0.05$ and $P < 0.01$, respectively, based on Dunnett's test for differences between treatments and a standard control. Data were analyzed before conversion to percentages. Values without asterisks do not differ from Fibermax 832.

todes/g soil threshold at all sites except Weslaco (Table 3). In 15 cases, however, Pf for resistant accessions in the top 30.5 cm of soil was above and in five cases at Baton Rouge was at least two-fold above the highest economic threshold (Table 2). No primitive accessions suppressed populations in the top 30.5 cm relative to either treatment threshold at Baton Rouge and only four of eight did so at Huxford. Subtracting nematodes observed in clean alleyways from nematode population densities measured in plots augmented calculated suppression values; resulting mean suppression values 0- to 122-cm deep across sites were 100% under A2–87 ($P < 0.01$), 97% under GB-713 ($P < 0.01$), and 76% under A1–17 ($P < 0.05$) (first column B, Table 3); corresponding suppression values for those accessions in the plow layer were 100% ($P < 0.01$), 83%, and 88% (first column B, Table 2). A2–87 had the lowest nematode per cm root value averaged across sites ($P < 0.01$) and was one of the two genotypes with the lowest value at every site (Table 1).

DISCUSSION

Our primary hypothesis was that roots of candidate sources of resistance to *R. reniformis* in *Gossypium* can

TABLE 5. Absolute final nematode population density (Pf) of *Rotylenchulus reniformis*, estimated root-length density, and estimated vermiform nematodes per cm root in controlled environment chamber experiment designed to elucidate factors influencing suppression of populations of *R. reniformis* from Weslaco, TX (TX pop), and Baton Rouge, LA (LA pop), by primitive cotton accessions that are known to be resistant to *R. reniformis* in pots. Each number is the mean of six replications.

	Nematodes/g soil				cm roots/g soil				Nematodes/cm root			
	TX pop		LA pop		TX pop		LA pop		TX pop		LA pop	
Plant genotype[a]	Field soil[b]	Sand	Sand	Mean	Field soil[b]	Sand	Sand	Mean	Field soil[b]	Sand	Sand	Mean
Fibermax 832 (*G. hi.*)	25 B	654 A	899 A	526	2.6 B	15.9 A	14.6 A	11.1	10.4 B	51.3 A	62.2 A	41.3
Suregrow 501 (*G. hi.*)	22 C	496 B	923 A	480	2.6 B	26.9 A	18.3 A	15.9	10.6 B	24.4 B	57.4 A	30.8
A2-87 (*G. ar.*)	16 B	104 A**[c]	87 A**	69	2.0 C	10.3 B*	17.9 A	10.1	8.9 A	11.8 A*	5.2 A**	8.6
GB-264 (*G. ba.*)	19 B	206 A*	91 A**	105	3.9 C	17.5 B	24.1 A	15.1	5.3 AB	13.4 A	3.9 B**	7.5
GB-536 (*G. ba.*)	14 B	124 A**	76 A**	71	3.5 B	20.3 A	18.9 A	14.2	5.8 A	6.5 A*	4.6 A**	5.6*
TX-110 (*G. ba.*)	19 B	190 A**	39 B**	83	2.3 B	19.1 A	21.0 A	14.2	8.6 A	11.5 A*	1.8 B**	7.3
GB-713 (*G. ba.*)	18 A	48 A**	27 A**	31*	4.4 C	21.6 B	30.2 A	18.6	4.9 A	2.3 AB**	0.9 B**	2.7*
Mean	19 B	260 A	306 A		3.0 B	18.7 A	20.7 A		7.8	17.3	19.4	

[a] *G. hi.* = *Gossypium hirsutum*; *G. ar.* = *G. arboreum*; *G. ba.* = *G. barbadense*.
[b] Sandy clay loam.
[c] Asterisks (*, **) indicate values within a column significantly different from the susceptible control Fibermax 832 at $P < 0.05$ and $P < 0.01$, respectively, based on Dunnett's test. Values for the same parameter (e.g., nematodes per g soil) within a row followed by the same uppercase letter do not differ by the LSD ($P < 0.05$).

