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# BREEDING AND GENETICS

## History of USDA-ARS Cotton Host Plant Resistance and Breeding Research at Mississippi State, MS

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### ABSTRACT

**Cotton host plant resistance research was initiated with the establishment of the Boll Weevil Research Laboratory in 1960. Laboratory objectives were to conduct research and develop technology that ultimately could be used to eradicate the boll weevil. Early research concentrated on developing techniques and screening germplasm for resistance. A full-scale boll weevil eradication trial began in southern Virginia and eastern North Carolina in 1978 and after initial success the USDA Animal and Plant Health Inspection Service established an eradication program. This led the host plant resistance program to broaden its research into other pests of cotton. During the 1980s, research continued to focus on tarnished plant bug, tobacco budworm, expanding the genetic diversity of cotton, basic genetic and cotton breeding studies. With the development of field infestation techniques for the tobacco budworm, in the 1990s the research team conducted the first field test of *Bacillus thuringiensis* (Bt) transgenic cotton for resistance. During this time, root-knot nematode research expanded. Cotton fruiting efficiency and distribution of harvestable bolls and the concept of plant mapping were developed. During the 2000s, research expanded with the use of chromosome substitution lines for the introgression of new alleles into Upland cotton. Nematode research remained active during this time. To date, the research program has developed and released more than 800 germplasm lines and four random-mating populations. Scientists in the program have trained more than 60 graduate students and countless others have been mentored. The full impact of the research team will only be revealed with time.**

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### INTRODUCTION

The beginning of cotton host plant resistance research coincided with the establishment of the Boll Weevil Research Laboratory at State College (renamed Mississippi State on 16 September 1972), MS, in 1960. Leaders of the cotton industry appealed to the U.S. Congress in 1958 for a program of research that would adequately deal with the destructive boll weevil. In response, Congress directed the Secretary of Agriculture to review the situation and submit a report of research and facilities needed to address the boll weevil problem. The Office of the Secretary appointed a study group to gather information on current research being conducted by states, federal government, and industry on the boll weevil. The group was further instructed to determine needs for a comprehensive research program with broad areas appropriate for the federal government to support. In the report to Congress the first recommendation was to increase support for current federal research programs that were underway. The second recommendation provided for the establishment of a new laboratory with particular emphasis on new approaches to boll weevil control. In 1960, Congress appropriated $1,100,000 for the construction of the Boll Weevil Research Laboratory. In addition, $165,000 was appropriated for initial staffing. The Boll Weevil Research Laboratory was formally dedicated 21 March 1962. The Mississippi Entomological Association asked Congress to rename the laboratory in honor of Professor R. W. Harned. Professor Harned, known as the father of entomology in Mississippi, directed cotton insect research for USDA from 1931 to 1953. In late 1981, Congress passed a bill that was signed by President Reagan changing the name from Boll Weevil Research Laboratory to Robey Wentworth Harned Laboratory. The laboratory was rededicated at the annual Mississippi Entomological Association meeting on 10 November 1982.

The new Boll Weevil Research Laboratory was designed and equipped for research conducted in the fields of insect toxicology, chemistry, soil science,

insect pathology, biological control, agricultural engineering, and plant resistance to the boll weevil. Dr. Theodore (Ted) Davich, laboratory director, assembled scientists representing different scientific fields to concentrate as a team on new areas of research to solve one of the major problems of cotton production. The challenge was to work cooperatively with other federal laboratories and state and industry research groups to eradicate or at least relegate the boll weevil to a status of minor importance.

**Cotton Host Plant Resistance Research Begins.** With the hiring of Dr. Johnie N. Jenkins in 1961, a geneticist and recent graduate of Purdue University, and Dr. Fowden G. Maxwell, an entomologist and recent graduate of Kansas State University, the new program was established. Jenkins grew up on a farm in Arkansas and was familiar with the destruction and damage of the boll weevil to cotton production. He had also worked as a cotton scout in the Arkansas cotton scouting program. Maxwell studied under Dr. Reginald H. Painter (considered the father of insect plant resistance) at Kansas State and was familiar with how to set up a plant resistance research program. At the 1962 Cotton Improvement Conference, Maxwell (Maxwell and Jenkins, 1962) gave a presentation on the general aspects of host plant resistance to insects, followed by a presentation by Jenkins (Jenkins and Maxwell, 1962) on the research plans of the cotton host plant resistance research team. They planned to divide the research into five major areas with some research falling into more than one area. These research areas were: 1. development of techniques to adequately measure resistance and to speed up the process of evaluating the available germplasm, 2. biochemistry and/or physiology of host plant resistance, 3. study of morphological characteristics of the plant that could confer and/or influence resistance, 4. boll weevil behavior and attractancy studies, and 5. evaluation of the available *Gossypium* germplasm in field cages. These broad areas of research were the focus as the research team began its work. The research team had adequate physical facilities in the new Boll Weevil Research Laboratory to conduct their research as well as greenhouse and field-plot space. Jenkins pointed out a feature of the program was the ability to work with students and that assistantships for students interested in host plant resistance would be available. Students would take their course work at Mississippi State University and conduct their research with the host plant resistance team. Graduate student training has been a major accomplishment of the team.

## THE EARLY YEARS: 1960S BOLL WEEVIL RESEARCH

The early tasks were to hire support staff and student labor to assist the senior scientists in conducting research. The assigned laboratories had to be equipped and organized. Equipment necessary to conduct field studies had to be obtained and modified to conduct field-plot research. Cotton germplasm had to be acquired for study. This was a new program in a new laboratory, and new techniques needed to be developed to evaluate all forms of resistance. The literature had to be reviewed to determine what was known about the boll weevil and its host. Because the Boll Weevil Lab was not immediately ready for occupancy, the summer of 1961 was spent by Jenkins and Maxwell visiting several locations around the U.S. that were involved in cotton genetics and entomology research. This is how they met the legendary cotton geneticists S. G. Stephens and T. R. Richmond. These contacts and discussions with Stephens and Richmond proved to be useful to these relatively new scientists.

Early research concentrated on chemical stimuli that were extracted from the cotton plant. This research was aided by J. C. Keller, a scientist from the toxicology section of the Boll Weevil Laboratory. Cotton flower buds (squares) that were extracted with organic solvent had no effect on boll weevil feeding; however, on squares that were extracted with water, the weevils failed to feed (Keller et al., 1962). Additional research showed the water extracts did not appear to contain an attractant, as distilled water attracted as many weevils as the extract. The water-soluble substance extracted appeared to be an arrestant, which caused insects to aggregate or stimulated feeding. The arrestant was extracted from plant parts, including flowers, squares, petals, calyx, bolls, bracts, leaves, roots, and stems, with quantitative differences existing between different parts (Maxwell et al., 1963a). Utilizing a bioassay, the water extract was found to be a strong arrestant and feeding stimulant to the boll weevil (Jenkins et al., 1963). They further reported that the boll weevil exhibited differences for the extracts from genetically different lines and species of *Gossypium*. The order of preference was the same as that exhibited for fresh squares from the cotton lines. The Asiatic species, *G. arboreum* L. and G. *herbaceum* L., were much less preferred by the boll weevil than Upland cotton, *G. hirsutum* L.

Keller et al. (1963) noticed that the water from a defrosted freeze-drying apparatus used in the process

of freeze-drying cotton squares contained volatile substances that smelled like living cotton plants (Fig. 1). Upon testing these substances, they discovered they were attractants for the boll weevil. The oily residue remaining after the separation of the attractant from cotton squares was biologically assayed and found to act as a repellent to the boll weevil (Maxwell et al., 1963b). The attractant was also collected from the atmosphere surrounding cotton growing in an enclosed greenhouse. The extraction method consisted of using a pump to pass air into a steel trap filled with dry ice and methanol and freezing out the water vapor and the cotton-derived volatile substances (Keller et al., 1965).

**Figure 1. Top photo, J. N. Jenkins and F.G. Maxwell examining freeze-dried square powder; bottom photo, J.N. Jenkins on tractor, Bill Parrott left, and F.G. Maxwell planting cotton research plots, 1962-1963.**

Maxwell et al. (1965) reported that a water-soluble and readily extractable feeding deterrent was found in the calyx of Rose-of-Sharon, *Hibiscus syriacus* L., an alternate host of the boll weevil. In follow-up studies, Parrott et al. (1966) showed that when the calyx was removed from the Rose-of-Sharon, weevils fed and oviposited at approximately the same rate as on cotton. Field observations showed that infestation of the alternate host occurred only when the plant grew near cotton.

Jenkins et al. (1964a) developed a technique for measuring certain aspects of antibiosis in cotton to the boll weevil. It used lyophilized cotton square powder as the basic ingredient. Using the technique, antibiosis was found to be present in *G. thurberi* Tod., which resulted in smaller weevils and a longer development time.

To study the rate of boll weevil oviposition on squares of various cotton lines, Jenkins et al. (1964b) collected squares, brought them to the laboratory, and placed them in glass jars with female boll weevils. Squares were changed twice daily, and oviposition was recorded. After screening more than 500 old cultivars and breeding strains, Jenkins et al. (1965) reported they found 15 lines where the female boll weevil oviposited approximately 80% as many eggs as on a commercial cultivar. On three of the lines, egg production was only 60% of normal. Buford et al. (1967) reported on a laboratory technique to evaluate boll weevil oviposition preference among cotton lines. Boll weevils were caged in glass jars (0.5 pt), and fresh squares were placed in the jars twice per day, and upon removal, the number of oviposition punctures on the squares were counted. The test was repeated daily for 8 days. They reported that boll weevil oviposition was an insect biological response that could be modified by host plant genotype. They also reported that Sea Island cultivars Triple Hallmark and Seaberry were less preferred for oviposition by the boll weevil than Deltapine Smooth Leaf. Buford et al. (1968) screened 252 cotton lines for rate of oviposition and reported that 26 lines had 50% as many eggs as the mean of all lines in the test. Sea Island Seaberry was found to be the most resistant. Sea Island Seaberry was crossed to Deltapine Smooth Leaf, and inheritance studies revealed the oviposition suppression factor was under genetic control. The low oviposition character appeared to behave as incomplete dominance to high oviposition, as the low-by-high cross $F_1$ was intermediate between the two parents.

Glandless cotton had been observed to be more susceptible to several phytophagous insects when growing in breeding nurseries with glanded cotton. Laboratory experiments were designed to measure feeding, oviposition, and development time of the boll weevil on glandless and glanded cotton lines (Maxwell et al., 1966). Weevils tended to feed more on the glandless cotton; however, there was no overall difference in oviposition between the glanded and glandless lines. Oviposition did vary depending on the genetic background of the trait. Also, there were no differences in boll weevil development time. Field evaluations of the glandless cotton lines revealed they were not any more susceptible to the boll weevil than their glanded counterpart (Jenkins et al., 1967). Antibiosis studies showed there was no difference in number or mean weight of emerged weevils. Holder et al. (1968) established the duplicate linkage groups of glandless and nectariless (*gl*2-*ne*1 and *gl*3-*ne*2) in Upland cotton.

Two techniques of implanting eggs of the boll weevil into cotton squares were used to compare antibiosis in 12 cotton lines (Bailey et al., 1967a). Antibiosis was found in *G. arboreum*, *G. thurberi*, *G. davidsonii* Kellogg, and one *G. hirsutum* line. Bailey et al. (1967b) reported that mortality of boll weevils in squares of genotypically different lines of cotton varied from 10 to 53%. The highest mortality occurred in the larval stage and was probably caused by a toxic substance, a lack of proper nutrients, or a feeding deterrent in the squares. Changes that occur in the cotton plant during the growing season had little effect on boll weevil feeding, oviposition, and development (Bailey et al., 1969). Coakley et al. (1969) reported that the second and third instars of boll weevils caused cotton squares to abscise. These two larval instars caused a reaction in the plant that resulted in abscission of the squares. The boll weevil molts twice during larval development, and measurement of the head capsules demonstrated that the insect has three well-defined instars (Parrott et al., 1970).