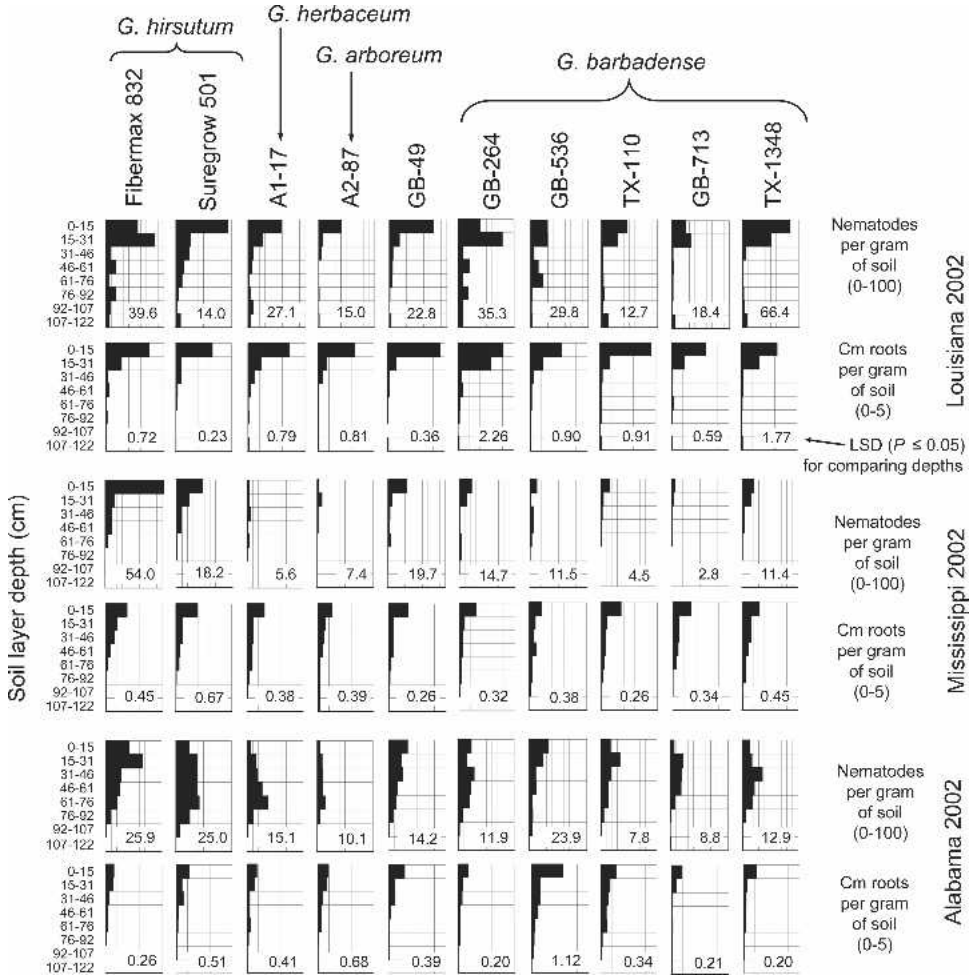

FIG. 2. Nematodes and roots collected in September 2002 from eight 15.25-cm layers of soil 0- to 122-cm deep in fields infested with *R. reniformis* at Baton Rouge, LA, Stoneville, MS, and Huxford, AL. Fields were planted to selected resistant and susceptible genotypes of cotton and related species. All graphs for each parameter (nematodes and roots) are to the same scale, and the number above the x-axis in each graph is the LSD for comparisons between depths within that graph. Each graph is the mean of three replications in Louisiana and four at the other sites, except for A1–17 and GB-536 at Huxford, which had two and three replications, respectively.

suppress the final population density (Pf) under field conditions sufficiently to merit introgression of resistance from them into commercial cultivars. We considered three criteria: 1) the candidate sources would need to colonize the soil profile well enough to expect that any population suppression observed resulted from a physiological factor inherent in roots rather than lack of roots in the soil; 2) Pf generally should be suppressed below Pf on a susceptible control, as observed in pot studies; and 3) Pf should be suppressed below the end-of-season treatment threshold, regardless of the initial population (Pi).

We further considered that, although a good resistance source would suppress the nematode population below that on a susceptible genotype, the required level of suppression would depend on the absolute population density. For example, if the final population density on a susceptible cultivar in a given field were 10 times the treatment threshold and a resistant accession in that field suppressed the population only 80%, then that accession would not have sufficient resistance to be economically competitive with nematicides or crop rotation as a nematode population management tool. On the other hand, failure to suppress low populations would not necessarily be bad. A good resistance source might suppress populations 95% relative to a susceptible genotype in a field at 10 times the treatment threshold, yet not measurably suppress sub-threshold populations in other fields if Pf on susceptible plants were sufficiently low or if nematode survival were high enough to mask effects of reduced reproduction. Furthermore, we did not test whether accessions with low to moderate levels of resistance (ability to suppress populations) are tolerant (able to yield well in the presence of nematodes).

The first condition supporting our hypothesis was met in the 2001 field experiment at Weslaco and at all locations in 2002. No resistant accession had less than 76% of the mean root-length density of the Fibermax 832 susceptible control 0- to 122-cm deep at any loca-

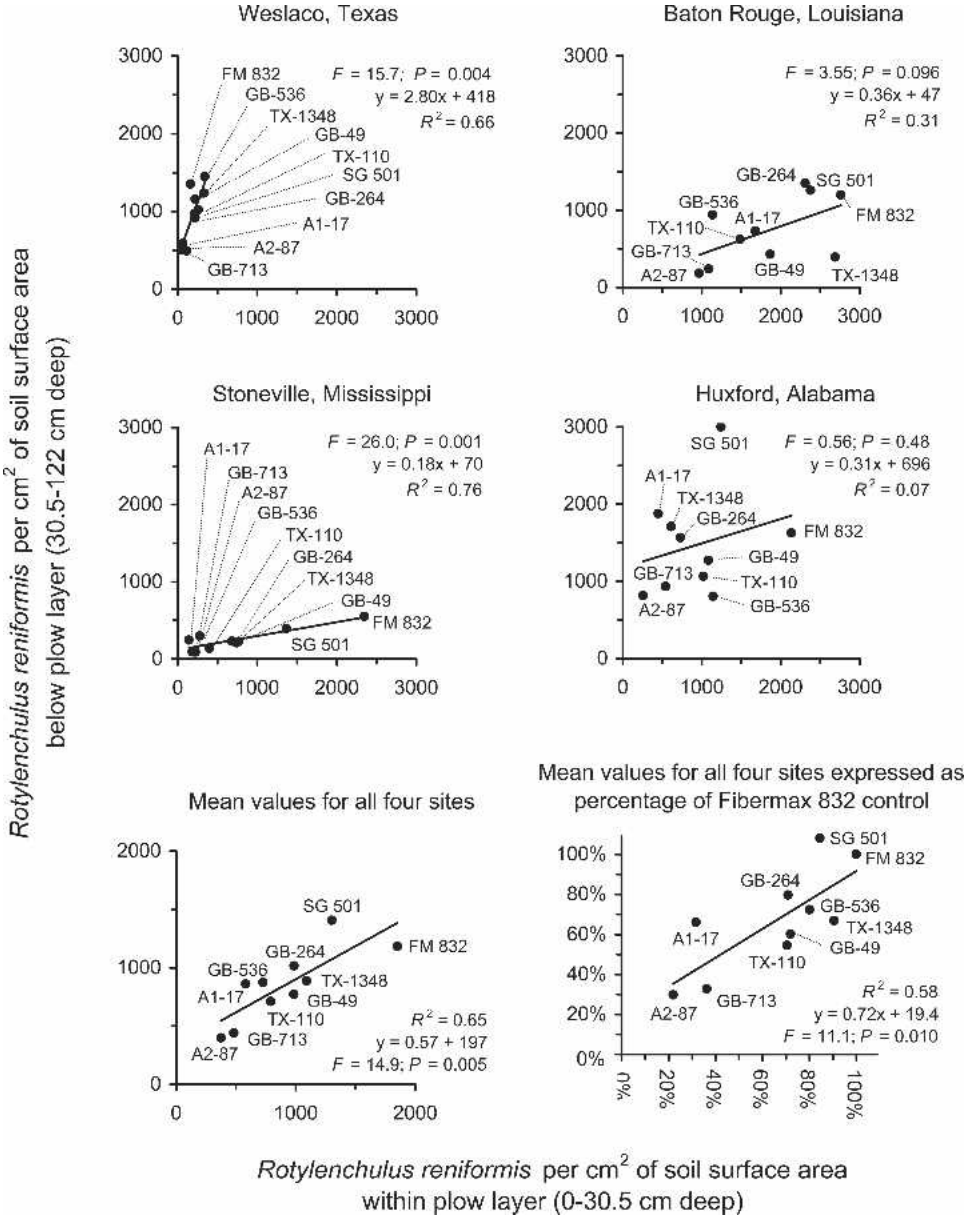

FIG. 3. Relationship between population density of *R. reniformis* in the top 30.5 cm of soil and that below 30.5 cm at the end of the growing season for two susceptible upland cotton cultivars (*Gossypium hirsutum*) and eight nematode-resistant accessions of *G. arboreum*, *G. barbadense*, and *G. herbaceum* planted at four sites in 2002. Each dot represents a different genotype and is the mean of four soil cores at Weslaco, Stoneville, and Huxford, and of three cores at Baton Rouge.