Ascorbic acid is a natural, water-soluble vitamin that is essential for boll weevil development. Hudspeth et al. (1969) reported that it would not be practical to develop cotton lines with low enough levels of ascorbic acid to inhibit boll weevil growth due to the minute quantities required for normal weevil development. Amino acids were investigated in host and non-hosts of the boll weevil (Parrott et al., 1969). All the amino acids essential for growth and development of the boll weevil except tryptophan were found in both host and non-host plants. Tryptophan was found present in cotton using a microbiological assay, but it was not analyzed for in the other plants. There were not sufficient differences in the amino acids to explain host versus non-host status.

Five frego, four red, and several Sea Island cotton lines received less boll weevil oviposition than the commercial check, Deltapine Smooth Leaf, after 3 years of testing under small field-plot conditions (Jenkins et al., 1969). In general, lines that had been selected for low oviposition in laboratory tests showed reduced oviposition in field tests. In laboratory tests, frego lines with bracts removed showed no reduction in oviposition; however, in field plots, frego lines showed a significant reduction in oviposition. The laboratory tests measured oviposition suppression caused mainly by chemical factors, whereas the field-plot tests measured general resistance to oviposition.

Considerable progress was made during the 1960s in the development of laboratory and field-plot techniques to measure resistance in cotton to the boll weevil. Several chemical stimuli were identified in the cotton plant, including an arrestant, a feeding stimulant, an attractant, and a repellent. Cotton lines were identified that exhibited antibiosis to the boll weevil. Furthermore, lines were identified that had reduced oviposition in laboratory and field-plot tests. The research team was able to recruit graduate students during this time, and the program was moving forward toward the development of boll weevil resistant cotton lines.

## THE 1970S

During the early 1970s, the cotton host plant resistance team continued its efforts to find resistance to the boll weevil. During this time, a trial boll weevil eradication experiment was conducted in south Mississippi. The results were evaluated, and the decision was made that eradication was feasible with the current technology that had been developed. This decision was not without controversy. The eradication effort moved forward with the first full-scale trial in 1978 in southern Virginia and eastern North Carolina. After initial success, the USDA's Animal and Plant Health Inspection Service (APHIS) established an eradication plan involving USDA and cotton producers jointly funding the eradication efforts. The host

plant resistance program broadened its research into other economic pests of cotton.

To determine if glandless cotton was more susceptible to cotton bollworm (*Heliothis zea* [Boddie]), Oliver et al. (1970a) compared 14 pairs of glanded/glandless cotton lines in field plots grown under a natural infestation. They reported that oviposition and damage to squares and bolls by larvae were not different; however, the high variability between lines contributed to no significant differences being detected. Several of the glandless lines had more square and boll damage than their glanded counterpart. In laboratory tests, food conversion of small larvae was less efficient versus large larvae when fed on glanded diets versus glandless diets (Oliver et al., 1970b). The amount of food consumed and net-weight gain on the glanded and glandless diets were directly related to the size of larvae when they were placed on the diet. All larvae fed from glanded diet gained less weight than similar-sized larvae fed glandless diets. Larvae also consumed less on a glanded diet than on a glandless diet. Growth of small larvae was most inhibited. The differential reduction in efficiency of food conversion was responsible for the smaller larvae produced by feeding glanded diets. In a related study, there was no difference in the growth of two strains of cotton bollworm larvae when they were fed on diets of lyophilized squares of 14 pairs of glanded and glandless cotton; however, all larvae were larger when they were fed on glandless diets and plants (Oliver et al., 1971).

Cotton with frego bract has shown resistance to the boll weevil when grown in small field plots (Jenkins et al., 1969). In 1970, boll weevil populations were measured when frego bract and a commercial variety were planted on four farms in large plots that ranged from 4 to 8 ha in size. Boll weevil oviposition was measured weekly during the summer; in frego bract plants, oviposition was suppressed 66, 71, 75, and 94% below that of the non-frego cultivars. The variation in suppression was due to the number of overwintering weevils and in-season management and supplemental control measures. The frego bract field with the lowest suppression had the most overwintering weevils as evidenced by the numbers recorded in pheromone traps. The largest suppression occurred on the farm with the fewest overwintering weevils (Jenkins and Parrott, 1971). Boll weevil population suppression was measured when frego bract cotton was used with and without a reproductive-diapause program the previous year (Jenkins et al., 1973). The test was conducted in 1971 in Yalobusha County, MS, using 22 fields. Frego bract fields were 1.6 to 2.0 ha each and normal bract fields were approximately the same size and were located adjacent or nearby. Fourteen fields received diapause control and eight did not. Population suppression was 69 and 79% with and without the diapause treatment. Application of insecticide was delayed 4 weeks in the frego fields (Jenkins et al., 1973). Insecticides (azinphosmethyl and methyl parathion), when applied to frego bract cotton for boll weevil control, left greater deposits and caused higher mortality to weevils than when applied to normal bract cotton (Parrott et al., 1973).

Frego bract cotton was observed to be more sensitive to the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), than normal bract cotton. An analysis of sugars in leaf tissue was conducted to determine if a taste preference might exist for frego bract cotton (Holder et al., 1974). No qualitative differences in sugar fraction were found between frego strain M64 and Deltapine 16.

The twospotted spider mite, *Tetranychus urticae* Koch., can be a serious pest of cotton when environmental conditions favor its establishment. Schuster et al. (1972a) developed a technique for mass screening cotton seedlings in the greenhouse for twospotted spider mite resistance. The greenhouse seedling rating agreed with the field rating and required 30 days versus 60 days for the field test. Fecundity was not a reliable indicator of resistance with few replications. Using the greenhouse screening method, Schuster et al. (1972b) evaluated 21 primitive accessions of *G. hirsutum*, 22 *Gossypium* species, 12 pairs of glanded and glandless lines, and 4 high-gossypol breeding lines for resistance to the twospotted spider mite. The highest level of resistance based on plant damage index was found in *G. barbadense* L. (Pima S-2), followed by *G. australe* F. Muell., and *G. lobatum* Gentry. All race accessions were damaged more than Pima, but a few damaged less than Upland cultivars were not considered resistant. The glanded/glandless lines and the high-gossypol lines suffered equal damage; however, the fecundity on the glandless lines was greater than that on the glanded lines. Plant damage indices and fecundity were not correlated. Antibiosis was demonstrated in Pima cultivars compared with Deltapine 16 by a reduction in fecundity (Schuster et al., 1972c). When reared on

Pima S-2, the life cycle was lengthened compared with Deltapine 16. Schuster et al. (1973) used a seedling screening technique to evaluate 994 cotton lines and cultivars for resistance to the twospotted spider mite. These included 429 Stoneville accessions, 330 *G. hirsutum* race stocks, 37 *G. barbadense* lines, 95 multiple-disease-resistant cultivars, 27 interspecies crosses, and 77 $F_1$ crosses between *G. hirsutum* races or Sea Island cultivars with Upland cultivars. Susceptible Stoneville 7A and resistant Pima S-2 were included in each test as checks. No resistance was found in the Upland cotton cultivars; however, resistance was found in *G. barbadense* lines and in some *G. hirsutum* race accessions.

To facilitate future research, improved techniques for rearing the tarnished plant bug were developed. Parrott et al. (1975) developed a technique to rear many tarnished plant bugs in small cages under controlled conditions in a laboratory using green beans as a source of food.

In 1970, 249 diverse cotton lines were grown at Mississippi State, MS, and the Red River Experiment Station, Bossier City, LA, and evaluated for tarnished plant bug resistance (Jenkins et al., 1977). Naturally occurring populations of the plant bug at both locations were not large enough to cause economic damage. The test was repeated in 1971 at the Mississippi Agricultural and Forestry Experiment Station, Northeast Branch Station, Verona, MS, and the Red River Experiment Station. The experiment was divided into treatment one, which consisted of 20-ft rows of cotton alternated with 20-ft rows of mustard; and treatment two was 20-ft rows of cotton alternated with a skip row. Treatment one was on one side of the field, and treatment two was on the opposite side with a four-row buffer in the center of the field. Insecticides were applied weekly in treatment two (no mustard plots) for plant bug control. Flowering rate was recorded weekly and used as a measure of resistance. The flowering rates for 30 of the 249 lines were not significantly different between the two treatments at each location. The resistance of the lines was found to be associated with leaf pubescence, with 27 of the 30 lines being rated as moderately hairy or greater.

Behaviors of the tarnished plant bug on cotton and horseweed, *Erigeron canadensis* L., were investigated in 1971 (Latson et al., 1977). Based on observation in a field cage containing cotton, tarnished plant bug spent 46% of the time in locomotion, 27% resting, 15% cleaning or grooming, 11% feeding, and 1% ovipositing. On horseweed, the plant bug spent approximately 35% of the time in locomotion, 27% resting, 2% cleaning or grooming, and 1% ovipositing. On horseweed, in contrast to cotton, more time was spent feeding and less time was spent cleaning. On cotton, tarnished plant bug spent approximately 45% of the time feeding on squares and 25% on the leaf nectary. Stipules, bract, and petiole made up approximately 15% of feeding time.

Jenkins et al. (1978) evaluated 191 primitive race accessions of *G. hirsutum* for resistance to the boll weevil. Because most of the accessions were photoperiodic, they were grown in Mexico and squares were shipped to a laboratory in Brownsville, TX, where they were evaluated for boll weevil oviposition. They found 69 accessions that had significantly fewer boll weevil eggs oviposited when compared with a susceptible check. From 16 to 78% as many eggs were oviposited on the resistant accessions as on M-8. To conduct field evaluations, these lines needed to be converted to flowering types. A backcross breeding program was used to eliminate the photoperiodic response of 20 selected accessions so they could be evaluated for boll weevil resistance under field conditions (McCarty et al., 1977). The accessions were crossed and backcrossed twice to the recurrent cultivar Deltapine 16. The resulting progeny were evaluated for boll weevil oviposition suppression in replicated field tests. The $BC_2$ progenies of T-25B-58, T-80, and T-209 had significantly less oviposition than the susceptible control Deltapine 16.

In 1974, 109 primitive race accessions of *G. hirsutum* were grown in single-row field plots at Mississippi State, MS, to classify the photoperiodic response. All the accessions were photoperiodic, and only a few plants in a few accessions flowered late in the growing season (Jenkins and Parrott, 1978). Field conditions and weather late in the season allowed *Cercospora gossypina* Cooke 1883 [synonym *Mycoshaerella gossypina* (G.F. Atk.) Earle 1900] and the leaf spot caused by the organism to be prevalent in the field plots, also verticillium wilt caused by *Verticillium dahlia* (Klebahn) was severe in the field. The accessions were rated for resistance to leaf spot and wilt. A scale (0 = immune to 5 = very susceptible) was used to score for resistance to leaf spot. No accession rated 0, but eight were rated 1 (Deltapine 16 was rated 2). Of the 109 accessions, 45 were rated 1 to 3 and considered resistant to leaf spot. Even though most of the cotton plants did not fruit, many showed symptoms of severe verticillium wilt to the

point of complete defoliation. Nineteen accessions were rated resistant to both Cercospora leaf spot and verticillium wilt (Jenkins and Parrott, 1978).

Kappleman et al. (1979) evaluated day-neutral derived lines from primitive race accessions of cotton for resistance to fusarium wilt. Materials with either accession 69 or 78 in their background expressed a high degree of resistance, both as race stocks and as crosses to Deltapine 16. Selections of advanced lines from crosses of Deltapine 16 and six other race accessions, 78, 80, 87, 113, 116, and 495, were also highly resistant to fusarium wilt.

A conversion program was initiated in the 1970s to incorporate day-neutral genes into photoperiodic *G. hirsutum* primitive race accessions of cotton (McCarty et al., 1979). The program involved crossing short-day race accessions with a day-neutral donor line at a tropical cotton nursery. The resulting $F_1$ was self-pollinated at the tropical nursery. The $F_2$ population was grown at Mississippi State, MS, where segregation for flowering occurred. Equal numbers of open-pollinated bolls were harvested from plants that set fruit, and the seed were bulked for each population and then increased for research purposes. One plant that set fruit at a low node and continued to fruit was selected from each $F_2$ population. The $F_3$ progeny from the plant was backcrossed to the race accession. This cycle was repeated for four backcrosses. Day-neutral converted accessions were evaluated for useful traits and released for use by cotton breeders and researchers.