tion either year, and genotype root density averaged across locations ranged only from 92% of the control for GB-713 to 116% for GB-536 (Table 1). Mean root depths of genotypes averaged across locations ranged only from 100% to 127% of the control. By comparison, location strongly influenced total root-length density (Table 1) and vertical root distribution, with Baton Rouge and Weslaco being the extreme cases. Roots were shallowest at Baton Rouge, with an average depth of 19 cm, and deepest at Weslaco, with an average root depth of 32 cm. Root-length density at Baton Rouge (112 cm roots/cm^2 soil surface) was three times that at Weslaco in 2002 (36 cm/cm^2), primarily due to more roots near the surface at Baton Rouge (Table 1, Figs, 1,2).

The second condition of the hypothesis was met by microplot but not by cotton field results in 2001, with up to 98% population suppression in microplots ($P < 0.01$), relative to the control, and none in the field. In 2002, suppression of *R. reniformis* population density 0- to 122-cm deep relative to Fibermax 832 varied greatly across sites but at all sites except Stoneville (Tables 2,3) was less pronounced than in microplots (Table 4), in sand mix pots in the controlled environment chamber (Table 4), or in previous pot studies (Yik and Birchfield, 1984; Robinson and Percival, 1997; Moresco et al., 2004; Robinson et al., 2004). At Weslaco in 2002, as in 2001 (Tables 2,3), there was no significant population density suppression relative to the Fibermax 832 con-

trol, whereas at Stoneville, all accessions suppressed *R. reniformis* populations ($P < 0.01$ or $P < 0.05$) by 66 to 90% overall (0 to 122 cm) and 67 to 94% in the top 30.5 cm. At Baton Rouge and Huxford, levels of population density suppression relative to the control were intermediate between those at Weslaco and Stoneville (Tables 2,3).