Parrott et al. (1978) developed a procedure to test newly hatched larvae of tobacco budworm, *Heliothis virescens* (F.), on small terminal leaves of cotton where they naturally feed. Using the procedure, 30 primitive race stock accessions and controls were evaluated. Larvae on 12 race accessions and a high-gossypol strain were significantly smaller than larvae on Deltapine 16. Hall et al. (1980) evaluated three methods for artificially infesting cotton with tobacco budworm. Method 1 used eggs suspended in corn meal applied to the terminal of plants. Method 2 also used eggs, but they were suspended in a 0.5% xanthane gum solution and applied with a hand sprayer to the terminal area; method 3 used 1$^{st}$ instars mixed in corn meal and applied with a plastic dispensing device to the terminal area of plants. Recovery of larvae after 10 days for method 1 was less than 1% and was not feasible for the establishment of field infestations. Methods 2 and 3 were effective in establishing field infestation of tobacco budworm.

## THE 1980S

During the late 1970s, there was a change in the USDA Agricultural Research Service (USDA-ARS) organizational structure at the Mississippi State, MS, location. The Crop Science Research Laboratory was organized containing the research units: engineering, forage crops, crop modeling, corn host plant resistance, and cotton host plant resistance, formerly under the Boll Weevil Research Laboratory, with Rex Colwick, an agricultural engineer, as director. There was no physical movement of personnel. During the 1980s, the cotton host plant resistance program continued to shift its focus away from the boll weevil as the eradication program continued its movement in a westward direction from the east coast. The cotton host plant resistance program expanded into root-knot nematode research as a result of the USDA-ARS Cotton Nematode/Pathology research program at Auburn, AL, being transferred to Mississippi State, MS. The USDA-ARS program at Auburn consisted of Raymond Shepherd, research agronomist, conducting root-knot nematode research and A.J. Kappleman, research pathologist, conducting research on fusarium wilt. Kappleman chose to retire, but Shepherd accepted the transfer in 1984 and retired in 1990. Paul Hedin and A. C. Thompson, both research chemists, joined the cotton host plant resistance unit in 1985 from the former Boll Weevil research unit. Thompson retired in 1987 and Hedin continued to support the cotton host plant resistance program until his retirement in 1997. Research continued to focus on the tarnished plant bug, tobacco budworm, expanding the genetic diversity of cotton through the conversion of photoperiodic stocks to day-neutrality, and basic cotton genetic studies (Fig. 2).

**Figure 2. Members of the cotton host plant resistance research team in 1986. Standing (L to R), Mustafa McPherson, Joe Mulrooney, Raymond Shepherd, Barry Knight, Jack C. McCarty, Valeria Allsup, William L. Parrott, Johnie N. Jenkins, and Paul Hedin (seated). Photo December 1986.**

**Bacterial Blight Studies**. Mahill et al. (1982) evaluated 50 populations of cultivar-cytoplasm reciprocal crosses for five species cytoplasms, *G. herbaceum*, *G. arboreum*, *G. anomalum* Wawr. & Peyer, *G. barbadense*, and *G. tomentosum* Nutt. ex Seem., and five cultivars, B3083, Coker 201, Delcot 277, Stoneville 213, and Deltapine 16, for resistance to bacterial blight. The populations were evaluated in a greenhouse test where seedlings were inoculated with a mixture of races 1, 2, 7, 10, and 18 of bacterial blight. The reciprocal differences and cytoplasmic effects were considered identical in this study. There were small differences in blight grade, but none of the five cytoplasms increased susceptibility to bacterial blight. In 1978 and 1979, 82 cotton lines involving 54 *G. hirsutum* primitive accessions, 10 $BC_2F_5$, and 119 $F_3$-derived lines were evaluated for bacterial blight resistance in greenhouse tests (Mahill et al., 1983b). The lower epidermis of seedling cotyledons was inoculated with a mixture of bacterial blight races 1, 2, 7, 10, and 18. Visual blight ratings were conducted following maximum disease reaction, which occurred from 9 to 13 days after inoculation. None of the lines were rated resistant; however, 11 lines were rated equal to Stoneville 213 and Deltapine 61, which were rated intermediate in resistance to bacterial blight. Resistance in the study was not associated with any primitive race or geographic origin.

Mahill et al. (1983c) evaluated 165 primitive race accessions for bacterial blight resistance. Day-neutral progeny derived from race accessions that scored between 4.1 and 6.4 for resistance, in the same range as Stoneville 213 and Deltapine 61, were also evaluated. Of the 165 race accessions evaluated, 54 were more susceptible than Stoneville 213 or Deltapine 61. Seventy-seven accessions with blight scores between 4.1 and 6.4 were considered potential sources of intermediate resistance, and their day-neutral progeny were evaluated. Only three day-neutral lines were more susceptible than Stoneville 213; whereas one, M-7914-0209, was significantly more resistant than both Deltapine 16 and Stoneville 213. The other day-neutral lines were generally equal to Stoneville 213 or more susceptible.

**Allelochemic Studies.** White et al. (1982a) determined the inheritance of several hypothesized allelochemics from cotton that are alleged to confer resistance to the tobacco budworm. Three crosses, DES-24 x SATU-65, DES-24 x BJA-592, and DES-24 x MOHG, and the six populations needed for a generation means analysis were developed. The populations were grown in field plots where young leaves were collected and analyzed for condensed tannins, catechin, total phenols, aniline reacting terpenes, and phloroglucinol reactive compounds at intervals during the growing season. The inheritance of gossypol, as measured by the phloroglucinol test, was predominately additive gene action; however, gossypol was inherited by dominant gene action when measured by the aniline-reacting terpene test. The two tests appeared to measure different gene products that were inherited in different ways. Tests used to determine condensed tannins appeared to measure diverse genetic products; however, genetic analyses were highly additive for tannins for all the tests used. A high degree of additive gene action was found also for flavonoid-anthocyanins and total phenolics.

White et al. (1982b) determined the effects of within-season environment and cotton strain on allelochemics alleged to be important in repelling the tobacco budworm. Twenty diverse strains of cotton were grown in replicated field plots and leaves were collected weekly for 10 weeks beginning on 13 June, approximately 1 week before squaring. The leaf tissue was freeze dried and analytical tests were conducted to measure total phenolic compounds, gossypol and its analogs, flavonoid-anthocyanin mixture, and condensed tannins. Data analyses detected significant differences among cotton strains, sampling dates, and significant interaction between these main effects. The interaction component was small relative to the main effects. The results of the study indicated significant genetic variation exists among cotton strains for allelochemics, and the genotype-by-week interaction within a season was small.

In another study, neonate larvae of tobacco budworm were fed on a commercial wheat-germ diet for 5 days that contained various concentrations of eight allelochemics that naturally occur in cotton (Jenkins et al., 1983). The level of each allelochemic in cotton required to reduce larval weight 90% was within the range of the amounts found in various cotton strains and primitive accessions.

**Miscellaneous Studies**. The yield potential and adaptability of nine nectariless-nectaried pairs of cotton were evaluated for 1 to 3 years, 1978 to 1980, at six locations with and without early-season insect control (McCarty et al., 1983). Early-season insect

control was a side-dress application of aldicarb at pin head square. Insecticides were applied late season as needed. Five of the pairs of cotton were in conventional Coker, Deltapine, Stoneville, or DES genetic backgrounds. The others were backcrossed-derived strains that combined the nectariless or nectaried trait with frego bract, okra leaf, smooth leaf, high gossypol, or glandless. The largest mean squares within a year's analyses were for locations, suggesting a wide range of environments were sampled. Nectariless cottons had significantly higher first harvest yields than nectaried ones in 1978 and 1979, and over the 3 years nectariless cottons averaged 5.7% higher total yield than nectaried cottons when grown with and without early-season insect control. However, no differences in total yield were detected between the nectaried/nectariless cottons when grown with early-season insect control. An environmental index used for the 18 environments studied was determined by the average performance of two nectaried cottons, Stoneville 213 and Deltapine 61, and two nectariless ones, Stoneville 825 and Deltapine 7146N. When grown with early-season insect control, the average regression coefficient for nectariless cotton was not different from nectaried ones (b = 0.81 vs. b = 0.79). However, when grown without early-season insect control, the average regression coefficient for nectariless was significantly higher than nectaried ones (b = 0.86 vs. b = 0.76). The average regression coefficients for the glandless, high gossypol, okra leaf, and frego bract were 0.64, 0.70, 0.76, and 0.43, respectively, when grown with and without early-season insect control. Results suggested that nectariless cottons used in this study had high adaptability potentials, but the other traits investigated did not.

**Root-knot Nematode Studies.** Shepherd et al. (1988b) conducted a study to compare resistance to egg production of root-knot nematode resistant breeding lines to commonly grown commercial cultivars of cotton. Cotton seedlings were grown in individual pots in the greenhouse and inoculated with 10,000 root-knot nematode eggs at planting. Eggs produced on the seedlings were collected 40 days after inoculation and counted. The commercial cultivars evaluated were all susceptible to root-knot nematode egg production except LA434, which was significantly more resistant than the other cultivars. Susceptible cultivars had 7.6 to 14 times more eggs produced on their roots than were applied to them as inoculum. The resistant breeding lines had one-fourth to one-eighth as many eggs produced as applied to them. Development of high root-knot resistance cultivars could prevent or greatly reduce economic losses in cotton from this nematode.

**Tarnished Plant Bug Studies**. Lambert et al. (1980a) evaluated 38 foreign and domestic cotton cultivars for tarnished plant bug resistance in field plots inter-planted with mustard. They identified five early-maturing cottons from Bulgaria that showed resistance to the tarnished plant bug.

The moderate level of tarnished plant bug resistance in Timok 811 was crossed to susceptible frego bract and subsequently crossed to nectariless to improve resistance of the frego (Milam et al., 1985). They developed frego bract strains with tarnished plant bug resistance and earliness comparable with that of Timok 811 and yield comparable to the original frego bract parent and the nectariless parent.

A 3-year study conducted in 15 environments evaluated the effect of aldicarb on early-season control of tarnished plant bugs (Parrott et al., 1985). Ten of the 15 environments had populations of tarnished bug sufficient to effect yield. Results showed that aldicarb used at 2.24 kg (AI) per ha reduced tarnished plant bug numbers and increased yield.

**Boll Weevil Studies**. Forty-four domestic and introduced cultivars and strains of cotton were evaluated in the laboratory for resistance to the boll weevil (Lambert et al., 1980b). A low level of resistance was found in some lines; however, oviposition was not significantly (0.05 level) lower than that of the cultivar Stoneville 213.

Four primitive race accessions of cotton that exhibited resistance to the boll weevil were each crossed to Deltapine 16 and subsequently selected for the day-neutral flowering habit. These progenies were then backcrossed twice to their respective primitive accession and selected for day-neutrality following each backcross. The resulting progenies were evaluated for boll weevil oviposition by McCarty et al. (1982b). Weevils oviposited less often on $BC_3F_3$ progeny of T-78 than on the controls, Deltapine 16 and Stoneville 213. The level of resistance in the day-neutral T-78 approached that of the original photoperiodic accession. No differences were found in oviposition among the controls and the other three day-neutral accessions. In the early 1970s, boll weevil resistance was identified in the photoperiodic primitive *G. hirsutum* accessions, T-326 and T-1180. These accessions were crossed to Deltapine 16 and progeny with day-neutral flowering habit were selected. The day-neutral progeny were

backcrossed twice to their respective primitive accession and selected for day-neutrality following each backcross. The resulting day-neutral progeny were evaluated for boll weevil oviposition (McCarty et al., 1987). Significantly less oviposition was found on $BC_2F_4$ progeny of T-326 and T-1180 than on the control, Stoneville 213. The rate of oviposition was 57 and 54%, respectively, of the control. Resistance was later confirmed in field-plot research in Louisiana and Brazil.

McCarty and McGovern (1987) measured oviposition preference of two laboratory colonies of boll weevils on day-neutral progenies of primitive cottons. These day-neutral progenies carried resistance to the boll weevil. Rate of oviposition was used to compare the two colonies of insects. Colony 1 had been in mass production for several years without infusion of wild types; Colony 2 had not been in mass production and wild weevils had been introduced yearly. No significant differences in oviposition rate were found between primitive cottons and the susceptible control, Stoneville 213, when weevils from Colony 1 were used for testing. However, significantly fewer eggs were laid on the primitive cottons than on the control when weevils from Colony 2 were tested. The long-term mass-reared boll weevil Colony 1 did not exhibit oviposition preference; these weevils lost their ability to discriminate between lines of cotton. Oviposition resistance and non-preference of boll weevils were measured on day-neutral lines of primitive accessions of cotton (McCarty and Jones, 1989). Six of nine lines (T-109DN, T-277-2-6DN, T-330DN, T-759DN, T-763DN, and T-790DN) had significantly less boll weevil oviposition and fewer damaged squares than the susceptible checks, Stoneville 213, Deltapine 41, or Deltapine 61, in both laboratory and field tests. The level of field resistance of DN lines approximated that of the frego bract–nectariless resistant check, LA81-560FN. Resistance of the DN lines was not attributed to any morphological trait.

**Tobacco Budworm Studies.** Techniques to achieve uniform field infestations of the tobacco budworm on cotton field plots were described by Jenkins et al. (1982). Detailed procedures and equipment needed for handling tobacco budworm pupae, eggs, and first-instar larvae and how to uniformly distribute the first-instar larvae to cotton plants in field plots were described. Use of these techniques achieved uniform damage levels to evaluate cotton lines and progeny rows for resistance.

Weights were determined for tobacco budworm larvae grown from hatching to 5 days of age on excised terminal leaves from 35 foreign and eight U.S. cotton cultivars or strains (Lambert et al., 1982). Larvae reared on BJA, 592, Laxmi, Satu 65, MO-HG, and HG-BR-8-N were significantly smaller than those on Deltapine 16, and larvae grown on Laxmi were also smaller than those on Stoneville 213. Feeding behavior and histological studies of newly hatched tobacco budworm larvae showed that first-stage larvae avoided consuming glands that contained gossypol (Parrott et al., 1983). Between 48 and 72 hours of age, larvae molt and then nonselectively consume the glands. Histological studies showed that gossypol glands are surrounded by an envelope that contains anthocyanins. The authors concluded that allelochemics were acting as feeding deterrents or as antifeedant compounds to first-stage tobacco budworm larvae.

Ramalho et al. (1984a) studied the distribution of tobacco budworm larvae within cotton plants from mid-June through August in a natural population. Approximately 75% of first instars were observed on the upper third of the plant. Second instars were found in the upper third of the plant until August. Instars three through six moved throughout the plant. All larval stages were found in higher numbers on structures that arise from sympodial position 1 from the main stem. First-instar larvae were found mainly on small squares. Second and third instars fed on squares in early season and on bolls in late season. Most of the fourth through sixth instars were found on small and medium bolls. The distribution of larvae within the plants was a function of the instars and phenological development of the plant. Movement of newly hatched tobacco budworm larvae on upper and lower leaf surfaces and petioles was observed (Ramalho et al., 1984b). The study revealed that pubescence provides a mechanism of resistance to movement of newly hatched larvae. With reduced movement, larvae increased exposure to biotic and abiotic factors in the field, thus increasing natural mortality.

The performance of 13 germplasm lines of cotton and seven cultivars was determined when grown with and without tobacco budworm in a 3-year trial (Jenkins et al., 1986). Plots were grown and inoculated with first-instar tobacco budworm larvae five to six times at weekly intervals, beginning the second week of squaring as determined in Stoneville 213. Worm-free plots were sprayed weekly

with an insecticide recommended for budworm control. Resistance was measured as the ability to resist yield loss when continually infested for 5 to 6 weeks. Resistance was identified in Stoneville 506 and confirmed in PEE DEE 875, PEE DEE 8619, and Tamcot CAMD-E. Regression analysis suggested that approximately 65% of the resistance was associated with early, rapid fruiting. Other unidentified factors were also involved in resistance.

To determine impact on yield reduction and maturity delay, two cotton cultivars were artificially infested with tobacco budworm larvae for different time intervals during the first 8 weeks of fruiting (McCarty et al., 1986c). The full-season cultivar, Stoneville 213, and short-season, Tamcot CAMD-E, were evaluated during two growing seasons. Treatments consisted of applying 12 first-instar larvae per foot of row in the terminal area of plants, once per week for the following combinations of weeks after fruiting has begun: none (control), weeks 1 to 2, 1 to 4, 1 to 6, 1 to 8, 7 to 8, 5 to 8, 3 to 8, 3 to 4, 5 to 6, and 3 to 6. Plots were protected with an insecticide when larvae were not applied. Plots were harvested three times for yield and maturity delay. Larvae application during the first 2 weeks of fruiting resulted in significant yield reduction compared to the control, for both cultivars at first harvest. Tamcot CAMD-E with larval treatments produced a larger percentage of its total yield at first harvest than did Stoneville 213. The total yield of Stoneville 213 was significantly reduced only when larvae were applied for at least a 4-week period. The yield of Tamcot CAMD-E was not reduced or delayed as much as that on Stoneville 213 when larvae were applied during early, mid, and full season. Larval application during the early stage of fruiting had a greater impact on reducing yield and delaying maturity than when larvae were applied during mid and late season.

An improved method for the production and collection of tobacco budworm eggs was developed by Parrott et al. (1986). With increased demand for large numbers of larvae for field-screening studies, a new oviposition cage that used screens for oviposition and an automated egg collection system for removing eggs from screens were developed. Using the new system, egg production increased four-fold compared with previous years with a reduction in labor required from 8 hours per day to only 4 hours per day.

Graham et al. (1987) studied the effects of mepiquat chloride on natural plant resistance to tobacco budworm in cotton for 2 years. Stoneville 213 cotton was grown with and without artificial infestation of tobacco budworm larvae and treated with recommended levels of mepiquat chloride. Significant yield increases were found at first harvest for mepiquat chloride treatments, but not in total yield, suggesting the typical induced earliness of plant growth regulation. No significant differences in yield were recorded either year among mepiquat chloride treatments and the presence of an artificial infestation of tobacco budworm, indicating no increased plant resistance to the insect.

Three doubled haploid cotton germplasm lines, M-DH-118, M-DH-126, and M-DH-128, tolerant to tobacco budworm were each crossed with Stoneville 213 and Stoneville 825, and the six populations necessary for a generation means analysis were made (Hsieh et al., 1987). Parents and crosses were grown with and without tobacco budworm infestation. Tolerance to tobacco budworm is considered as the ability to resist fruit loss due to tobacco budworm larvae. Each of the M-DH lines was more tolerant than either cultivar parent. The variance for tolerance was primarily additive in each of the six crosses. Additive effects were much larger than dominance or epistatic effects. Small dominance effects were present in four of six crosses. Additive genetic effects predominated for most fiber traits.

Tobacco budworm larvae fed diets containing 0.06 and 0.2% gossypol or tannin had significantly depressed growth rates, but there was no increase in mortality (Parrot et al., 1987). When 6- to 8-day-old larvae were fed for 1 to 3 days on diets containing 0.2% gossypol or tannin, the recovery of gossypol in the digestive tract, haemolymph, and feces was near zero, and recovery levels for tannin were less than 0.06%.

Parrott et al. (1989) determined that young tobacco budworm larvae prefer to feed along the margin area of the calyx crown of cotton squares. Resistant cotton lines contain glands in the calyx crown area that are avoided by young larvae. The numbers of glands on bracts, small squares, calyx crown, and the entire calyx differed significantly between a susceptible and three resistant cotton lines. Cotton lines with greater than 80 glands per small square bract or 30 glands per calyx produced larvae significantly smaller than did lines with fewer glands after 12 days of feeding.

## THE 1990S

During the early 1990s the cotton research team conducted the world's first field test of *Bacillus thuringiensis* (Bt) transgenic cotton for resistance to the tobacco budworm. This marked the beginning of a new era of insect control in cotton and other field crops. New constructs of the truncated form of the delta endotoxin gene from Bt continued to be evaluated for resistance to the tobacco budworm throughout the 1990s. Root-knot nematode research expanded during this time. Fruiting efficiency and distribution of harvestable bolls and the concept of plant mapping (or box mapping) was developed. Breeding and genetic studies continued with the aim of expanding useful genetic diversity for cotton improvement.

**Cotton Fruiting Efficiency and Plant Mapping.** Jenkins et al. (1990a) determined the fruiting patterns of eight cultivars of cotton in terms of fruiting sites of harvestable bolls when planted in a conventional pattern of rows spaced 1 m apart with a population of approximately 95,000 plants per ha for 2 years in Mississippi. Descriptive terms used in the study were: 1. sympodium, a fruiting branch; 2. monopodium, a vegetative branch; 3. node, the place on the main stem where sympodia or monopodia arise (nodes were numbered beginning with the cotyledonary node as number one); 4. position, the order in which buds are produced on a sympodium branch; and 5. fruiting site, a specific node position combination. The eight cultivars used in this study and year of release were: Stoneville 213, 1962; Stoneville 506, 1980; Stoneville 825, 1979, Tamcot CAMD-E, 1979; Deltapine 50, 1984; McNair 235, 1975; DES 119, 1986; and Deltapine 20, 1985. Stoneville 213 is representative of cotton grown during the 1970s. Tamcot CAMD-E is a short-season cultivar adapted to the Coastal Bend area of Texas. The others are early-season cultivars adapted to the Mississippi Delta and mid-South growing area. Bolls at position one on fruiting branches produced 66 to 75% of the total yield; bolls at position two produced 18 to 21% of the total yield; all other positions on fruiting branches contributed only 2 to 4% of the total yield. Vegetative branches produced 3 to 9% of the total yield. The bulk of the lint yield in all cultivars was produced on fruiting branches from main-stem nodes 8 through 14. The newer, early-maturing cultivars produced significantly more lint from fruiting branches at node 6 through 8 than the older cultivar Stoneville 213. Tamcot CAMD-E, McNair 235, and Deltapine 20 also produced less lint on vegetative branches than Stoneville 213. This study generated valuable data that have been used to better manage cotton production.

Boll set percentage and boll size by fruiting site in a population of cotton plants were quantified by Jenkins et al. (1990b). This, the second part of a fruiting efficiency study in cotton used the cultivars and methods reported by Jenkins et al. (1990a). Fruit retention was similar among cultivars; however, the early-season cultivars Deltapine 50, Deltapine 20, and DES 119 retained bolls at nodes 6 through 8 more so than the older cultivar Stoneville 213. The percentage of plants with a harvestable boll at position 1 on fruiting branches increased from 9.6% at node 6 to 48.7% at node 12 and declined thereafter. At position 2, retention varied from 0.2 to 21.2%. Less than 5% of the plants retained a harvestable boll at position 3. Peak boll retention was at node 11 for position 1, node 9 for position 2, and node 8 for position 3. Boll set percentage began decreasing 15 to 18 days after first flower assuming a 3-day vertical flowering interval. Bolls at position 1 were 14 and 21% larger than those at positions 2 and 3. Also, the smaller bolls had fewer and smaller seed. The partitioning of photosynthate to older bolls resulted in fewer harvestable bolls at positions 2 and 3 for all nodes. The data generated for boll retention and distribution by this study provided insight into possible ways to increase earliness and overall yield of cotton.

The evaluation of cotton at harvest by plant mapping was described by McCarty et al. (1994). Plant mapping is a numerical description of the average plant in a field or of the crop as a whole. A detailed description of plant mapping technique was provided. Commonly used terminology was provided along with how to construct a data collection box, sample data sheet, and samples of data tabulation. The crop evaluation system described was designed to provide all essential data necessary to completely evaluate all components of a cotton crop. This method has been adopted by researchers, farmers, extension personnel, and consultants as a useful tool in managing cotton production.