At Weslaco, poor Pf suppression by resistant accessions relative to the control appeared to be associated with a low site population density (Tables 2,3). However, when comparing only Stoneville, Baton Rouge, and Huxford sites, the level of Pf suppression relative to the Fibermax 832 control was not associated with site population density, because the Pf 0- to 30.5-cm deep under Fibermax 832 at Stoneville, where the greatest suppression occurred, was intermediate between Pf on Fibermax 832 at Baton Rouge and Huxford (Table 2). Thus, unknown factors other than population density appeared responsible for the marked differences observed at field sites in the level of population suppression, relative to the control. Subtraction of Pf values measured in clean alleyways from those in plots with plants (Tables 2,3) gave adjusted Pf relative to the control for A2–87 and GB-713 that were comparable to those measured in microplots and sand mix pots (Table 4), suggesting that nematode survival from the previous year was an important factor masking resistance. Thus, the second condition of the hypothesis, that *R. reniformis* populations should be suppressed relative to a susceptible control as observed in pot studies, was met at three sites, but the level of suppression was less than that typically observed in pots, possibly due in part to high survival in the field. *Rotylenchulus reniformis* persists long periods in soil as eggs and as quiescent, molting or anhydrobiotic stages (Heald and Robinson, 1987; Heald and Inserra, 1988; Womersley and Ching, 1989; Caswell et al., 1991). Genetic variance in virulence among nematode populations is another possible factor. Davis et al. (2003) noted that cotton rotation to corn or resistant soybean, which support little or no reproduction by *R. reniformis*, does not suppress populations well in some fields. An examination of reproduction by 13 populations of *R. reniformis* on susceptible cotton cultivar Deltapine 50, susceptible soybean cultivar Braxton, and resistant soybean cultivar Forrest under greenhouse conditions indicated significant variance among populations, although no geographical component to variability among populations from cotton growing areas of the United States was apparent (Agudelo et al., 2005).

The third condition of the hypothesis, that Pf be less than the treatment threshold in the top 30.5 cm of soil, where samples are usually collected as a basis for treatment recommendations, was not met in most cases (Table 2). As noted, the high and low treatment thresholds of 16.2 and 8.1 nematodes/g soil to which data were compared are equivalent to 10,000 and 5,000 nematodes/pint (473 cm^3) of soil, respectively, at 1.3 g/cm^2 bulk soil density, and are the upper and lower end of the range of end-of-season densities within which recommendations for *R. reniformis* management in cotton under various growing conditions are currently made in states of the US where *R. reniformis* is problematic (Overstreet, 2001; Koenning, 2002; Komar et al., 2003; Sciumbato et al., 2004).

Sub-threshold populations under resistant accessions at Weslaco would be expected even if resistant accessions had no suppressive effect because populations under controls at Weslaco were sub-threshold (Table 2). At the three sites where populations in control plots were consistently above treatment thresholds, final populations in the top 30.5 cm were sub-threshold in only nine of 30 possible accession × site combinations; five accessions at Stoneville, four at Huxford, and none at Baton Rouge had sub-threshold populations (Table 2).

In sum, our primary hypothesis was that candidate sources of resistance suppress field populations of *R. reniformis* sufficiently to merit introgression. A first condition of the hypothesis, that candidate accessions develop enough roots to implicate physiologically based resistance when the final nematode population under an accession is low, was met at all locations. A second condition, that populations under resistant accessions be lower than on a susceptible control, was met for some accessions at three sites but the degree of suppression relative to the control was less than in pots. A third condition, that final populations under candidate accessions be less than the treatment threshold, was met for certain accessions at certain sites and was depth-dependent. Our results, consequently, support the hypothesis conditionally and provide additional information regarding which accessions are likely to be most useful, where, and when. Two accessions, *G. barbadense* GB-713 and *G. arboreum* A2–87, consistently exceeded other accessions in ability to suppress populations of *R. reniformis* in the soil and so would seem the best initial candidates for introgression among those tested.