Jenkins and McCarty (1995) compared 12 cotton lines for fruiting sites that produced an open harvestable boll. Cotton lines were grown for 2 years in a randomized complete design with six replications. Plants in a 10-foot section of each plot were mapped to record the number of bolls and seed cotton by

fruiting site. When averaged over 2 years and 12 cotton lines, lint yields averaged 1,535 lb per acre (1719 kg $ha^{-1}$). There was no significant difference in yield among the lines except for the experimental line DH 126, which was significantly lower. The 2-year means showed that 73.8, 17.1, 2.1, and 6.6% of the lint was produced at positions 1, 2, 3, and on vegetative branches, respectively. There was little variation among cotton lines for the percentages of yield produced at the three positions. The amount of lint produced by nodes varied significantly among cotton lines, reflecting their differences in maturity. Data from this study with average yields slightly more than three bales per acre (1613 kg $ha^{-1}$) were compared to a previous study of eight cotton lines that averaged approximately two bales per acre (1075 kg $ha^{-1}$). There were three additional open bolls per plant in the three-bale cotton compared to the two-bale cotton. One boll was produced between nodes 5 and 8, one between 9 and 12, and one from all nodes above 12. These comparisons indicated that good season-long management is required to produce three bales per acre and not a longer growing season. The expression of the yield in terms of dollar value per fruiting site (money tree) became a popular teaching tool by extension personnel and consultants to help producers better manage for profit.

**Transgenic Cotton Studies**. Four transgenic cotton strains were evaluated in field plots and their performance compared with their near-isogenic, non-genetically engineered parent cultivar, Coker 312, and locally adapted cultivar, DES 119, by Jenkins et al. (1991). This was the world's first field test of cotton genetically engineered to express the delta endotoxin from *Bacillus thuringiensis*. Agronomic performance, fiber properties, and resistance to tobacco budworm were compared in field plots artificially infested with and without tobacco budworm. Laboratory feeding assays were used to test the ability of the tobacco budworm and cabbage looper, *Trichoplusia ni* (Hübner), to survive on leaves, squares, and reproductive structures. The *Bacillus thuringiensis* gene construct used in this study did not produce enough of the delta endotoxin in the desired plant parts to provide an adequate level of protection in the field. No major effects on survival or growth of tobacco budworm or cabbage looper were detected in laboratory assays. Lint yield of the transgenic strains were not significantly different from Coker 312 in infested versus uninfested plots. Three of the four transgenic strains produced significantly lower yields than DES 119. Boll and seed weights of all transgenic strains were significantly lower than Coker 312. In this study the gene construct used did not improve resistance of cotton plants to tobacco budworm; however, some important biological properties of these genetically engineered cotton strains derived from independent transformation events were detected.

Umbeck et al. (1991) determined the movement of pollen from a field test site of genetically engineered cotton grown in 1989 at the Plant Science Research Farm at Mississippi State University. Transgenic cotton was planted in a field plot measuring 136 by 30 m and was bordered on all sides by 25 m of commercial non-transgenic cotton. All border rows were sampled from the lower, middle, and top fruiting positions. Seeds were analyzed for the expression of the dominant selectable marker neomycin phosphotransferase (*npt II*). There was a consistent and significant reduction in pollen dissemination as distance from the test plot increased. Outcrossing decreased from 5% to less than 1% 7 m away from the test plot. A low level of pollen dispersal (less than 1%) occurred sporadically in the remaining rows out to 25 m. There were no significant differences between the lower, middle, and top fruiting positions sampled on the plant, indicating no consistent season effects on pollen dissemination. In this study, the borders were effective in serving as a pollen sink to significantly reduce the amount of pollen from a test plot of transgenic cotton.

Transgenic cotton lines that contained a truncated version of the delta-endotoxin gene from *Bacillus thuringiensis* were evaluated in laboratory tests for effects on growth and survival of the tobacco budworm (Jenkins et al., 1993a). Five of the six transgenic lines evaluated contained the *cry1A(b*) gene from bacterial strain HD-1, and one line (MON-249) had the *cry1A(c)* gene from strain HD-73. For the laboratory feeding assays, the plant structures used from field-grown plants were: cotyledons, seedling stems, first true leaves, terminal leaves, mature leaves, squares without bracts, squares without bracts and petals, and petals. Neonate larvae of tobacco budworm were grown on the different plant parts for the six transgenic lines and the non-transgenic parent Coker 312. The mean growth and survival of larvae after 6 days for the transgenic lines as a group were significantly less than Coker 312 for every plant structure. Variation in larval survival to 6 days on terminal leaves, small squares, and bracts among the transgenic lines was observed; however,

insect weights were low and not different among the transgenic lines. When larvae were fed for 6 days on artificial diet before being placed on leaves from transgenic plants and non-transformed Coker 312 and held to pupation or death, none of the larvae on transgenic leaves pupated, whereas 40% survived and pupated on Coker 312. This study indicated great potential for using transgenic cotton to control the tobacco budworm.

Various transformation events of the *cry1A(c)* and *cryIIA* genes in transgenic cotton were investigated for their effects on selected agronomic traits and for resistance to tobacco budworm and cotton bollworm in laboratory and field tests (Jenkins et al., 1997). Field and laboratory tests were designed to evaluate transformation events of the *cry1A(c)* and *cryIIA* genes from Monsanto Agricultural Company; events of the *cry1A(c)* gene from Calgene; experimental lines and cultivars from Delta & Pine Land Co. that contained transformation event M531 Bt from Monsanto; and experimental lines from Paymaster Technologies (formerly Jacobs Hartz Seed Co.) that contained event M757 Bt from Monsanto. Monsanto transformation events with *cry IIA* were as resistant to tobacco budworm and cotton bollworm as the M531 Bt event of *cryIA(c)*, but they showed some yield loss. Events ST 807, ST 808, ST 317 from Calgene expressing *cryIA(c)* were similar to event M531 in control of tobacco budworm and cotton bollworm. Cultivars NuCOTN 33B and NuCOTN 35B from Deltapine with event M531 Bt were highly resistant to tobacco budworm when grown under heavily infested field plots and compared with their non-transgenic recurrent parents. The NuCOTN cultivars yielded 450 to 550 kg $ha^{-1}$ more lint in infested plots versus their recurrent parent. In the absence of tobacco budworm, NuCOTN yields were equal to or exceeded the recurrent parents. The Paymaster lines with *cryIA(c)* event M757 were not pure for the gene, but they showed excellent field resistance to tobacco budworm. Lines HX2 BG and HX3 had resistance equal to M757 and yields equal to the cultivar H1244. Laboratory tests revealed that survival of cotton bollworms after 7 days on transgenic leaves and squares was greater than survival of the tobacco budworm. Weights of surviving larvae of each species were only 10 to 15% of the non-transgenic controls. Survival and weights of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith), at 7 days were only slightly lower than on non-transgenic controls. Evaluation of transgenic events and cultivars help ensure that when a cultivar is released to producers it is resistant to the target pest and has acceptable yield.

**Allelochemic Studies**. Hedin and McCarty (1991) determined whether candidate growth regulators affected yield and levels of allelochemics in cotton. Twelve candidate plant growth regulators were applied to Deltapine 50 at early flowering and 2 weeks later. Leaves and squares were collected for analysis of allelochemics (gossypol, tannin, anthocyanin, flavonoids) at 3 and 5 weeks after the first treatment. Leaf gossypol and square gossypol were most frequently increased by the bioregulators. Kinetin, kinetin plus $CaCl_2$ or $Na_2SeO_3$, and mepiquat chloride alone or with a commercial cytokinin preparation Foliar Triggrr (Westbridge Agricultural Products, San Diego, CA) all increased gossypol and one or more of the other allelochemics. The growing season initially was very wet before it turned dry during the fruiting period. The results suggested that plants under stress could respond positively to bioregulators with increases in allelochemics. Some trends toward yield increases were noted; however additional studies are needed to confirm this.

Hedin et al. (1991) determined the effects of cotton plant allelochemics and nutrients on behavior and development of the tobacco budworm. Neonates of tobacco budworm larvae that hatch on terminal leaves migrate to the terminal area, feed, and move to small squares on which they feed, and finally burrow into the anthers where they grow and develop. Chemically related evidence explained, in part, these observations. Young tobacco budworm larvae avoid the calyx crown area that is high in terpenoid aldehydes, including gossypol, of resistant cotton lines. Data from high-pressure liquid chromatography showed that gossypol content of both susceptible and resistant glanded cotton lines was equal, whereas the hemigossypolone and heliocides $H_1$ and $H_2$ were greatly increased in resistant lines. Analysis of total amino acids in cotton square tissue showed a graduation from the calyx crown, which was lowest, to the anthers, the site of insect development and highest levels. Artificial diets mimicking amino acid distribution in anthers were found to be successful for larval growth and development.

Hedin et al. (1992) investigated the allelochemics in *G. arboreum* lines as potential sources of resistance to tobacco budworm. They found that larvae fed on *G. arboreum* grew approximately equally compared with those fed squares from commercial *G. hirsutum* lines. Allelochemics of *G. arboreum*

lines were found to contain much less gossypol in leaves, squares, and petals than in *G. hirsutum* lines. Flavonoids were significantly higher in petals of *G. arboreum* lines. When square flavonoids were isolated and incorporated in laboratory diets for the tobacco budworm, moderate toxicity was observed; however, the toxicities were not greater than those of the same flavonoids isolated from *G. hirsutum* lines. The most prevalent flavonoids found were gossypetin 8-0-glucoside and gossypetin 8-0-rhamnoside, neither of which were found in *G. hirsutum*. The role of these compounds as resistance factors has not been determined.

**Root-knot Nematode Studies**. Cotton cultivars offered for sale in Mississippi were evaluated for resistance to the root-knot nematode (Jenkins et al., 1993b). Seedlings were grown in the greenhouse in pots that were inoculated with 7,500 root-knot nematodes 7 days after planting. Forty days after inoculation, plants were removed from pots, roots were washed free of soil, and eggs were extracted and counted. Eggs per plant ranged from 111,000 on LA 887 to 242,000 on Terra C 40. There were significant differences among the cultivars for susceptibility. Widely grown Deltapine 50 and DES 119 were among the less susceptible cultivars. The susceptible check M-8 produced 239,000 eggs in contrast to the resistant breeding line M-315 that produced only 2,500 eggs. The use of resistance genes in M-315 should allow for the development of cultivars resistant to the root-knot nematode.

The post-infection development of the root-knot nematode on cotton was investigated by Tang et al. (1994). The developmental stages of the root-knot nematode juveniles (J2) in 2-day time sequences following infection of susceptible M-8 cotton were described. The developmental periods were divided into seven stages, based mainly on nematode body shapes. During Stage A the juveniles penetrated the roots. The juveniles became sedentary and established a parasitic relationship with the plant during Stage B. Plant cells began to enlarge into giant cells, and root gall formation began. Stages C and D were considered transition stages from late juveniles to early adults. During this period giant cells rapidly increased in size and significant enlargement of root galls were noted, which are characteristic of root-knot nematode infection. Stages E, F, and G are adult stages that determine nematode reproduction. Egg production was observed 16 days after inoculation. The life cycle of the root-knot nematode in susceptible M-8 cotton was completed in 28 to 30 days. When juveniles were crowded in a small root portion, development was retarded. The proportion of juveniles that developed into males was higher in crowded areas of the root.

Creech et al. (1995) investigated penetration and reproduction of root-knot nematodes at sequential time intervals when cotton genotypes with different levels of resistance were inoculated with juvenile nematodes. Penetration and reproduction of root-knot nematodes were compared on three cotton genotypes with different levels of resistance (M-8, susceptible; M-78, moderately resistant; and M-315, highly resistant). Responses were characterized by penetration of roots by juveniles and by reproduction. Susceptible, moderately resistant, and highly resistant genotypes were penetrated approximately equally by the juveniles. Reproductive measures were different among the genotypes. The development of egg masses was delayed in M-78 and M-315 compared to M-8, with the greatest delay and a significant reduction in egg masses formed in M-315. Production of eggs and second-stage juveniles were sufficient in M-78 to contribute to the build-up of the next generation of root-knot nematodes in production fields. Reproduction on M-315 was so low that nematode populations would be expected to decrease under field conditions. The two major genes for resistance in M-315 do not alter penetration of juveniles into cotton roots but do have major negative effects on survival and reproduction of the nematode.