At Baton Rouge, no primitive accession suppressed populations in the plow layer below the economic threshold, even though several of the resistant accessions tested were identified originally in greenhouse studies utilizing nematodes from the Baton Rouge field (Robinson et al, 2004). The best relative suppression levels overall were at Stoneville. Baton Rouge and Stoneville sites have similar soil textures (loam/silty loam at Stoneville vs. silty loam at Baton Rouge) and had similar population densities on Fibermax 832 in the plow layer (59 and 70 nematodes/g soil, respectively) (Table 2). They also are representative of the Mississippi Delta production region where *R. reniformis* is most problematic, and thus a rigorous comparison of factors responsible for differences in performance of

primitive accessions at the two sites could provide valuable practical information for implementing resistant cultivars when available.

Our first field experiment at Weslaco in 2001 indicated that all primitive accessions had total root-length values (cm roots per cm^2 soil surface) (Table 1) that were similar to the susceptible, agronomic control (77–107% of Fibermax 832), and the *G. barbadense* accessions had similar mean root depths, ranging from 96 to 111% of Fibermax 832. Only *G. herbaceum* A1–17 and *G. arboreum* A2–87 were unusual in having mean root depths 74 and 56% deeper, respectively, than Fibermax 832. However, no primitive accession suppressed end-of-season nematode populations at Weslaco in 2001 (Tables 2,3), even though all did in previous pot studies (Carter, 1981; Yik and Birchfield, 1984; Robinson et al., 2004). Microplot experiments outdoors the same year at College Station, on the other hand, showed strong suppression by all accessions (Table 4). Thus, the discrepancy was not due to a greenhouse light-quality effect. Known differences between conditions in the field and microplots, respectively, included: origin of nematodes (Weslaco vs. Baton Rouge); soil (natural sandy clay loam profile more than 122-cm deep vs. shallow, homogeneous sandy loam); soil microflora (those in soil vs. those associated with nematodes introduced to it); latitude and climate (4°, 7′ latitude difference between sites); frequency of irrigation (3 times/season vs. 2 to 3 times/week); time of year (March to July vs. June to November); Pi (1 nematode/g soil vs. 10,000/83 liter microplot, equivalent to 0.1 nematode/g soil); and method of nematode introduction (naturally present vs. introduced via syringe). The experiment in a controlled environment chamber employed a factorial design to separate nematode from soil effects while eliminating many differences between field and microplot environments (Table 5). Results ruled out Pi because initial populations were similar (6,000 nematodes/pot in soil vs. 4,000 nematodes/pot in sand), as well as nematode genetic makeup, because the LA and TX population Pi in the sand mix were not different. Photoperiod differences due to latitude also were eliminated. Instead, a soil-specific factor in the North farm field soil was implicated because, compared to the control, resistant accessions suppressed populations in sand mix but not in field soil.

Another striking result of the controlled environment chamber experiment was 15-fold greater mean Pf in sand mix than in field soil (Table 5). The 25 nematodes/g soil Pf for the control was 2.5 times the Pf in the field experiment (in the same soil) when averaged 0- to 122-cm deep (10 nematodes/g soil) (Table 3), four times that in the top 30.5 cm (6 nematodes/g soil) (Table 2), and above the higher economic treatment threshold that we considered. The mean sand mix population density (777 nematodes/g soil) for the Fibermax 832 control (Table 5) was probably higher than ever encountered in cotton fields and 11 times the density in the top 30.5 cm under Fibermax 832 at Baton Rouge (Table 2), which in turn was the greatest density at any depth at the four infested field sites in 2002 (Figs. 1,2) and seven times the mean density 0- to 122-cm deep at Weslaco in 2001 (Tables 3). The 148 nematodes/g soil on the control in microplots also was exceptionally high compared to most field populations. Consequently, it can be interpreted that root growth and nematode population development in pots containing naturally infested field soil were realistic when compared to development in the field, whereas pots with sand mix and microplots into which nematodes were injected favored exceptional development atypical of field conditions.