The effects of three levels of resistance to root-knot development on post-penetration development of nematodes were compared by Jenkins et al. (1995a). Three genotypes of cotton, susceptible M-8, moderate resistant M-78, and highly resistant M-315, were grown in greenhouse pots and inoculated with second-stage juvenile root-knot nematodes. Developmental stages of the nematode were counted every 2 days for 44 days. At 18 days after inoculation, 70, 45, and 6% of the nematodes present were adults in M-8, M-78, and M-315, respectively. On the resistant M-315, nematodes developed more slowly, with fewer third and fourth stages at 8 days after inoculation and fewer developing-to-mature females at 24 days after inoculation. Most nematodes that penetrated M-315 failed to establish or maintain giant cells. The number of egg-laying females on M-8, M-78, and M-315 were 299, 144, and 5, respectively, at 44 days after inoculation. Significantly fewer galls developed on M-315 than on M-78 and M-8 begin-

ning 10 days after inoculation, and fewer developed on M-78 at 40 days after inoculation compared with susceptible M-8. The post-penetration development of root-knot nematodes on resistant lines was slower, fewer developed to adult females, and root galls were fewer and smaller than those on the susceptible M-8.

McPherson et al. (1995) determined combining abilities among a susceptible root-knot nematode line M-8, six converted primitive lines with varying levels of resistance, and the highly resistant M-315. The 28 single crosses among the eight lines were evaluated for resistance in two greenhouse environments. Seeds were planted in pots and inoculated with 10,000 root-knot nematode eggs 7 days after planting. At 40 days, plants were dug and number of eggs per plant were determined. The general combining ability effects were highest for M-315, whereas specific combining ability effects of six hybrids were significant in both environments. The specific combining ability effects for M-8 crossed to M-315 or M-75 were negative. Because relative plant resistance to root-knot nematode is inversely proportional to reproduction, negative effects indicate resistance. The specific combining ability effects of M-315 crossed with M-75 were positive. Even though M-315 and M-75 had high general combining ability effects, they combined poorly, suggesting they could have the same resistance genes. The specific combining ability effects for M-8 crossed to M-78 and M-188 were positive, but the specific combining ability effect for M-78 crossed with M-188 was negative, suggesting they could have different resistance genes.

A study conducted by Robinson et al. (1997) determined if $F_2$ populations developed from crosses among eight root-knot nematode germplasm lines and five cultivars were competitive in yield and provided useful levels of resistance to the nematode. Two $F_2$ populations were evaluated in greenhouse tests for nematode resistance. Nematode resistance for those two populations was greater than the cultivar parent but less than the resistant germplasm parents. The level of resistance of the $F_2$ population was nearer the resistant parent than the cultivar parent, indicating that the $F_2$ population possessed a useful level of resistance. Several $F_2$ populations produced yields and fiber quality equivalent to cultivar parents in field tests. Results of the study showed the potential of using $F_2$ populations as a rapid way to combine root-knot nematode resistance with acceptable yield and fiber quality.

Callahan et al. (1997) reported that increases in the levels of a specific polypeptide were induced by root-knot nematodes in resistant cotton lines. Root-knot nematodes penetrate resistant and susceptible cotton lines in similar numbers; however, nematode development is arrested in the resistant lines soon after infection. Analyses of root proteins extracted from galls revealed a relatively abundant 14 kilodalton (kDa) polypeptide that was differentially expressed in resistant cotton isoline 81-249 at 8 days after inoculation. Analyses showed that the 14 kDa polypeptide was a plant protein, and expression was localized to the nematode-induced galls. This protein's expression is temporally correlated with the resistance response to root-knot nematode.

McCarty et al. (1998c) screened 79 day-neutral primitive accessions of cotton for resistance to the root-knot nematode. The $BC_4F_5$ day-neutral progeny were evaluated in a greenhouse test. Seeds were planted in pots inoculated with approximately 5,000 nematode eggs. At 40 days after planting, plants were removed and assessed for egg masses. None of the lines produced as few egg masses as the resistant check M-315. Twenty-four lines had significantly fewer egg masses than the highly susceptible M-8, an indication they have an intermediate level of resistance to egg mass formation.

Khoshkhoo et al. (1993) tested whether some naturally occurring and synthetic plant growth regulators induce increases in terpenoid aldehydes in root-knot nematode inoculated and uninoculated cotton lines. Terpenoid aldehydes, namely gossypol and hemigossypolone, have been associated with plant defense mechanisms. Salicylic acid, mepiquat chloride (PIX), and Burst (Burst Agritech, Overland Park, KS) a mixture of cytokinins increased the terpenoid aldehyde content of cotton roots, whereas kinetin and gibberellic acid either had no effect or a decrease occurred. If plants were inoculated with root-knot nematodes, additional amounts of gossypol and hemigossypolone were induced by treatment with salicylic acid, mepiquat chloride, and a mixture of cytokinins. Khoshkhoo et al. (1994a) investigated the relationship between terpenoid aldehyde concentrations in the roots and/or leaves of several root-knot nematode resistant glanded and glandless lines. Root terpenoid aldehyde contents increased in three resistant lines by the fourth day after root-knot nematode inoculation. However, two of the resistant lines, one glanded and one glandless, had low intrinsic terpenoid aldehyde contents. Although terpenoid

aldehyde contents increased after inoculation, they were still lower than those of a susceptible glanded line. Increases in terpenoid aldehydes or terpenoid aldehyde level alone cannot explain root-knot nematode resistance in all lines. Analysis of terpenoid aldehydes in leaves could not be correlated with resistance. Khoshkhoo et al. (1994b) identified free sugars in root-knot nematode resistant and susceptible cotton lines and investigated the relationship between resistance and concentration. The sugars, glucose, fructose, sucrose, and raffinose, were present in both roots and leaves of susceptible and resistant cotton lines. The concentrations of sugars varied in the roots, and there was no clear association with nematode resistance. This was the first report of raffinose being present in cotton roots and leaves.

**Tobacco Budworm Studies.** A 2-year study was conducted to compare 18 cultivars of cotton developed between 1890 and 1986 for yield potential when grown with and without tobacco budworm (Wharton et al., 1991). The mean yields of cultivars grown without tobacco budworm larvae infestations ranged from 779 kg $ha^{-1}$ for King (released in1890) to 1768 kg $ha^{-1}$ for DES 119 (released in 1986). As yields increased, both lint percentage and boll numbers increased and made major contributions to lint yield. The newer cultivars yielded more than the older cultivars. When lint yields with tobacco budworm were regressed on lint yields without tobacco budworm, the regression equation ($R^2 = 0.84$) revealed that for every 1.00 kg of lint yield increase due to breeding during this study, there was a corresponding lint yield increase under tobacco budworm of only 0.69 kg. Some of the newer cultivars (DES 119 and Deltapine 50) yielded as much with tobacco budworm as some of the older cultivars yielded without tobacco budworm.

How tobacco budworm infestations at different growth stages of plant development affected fruit distribution on the cotton plant was studied by Mulrooney et al. (1992). Plants at different developmental stages were infested with five neonate tobacco budworm larvae per plant, and the position of each open boll produced was recorded at harvest. Infestations, regardless of the developmental stage of the plant, reduced boll numbers at the first fruiting positions from the main stem. Early infestations reduced total numbers of bolls more than all other infestation dates. Plants infested at the 15$^{th}$-node growth stage set a greater number of bolls at position 2 than plants infested at the 5$^{th}$-node stage of growth. Only plants infested at the 5$^{th}$ node had fewer total bolls than the control. The early-maturing cultivar, DES 119, set more bolls at position 1 and 2 on lower nodes than Stoneville 825, a later-maturing cultivar, when plants were infested at the 7$^{th}$ node.

An improved machine used to harvest tobacco budworm eggs was constructed and evaluated (Parrott and Jenkins, 1992). The machine automatically removes eggs oviposited on screens, recycles the sodium hypochlorite wash solution for reuse, and rinses the eggs with tap water. Results of laboratory test showed the eggs removed mechanically hatched as well as eggs removed manually. Daily collection rates during a 60-day test period averaged 360,000 eggs. The improved machine incorporates features for limiting the time eggs are exposed to sodium hypochlorite solution by immediately rinsing the eggs with tap water. The machine should be useful for collecting eggs from any species of Lepidoptera that will oviposit eggs singly on screens or cloth panels.

Tang et al. (1993a) compared the differences in tobacco budworm resistance among generations ($F_5$, $BC_1F_5$, $BC_2F_5$, $BC_3F_5$, and $BC_4F_5$), estimated broad-sense heritability, and examined plant-to-plant variability for resistance in crosses involving primitive *G. hirsutum* accession T-119. The photoperiodic-resistant accession T-119 was crossed to Deltapine 16, and day-neutral progeny were selected and subsequently backcrossed to T-119. The only selection was for day-neutrality following each backcross. Twenty-four random plants from each of the five generations, the resistant-backcross parent T-119, susceptible parent Deltapine 16, and the cultivar Deltapine 50 were evaluated in replicated greenhouse tests. Tobacco budworm resistance was evaluated by comparison of larval weight after 7 days of feeding on leaf tissue. Larvae were smaller on T-119 (5.05 mg per larvae) than any other genotypes (range 7.81-11.09 mg per larvae), and resistance was found in the $BC_3F_5$ (7.81 mg per larvae) compared with Deltapine 50 (9.67 mg per larvae). Low heritability estimates of 22 to 38% indicated potential difficulties in breeding for resistance. This relatively low heritability estimate was expected because no selection had been practiced for tobacco budworm resistance. Plant-to-plant variability was significant for four of the five generations, and selection of individual resistant plants for use as parents should improve heritability. Generally, the percentage of resistant plants within each $F_5$ generation increased with more backcrosses to T-119.

A 2-year study compared two strains of cotton putatively resistant to the tobacco budworm with two adapted cultivars, Deltapine 50 and DES 119, in field plots infested and not-infested with tobacco budworm (Jenkins and McCarty, 1994). The differences in lint yield between the infested and budworm-free plots were used as a measure of resistance. The strain LA 850082 was significantly more resistant each year than the cultivars and strain ST 69132. Strain ST 69132 was more resistant than DES 119 in both years and more resistant than Deltapine 50 in 1 year. Results of these field tests confirmed the resistance of the two cotton strains. LA 850082 was significantly higher in yield than the two cultivars, but it has shorter and weaker fibers. LA 850082 should be a good source of germplasm to use in developing cultivars that resist the tobacco budworm.

Seven field tests were conducted between 1988 and 1992 to evaluate cotton cultivars performance under two levels of the tobacco budworm (McCarty and Jenkins, 1994). Cultivars were grown under artificial infestation with and without tobacco budworm (control of insect pests). Cultivar yields were significantly reduced in the tobacco budworm plots, which varied among years. McCarty and Jenkins (1995) regressed lint yield with tobacco budworm on lint yields without budworm, and the resulting equation was $Y = -111.0 + 0.6X$ ($r^2 = 0.57$). Thus, for every 1.0 kg $ha^{-1}$ of lint increase due to cultivar improvement, the corresponding increase under artificial tobacco budworm infestation was only 0.6 kg $ha^{-1}$. When growing conditions were favorable for rapid growth and fruit set, yields were not reduced by the budworm to the extent they were when conditions were less favorable. Cultivars that are high yielding under good insect management also tend to be the best performers when grown with high tobacco budworm pressure.

A report by Jenkins et al. (1995b) described in detail the rearing of tobacco budworm and cotton bollworm for host plant resistance research. Screening to develop resistant germplasm requires insects in large numbers and of uniform age. The laboratory-reared insects needed to maintain genetic diversity representative of natural field populations. Detailed explanations of adult handling, egg production, collection, and hatching into first-stage larvae for field infestation studies are given. The procedures provided should be useful to other plant resistance programs and research studies that require large numbers of insects for field tests.