High nematode populations in containers with sand mix were associated with six times the root growth measured in field soil (Table 5). However, the mean number of nematodes per cm root on resistant accessions in field soil (6.7) was similar to that (6.2) in sand, while the number for the susceptible Fibermax 832 control in field soil was only 18% that in sand, suggesting again the presence of an additional important factor suppressing nematode population increase on susceptible plants in field soil. If it consistently suppressed population increase more on the cultivars than on primitive accessions, it would explain the difference between apparent levels of resistance in field soil vs. sand mix in the controlled environment chamber, as well as differences between field and microplot results.

The unidentified soil-specific factor responsible for failure of resistant accessions to suppress *R. reniformis* populations as well in cotton fields as in pots and the inability of those accessions to keep the Pf in the plow layer below the economic threshold at Baton Rouge would imply that future resistant cultivars of cotton developed from the available resistant primitive accessions of *G. arboreum*, *G. herbaceum*, and *G. barbadense* will not provide a reliable substitute for nematicide treatment of the upper soil layers in many fields. However, the economic threshold is the population level at which there is likely to be an economic return sufficient to cover the cost of fumigant and its application, costs that do not apply to the use of a resistant cultivar. In studies examining high rates and deep placement of fumigant at the Weslaco North farm and other Lower Rio Grande Valley sites (Westphal et al., 2004; Robinson et al., 2005a) at population densities of *R. reniformis* comparable to those measured at Weslaco, TX, in this study, 100% yield increases were obtained by applying 1,3-dichloropropene at 168 liters/ha or by spot-injecting fumigant at various points 30- to 120-cm deep. Although these methods are not economic, they demonstrate that resistant cultivars might yield much better than susceptible cultivars in many infested fields, even in fields with population densities below the economic threshold for nematicide treatment, if resistance (poor

ability to support nematode reproduction) confers tolerance (retention of high yield at high nematode population density). The relationship between resistance and tolerance to *R. reniformis* in cotton has not been studied; this examination will be essential for future research as resistant cultivars become available.

Several testable hypotheses explain the deeper distribution of nematodes than roots observed at Weslaco, Baton Rouge, and Huxford as well as in other fields (Robinson et al., 2005a). These include greater suitability of deeper, younger roots for nematode reproduction, downward movement of nematodes during the season, and high rates of mortality near the surface due to repeated wetting and drying, high temperature, and natural enemies. Perhaps the explanation is linked to the observation that the site with the least population suppression by resistant accessions, Weslaco (Tables 2,3), had nematodes 37-cm deeper than roots on average, while the site with the greatest population suppression by resistant accessions, Stoneville, had mean root depths similar to the mean nematode depth. Stoneville also had the most northern latitude of all sites, and the possible contribution of latitude and related factors, such as soil surface temperature, to differences between root and nematode depths could be tested in additional fields. High surface temperatures can drive *R. reniformis* downward in containers (Robinson, 1994).

In spite of marked changes in the ratio of nematodes to roots with depth, suppression of nematode population densities relative to the susceptible control by specific resistant accessions 0- to 30.5-cm deep at Weslaco, Stoneville, and Baton Rouge was a predictor of suppression 30.5- to 122-cm deep (Fig. 3). Also, absolute suppression 0- to 30.5-cm deep at a site gave an indication of the suppression achievable deeper in the soil at that site; at both depths the greatest suppression was achieved at Stoneville and the poorest at Weslaco, with intermediate levels at Huxford and Baton Rouge. Thus, our results finally indicate that future evaluations of the performance of resistant breeding lines and cultivars derived from resistant *Gossypium* spp. probably will not require collection of soil samples 122-cm deep.

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