**Breeding and Genetic Studies.** Day-neutral derived lines for agronomic and fiber traits were evaluated by McCarty and Jenkins (1992a). Seventy-nine *G. hirsutum* primitive accessions were each crossed to Deltapine 16, and progeny with day-neutral flowering were selected. These progeny were backcrossed to their primitive accession and selected for day-neutrality in the $F_2$ following each backcross. The resulting $BC_4F_3$ and $BC_4F_4$ were evaluated in field plots in 1990 and 1991. In 50% of the day-neutral lines, the node of the first fruiting branch was significantly higher than in check cultivars. The day-neutral lines also had more main-stem nodes and were taller than commercial cultivars. Lint percentage was in the low to mid 30s for day-neutral lines, whereas commercial cultivars were near 40%. Commercial cultivars produced more seed cotton than most day-neutral lines. Seed size in general was equal to commercial cultivars; however, a few lines had larger seed than commercial cultivars. Commercial cultivars generally had a higher tannin level in seed, whereas seed gossypol level was in the same range as commercial cultivars. Five day-neutral lines had fiber strength higher than cultivars developed for the mid-south; however, none were stronger than Acala 1517-75. Most day-neutral lines had shorter fibers and higher micronaire values than commercial cultivars. Useful genetic variability was measured for several traits in this set of 79 day-neutral derived lines.

Tang et al. (1993b) reported the potential value of $F_2$ heterosis for yield and yield component traits among a selected group of 16 lines that carry useful levels of resistance to certain pests. Four cultivars as female parents were crossed with 16 germplasm lines. The 64 $F_2$ hybrids and 20 parents were evaluated in field plots for yield in four environments. Several parents showed negative general combining ability effect, whereas others showed positive general combining ability effects. The cultivar Delcot 344 gave significant, positive general combining ability effects for all traits studied. Specific combining ability effects were smaller and less significant than general combining ability effects. Heterosis of the $F_2$ over the high-cultivar parent was observed in six $F_2$ hybrids. Heterosis for yield of $F_2$ hybrids resulted mainly from increased boll number and boll weight rather than increased lint percentage. In terms of combining ability for yield, the best two parents were Delcot 344 and Coker 315. Heterosis and combining ability for fiber properties for the above study were determined

(Tang et al., 1993c). Environment by hybrids were significant for fiber strength and micronaire, but not for length, uniformity, or elongation. General combining ability effects were more important than specific combining ability effects. Only one of the 20 parents, DES 119, had significant and positive general combining ability effects for four of the five fiber properties measured. In general, fiber traits of $F_2$ hybrids were similar to mid-parental values, with few superior to the high-cultivar parent. Results showed the potential of using pest-resistant germplasm as parents with cultivars to produce $F_2$ hybrids that combine acceptable yield and fiber quality. Tang et al. (1996) using mixed model approaches, estimated genetic variances, covariances, heritabilities, and genetic correlations for the 64 $F_2$ hybrids. Dominance variance accounted for the major proportion of the phenotypic variance for lint yield, lint percentage, and boll size. The proportion of additive variance was low for fiber traits, and a significant additive-variance-by-environment component indicated a lack of useful additive variance for fiber traits. For most pairs of traits studied, the genetic and phenotypic correlations were of comparable magnitude. The genetic correlation of fiber strength with boll weight was positive; however, the fiber strength correlation with yield and lint percentage was negative.

McCarty et al. (1995 evaluated the relationships among yield and fiber traits among 80 populations from five generations of each of 16 primitive photoperiodic *G. hirsutum* accessions originally crossed with Deltapine 16. The 80 $F_5$ populations consisting of $F_5$, $BC_1F_5$, $BC_2F_5$, $BC_3F_5$, and $BC_4F_5$ were grown in field plots for 3 years and evaluated for yield and fiber properties. Year, accession, and accession by generation were significant sources of variation for all traits measured. Lint yield and lint percentage tended to decrease with more than two successive backcrosses to the primitive accession, whereas seed size and fiber strength tended to increase with additional backcrosses. Yield components and fiber traits were relatively independent of lint yield. The day-neutral lines contained a broad range of genetic variability. The genetic variances and correlations were determined for the above study (McCarty et al., 1998a). Variation for accession generation was highly significant for all traits studied. The variation of main effects for accession or generation were significant; however, the magnitude was relatively small compared with the interaction variation. Lint yield had highly significant but small, positive phenotypic correlations with lint percentage, boll size, and 2.5% span length, but not with other traits. Strong positive correlations were found for effects of accession, generation, and accession by generation between lint yield and lint percentage. There were strong negative correlations between lint yield and seed size. Because large interactions between accession and backcross generation occurred in this study, evaluation of accession should be considered for specific generations. The second part of the above study was the prediction of genetic effects (McCarty et al., 1998b). Data for yield and fiber traits were analyzed by mixed linear model approaches, and effects were predicted by using an adjusted unbiased prediction method. Significant accession effects were detected for all traits studied. Significant generation main effects were detected for lint yield, lint percentage, and boll size, but only for one fiber trait. Lint yield decreased with more cycles of backcrossing to the accessions, as expected. For some traits, accession-by-generation interactions were detected, which indicated that not all generations were having equal effects. Genetic analysis of primitive accessions results in a better understanding of the breeding merit for specific mating generation of different accessions.

A 2-year study to estimate genetic variances for 13 yield, fiber, and other agronomic traits in 79 day-neutral $BC_4F_4$ primitive accessions and 11 diverse commercial cultivars was conducted by McCarty et al. (1996). A minimum norm, quadratic, unbiased estimation method was used for estimating genetic variance components and an adjusted unbiased prediction method for predicting genetic effects. Additive-by-environmental variances were significant for lint yield and node of first fruiting branch. Additive variance was the major component of phenotypic variance for lint percentage and boll size. Additive variances for other traits were significant but relatively low. Narrow-sense heritabilities ranged from 8 to 50% for the traits studied. Additive effects were positive for yield, lint percentage, and fiber traits, except micronaire, and were negative for node of first fruiting branch, number of main-stem nodes, and plant height. Results from this study indicated that many day-neutral accessions can be used in crosses with commercial cultivars without serious loss of agronomic potential in the progeny.

**Gene Expression and Molecular Marker Studies.** A full-length cDNA clone, GH3, was isolated from a cotton fiber library using a differential

screening method (Ma et al., 1995). The nucleotide and derived amino-acid sequence data showed that GH3 encodes a lipid transfer protein of 120 amino acids. Northern analysis indicated that the GH3 gene is developmentally regulated. Ma et al. (1997) screened a cotton genomic library for the lipid transfer protein. One clone containing the *Ltp* gene (*Ltp6*) was sequenced and characterized. *Ltp6* contains an open reading frame of 360 base pairs, which is interrupted by a single intron located in the region corresponding to the C-terminal of the protein. The amino-acid sequence of *Ltp6* was 64% homologous to that of GH3. *Ltp6* is specifically expressed in fiber cells, but its expression level is lower than GH3. The 447 base-pair *Ltp6* promoter and a series of 5′ deletions of the promoter were generated and cloned into a pB1101 plasmid upstream of the β-glucuronidase (GUS) reporter gene (Hsu et al., 1999). These constructs were introduced into transformed *Agrobacterium tumefaciens* strain LBA4404 and this strain was used to transform leaf disks of tobacco (*Nicotiana tabacum* L.). Histochemical analyses of the transgenic tobacco seedlings indicated that the *Ltp6* promoter directed GUS expression only in trichomes. Sequential deletions of the promoter gradually decreased the expression of the GUS gene.

Shappley et al. (1996) determined the inheritance of restriction fragment length polymorphisms and their linkage relationship in two Upland cotton $F_2$ populations. The two crosses characterized for restriction fragment length polymorphisms were HyPerformer HS 46 x MAR-CABUCAG8US-1-88 (MAR) and HyPerformer HS 46 x PEE DEE 5363 (PD5363). Individual plants from the MAR cross were analyzed with 73 probe/enzyme combinations, which resulted in 53 polymorphic fragments. Of these, 42 were considered informative for linkage analysis. The 42 fragments or molecular markers constituted 26 polymorphic loci. Fifteen loci showed codominance and the remaining 11 were termed dominant. The loci fit expected ratios of 1:2:1 and 3:1 as determined by chi-square analyses. The MAPMAKER software program established four linkage groups with 4, 2, 2, and 2 loci as well as 16 unlinked loci. Eleven polymorphic markers were identified in the HS 46 x PD5363 cross. The 11 fragments represented six polymorphic loci: 1 dominant and 5 codominant genotypes. MAPMAKER analysis identified two linked loci. To establish a detailed linkage map of restriction fragment length polymorphism markers in Upland cotton, 96 $F_2$-$F_3$ bulked sampled plots of the HyPerformer HS 46 x MAR cross (see above study) were analyzed (Shappley et al., 1998a). In this study, 129 probe/enzyme combinations were used resulting in 138 restriction fragment length polymorphism loci. Seventy-six of the 84 loci that segregated as codominant fit a normal 1:2:1 ratio. Fifty-four loci segregated as dominant genotypes, of which 50 fit a normal 3:1 ratio. MAPMAKER was used to determine linkage relationships among the 138 loci. There were 120 loci arranged into 31 linkage groups that covered 865 cM. Linkage groups ranged from 2 to 10 loci each, with 18 loci being unlinked. Shappley et al. (1998b) analyzed qualitative traits loci (QTL) associated with agronomic and fiber traits across 96 $F_2$-derived families from the HyPerformer HS 46 x MAR cross (see above studies). The fiber and agronomic traits, except seed index and bloom rate, were measured in $F_2$-derived $F_5$ families. A total of 100 QTLs were mapped to 60 maximum likelihood locations in 24 linkage groups. At least one QTL was identified for each of the 19 agronomic and fiber traits, except for fiber perimeter. Several QTLs influenced more than one trait and most frequently were associated with fiber traits.

Agrawal et al. (1999) determined whether commercially available simple sequence repeat (SSR) primers from other species could be used to detect polymorphisms in cotton. Polymerase chain reaction, agarose gel electrophoresis, and ethidium bromide staining were used to generate DNA fingerprints. Markers varied from 40 base pairs to more than 1,000 base pairs. Numbers of bands per primer combination and percentage of polymorphism varied widely. The SSR-generated markers from primer combinations specific to cotton produced the fewest number of bands, 2.2 and 2.6, at inter- and intraspecific levels. In contrast, SSR primers from sweet potato, *Ipomoea batatas* (L.) Lam., produced 20.5 and 19.5 bands at inter- and intraspecific levels. Polymorphic markers generated by SSR primers from species other than cotton were dominant, whereas those specific to cotton produced both codominant and dominant markers.

## THE 2000S

Breeding and genetic research continued to expand throughout the 2000s (Fig. 3). Boll weevil research was no longer conducted due to the success

of the eradication programs. Limited work continued with tobacco budworm as the *Bacillus thuringiensis* (Bt) transgenic technology was highly effective in controlling this pest. Nematode research remained an active part of the program.

**Figure 3. Left to right, Sukumar Saha, Jack C. McCarty, Martin J. Wubben, and Johnie N. Jenkins research scientists currently assigned to the cotton genetics CRIS project. Photo Oct. 2020.**

**Breeding and Genetic Studies.** The molecular variation in day-neutral converted race accessions by SSR DNA markers was surveyed and their genetic distance from a typical *G. hirsutum* cultivar was determined by Liu et al. (2000b). Fifty-six SSR primer pairs were used to genotype 97 $BC_4F_4$ race accessions. The day-neutral converted accessions had genetic distances from the *G. hirsutum* standard, TM-1, that ranged from 0.11 to 0.33, with the majority below 0.25. Data for each day-neutral accession were collected from a five-plant bulk sample. Close observation of alleles amplified for many of the accessions revealed possible heterozygosity or heterogeneity. When 10 individual plants comprised genotypes from nine of the most diverse accessions (distance greater than 0.25 from TM-1), the genetic distance in all cases for the most diverse plant relative to TM-1 exceeded the genetic distance derived from the bulk template sample of the accession. The diversity of the primitive photoperiodic parent was recovered in some accessions, whereas in others, there was extensive linkage drag from the day-neutral donor parent.

Sixteen day-neutral primitive accessions derived from *G. hirsutum* were evaluated for yield and fiber traits (McCarty and Jenkins, 2001). The 16 day-neutral $BC_4F_5$ lines and four cultivars were evaluated in field-plot tests from 1997 through 1999. The day-neutral lines tended to produce bolls that were smaller and seeds that were larger than the cultivars. Lint percentages for the cultivars (37-40%) were significantly higher than the day-neutral lines (28-34%). Several day-neutral lines produced seed cotton yield in the range of cultivars; however, lint yields were significantly lower for the day-neutral line compared with cultivars because of their low lint percentages. Day-neutral lines produced fibers shorter than those produced by cultivars, whereas fiber strength tended to be similar to cultivars.

Gutierrez et al. (2002) estimated genetic distances using SSRs among selected cotton genotypes. They also investigated the association between genetic distance and $F_2$-bulk population performance. Eleven genotypes (five U.S. and four Australian cultivars and two day-neutral *G. hirsutum* converted lines) were assessed by 90 SSR primer pairs. The genetic distance coefficients ranged from 0.06 to 0.34 for the 11 genotypes. The highest genetic distance (0.34) was detected between Stoneville 474 and day-neutral B1388, and the lowest (0.06) was between FiberMax 832 and FiberMax 975. Genetic distance between Australian cultivars (range 0.06-0.19) was lower than U.S. cultivars (range 0.10-0.22). Correlations between agronomic and fiber traits of $F_2$-bulk populations and genetic distance were not consistent and ranged from negative to positive, depending on trait, environment, and genetic background. Genetic distance based on the SSR makers used in this study revealed a lack of genetic diversity among all genotypes and was a poor predictor of overall $F_2$ performance.

Zhong et al. (2002) assessed the relationships among 20 day-neutral populations, four accession parents, and the day-neutral donor parent, Deltapine 16, using amplified fragment length markers. Primitive accessions T8, T74, T326, and T1149 were each crossed to Deltapine 16 and progeny with day-neutral flowering were selected. These progeny were backcrossed to their primitive accession and selected for day neutrality in the $F_2$ following each backcross. The 20 populations ($F_6$, $BC_1F_6$, $BC_2F_6$, $BC_3F_6$, and $BC_4F_6$), accession parents, and Deltapine 16 were planted in field plots to provide materials for amplified fragment length marker analyses. Young leaves from approximately 35 plants were bulk sampled for each entry for DNA extraction. Forty-three amplified fragment length primer combinations detected 251 polymorphisms among the four photoperiodic accessions and Deltapine 16. From 91 to 129 polymorphic markers were found within each of the five populations of the four sets of crosses and backcrosses. The recovery of markers from accession parents among

the backcrosses ranged from 27 to 92%, whereas recovery of markers from Deltapine 16 was 71 to 91%. The genetic distance among the five parents ranged from 0.35 to 0.63. Many of the amplified fragment length markers tended to stay together and were selected with the day-neutral phenotype. This indicated that linkage drag was occurring during introgression of the day-neutral trait. In a follow-up study using this data set, Wu et al. (2007) found a number of amplified fragment length markers were significantly associated with lint yields, lint percentage, boll weight, and fiber strength. Results suggested that several amplified fragment length markers were closely linked because they were highly associated with the same traits. Amplified fragment length markers associated with micronaire, elongation, and fiber strength were fewer in number and appeared not to be associated with yield.

A 2-year study measured agronomic and fiber properties and detected genetic variation and genetic effects associated with five U.S. cultivars, two Australian cultivars, and two day-neutral converted accessions and their $F_2$ populations (Cheatham et al., 2003). Parents and $F_2$s from a half-diallel cross were evaluated in field plots for yield and fiber quality traits in 1999 and 2000. The $F_2$ hybrids had significantly higher lint yield, heavier bolls, and longer fibers than parents. The parents used in this study varied in general combining ability. Australian cultivar, FiberMax 832, had the best overall general combining ability for yield and fiber quality, whereas Stoneville 474 was best for yield. FiberMax 975 and Paymaster 1560 exhibited good general combining ability for fiber length. The experimental line B1388 was a good combiner for fiber strength; however, general combining ability was low or negative for other traits. Lint percentage and fiber strength exhibited primarily additive genetic effects, whereas lint yield, boll weight, and fiber elongation had approximately equal additive and dominance effects. Micronaire and fiber length showed primarily dominance genetic effects. Australian cultivars and wild accessions can combine with U.S. cultivars to provide genes for fiber and yield improvements.

McCarty et al. (2003) compared yield and fiber properties when exotic cotton lines were crossed with commercial cultivars. Fourteen lines derived from primitive *G. hirsutum* accessions with high fiber strength were crossed as male parents to each of five cultivars used as female parents. The $F_2$ populations and parents were evaluated for yield, yield components, and fiber quality traits at two field locations in 1998 and 1999, and parents and $F_3$s were evaluated in 2000. All traits measured were significantly affected by environment. The cultivars had higher yield and lint percentages than the primitive derived lines; however, fiber strength for germplasm lines exceeded that of cultivars. The mean lint yield for $F_2$ hybrids exceeded the parent average value. Lint percentage, boll weight, fiber elongation, and fiber length were similar between $F_2$ and $F_3$ hybrids and near parent average values. Most traits were highly correlated between $F_2$ and $F_3$ generations, except seed cotton yield and lint yield. Phenotypic values and variance components were reported by McCarty et al. (2004a). Both additive and additive-by-additive epistatic effects controlled all agronomic and most fiber traits. Significant dominance effects were detected for all traits except fiber elongation. A significant additive-by-environment effect was detected, but it made a small contribution to the total variance. The genetic analyses suggest that crosses between day-neutral derived primitive accessions and cultivars can use both heterosis and genetic variation for pure line development. Genetic effects and genotypic values in different generations for agronomic and fiber traits were predicted using a mixed linear model approach (McCarty et al., 2004b). Generally, female cultivar parents had higher additive effects for lint percentage and lint yield; however, they generally had lower additive effects for fiber strength. The correlation coefficients between observed and predicted values were mainly high among traits and environments. This study showed that fiber strength can be improved over that of the female cultivar parents, whereas lint yield was slightly but not significantly predicted to be less than their female parent.

Twenty-one day-neutral primitive accession were grown and evaluated in field plots in 2001 and 2002 (McCarty and Jenkins, 2004). Seeds for the majority of the day-neutral lines were larger than the check cultivar. Lint percentage for the day-neutral lines were in the low 30s, whereas cultivars were in the low 40s. As expected, lint yields were low for the day-neutral lines because of their low lint percentages. The fiber length for the day-neutral lines was shorter than cultivars; however, many of the day-neutral lines had fibers that were stronger than cultivars. Day-neutral lines derived from primitive accessions are useful for the diverse germplasm they

contain and can be used to expand the genetic base of cotton, especially for fiber strength.

Lint yield and its three component traits (boll number, boll weight, and lint percentage) were measured in 188 recombinant inbred lines (RILs) derived from the cross of HyPerformer HS 46 by MARCABUCAG8US-1-8 and the parents in 1999 and 2000 (Wu et al., 2004). The analyses used an extended conditional mixed linear model approach. Boll number per unit of area made the largest contribution to genotypic and genotypic-by-environment variations for lint yield. More than 70% of the genotypic and genotypic-by-environment variations were accounted for by both boll number and lint percentage, and boll number and boll weight jointly. Ninety-nine percent of the genetic and phenotypic variation in lint yield could be explained by the three component traits. Boll number and boll weight interacted to affect lint yield, indicating balanced selection for boll weight and boll number is needed in high-yielding line development. Wu et al. (2005) analyzed boll retention in the above data set using a mixed linear model and a logistic regression model. Boll retention for the first position was significantly different among nodes but expressed similar total numbers from the first position among RIL lines. The estimates for boll retentions were similar for both models; however, the logistic regression model gave smaller confidence intervals for each estimate compared with the mixed linear model. The above 188 RILs and parents were screened with 141 polymorphic markers, and 125 markers were used to construct a linkage map (Wu et al., 2009a). Twenty-six linkage groups were constructed, and 24 of the 26 were assigned to specific chromosomes. Results from quantitative analysis showed that the genotypic effects accounted for more than 20% of the phenotypic variation for all traits, except fiber perimeter. Fifty-six QTLs (logarithm of the odds-LOD > 3.0) associated with 14 agronomic and fiber traits were located on 17 chromosomes. Nine chromosomes in A subgenome harbored 27 QTLs (10 associated with agronomic traits and 17 with fiber traits), and eight chromosomes in D subgenome harbored 29 QTLs, with 13 associated with agronomic traits and 16 with fiber traits.

Gutierrez et al. (2006) reported on the development of random-mated populations using bulked pollen. To test the bulked-pollen method, they used glanded and glandless cotton lines, collected different numbers of flowers from the two cotton lines, mixed the pollen, and then used the mixed pollen to pollinate emasculated flowers on the glandless line. Observed progeny genotypic ratios were nearly as expected. The results of their study indicated the use of pollen mixtures and bulk pollination could be used to develop random-mated populations in cotton.

A study was conducted using 114 day-neutral derived lines from primitive accessions that were used as male parents, with two commercial cultivars, Stoneville 474 and Sure-Grow 747, as female parents. The parents and $F_2$-bulks were grown in field plots during 2001 and 2002, and yield, yield components, and fiber traits were determined (McCarty et al., 2005). The yield for most of the $F_2$-bulks was not significantly higher than the high-yielding cultivars. All day-neutral derived lines had lint percentages lower than cultivars. Most male parents had micronaire values lower than female cultivars. Many of the $F_2$-bulks had fiber length that was equal to or longer than the cultivars, and none of the $F_2$-bulks produced fibers that were weaker than Sure-Grow 747. Variance components, genotypic values, and genotypic correlations were calculated for the 114 day-neutral derived germplasm lines from the above study (McCarty et al., 2006a). Genotypic effects for all traits studied made significant contributions to the phenotypic variation, indicating genetic diversity or variations among these lines. The predicted genotypic values relative to the population mean showed a wide range of variation for yield and fiber traits in the 114 day-neutral lines. Weak genotypic correlations were found between cotton yield and two fiber traits: 2.5% span length and fiber strength. Data for the parents and $F_2$ hybrids were analyzed using an extended additive-dominance genetic model based on the mixed model approach (McCarty et al., 2007). Dominance effects were the primary genetic effects controlling yield and fiber traits, whereas additive effects were small for most traits. Even though dominance effects were significant and common, they can be used in conventional breeding; however, selection would be done in later generations. Both cluster and discrimination analyses were conducting using both additive effects and genotypic values for the 114 day-neutral male parents to test for any association with geographic origins of the lines. Results showed no consistent effects of collection location or geographic race based on the traits measured in this study.

**Statistical Models for Data Analyses.** Several new statistical models were developed to aid breeders in data analyses. Wu et al. (2006a) developed a

method for the estimation of variance components using the additive, dominance, and additive-by-additive model when genotypes vary across environments. Monte Carlo simulations were used to compare the estimated variance components between four partial and two complete genetic designs. Simulations results showed that the estimated variance components were unbiased for the six designs. Results from using an actual data set agreed with the simulation studies. Wu et al. (2006b) also developed an additive-dominance model to determine chromosomal effects in chromosome substitution lines and other germplasms. The modified additive-dominance model can predict additive and dominance genetic effects attributed to a substituted alien chromosome in a chromosome substitution line as well as the overall genetic effects of the non-substituted chromosomes. Actual field data from the substitution of chromosome 25 from *G. barbadense* line 3-79 into TM-1 (*G. hirsutum*) were used to illustrate the new genetic model. The chromosome substitution line (CS-B25) had positive genetic associations with several fiber traits. Wu et al. (2006c) developed a recursive approach for deriving a random vector that can be used equivalently to detect multivariable conditional variance components and random effects under a general mixed linear model. End-of-season plant mapping data, including lint yield and three components of Upland cotton, were used to illustrate this method. The results suggested that the constructed random variables were independent of yield component traits and, thus, were appropriate for multivariable conditional analysis. Lint yield and all three yield components were controlled by both genotypic effects and genotypic-by-environment effects. The recursive approach offers a new method for dissecting gene expression of a complex trait.

Molecular markers were used to locate QTLs for node of first fruiting branch, a trait closely related to flowering time in cotton (Guo et al., 2008). A photoperiodic primitive accession, Texas 701, was crossed to a day-neutral cultivar, Deltapine 61, and the $F_2$ population was classified for node of first fruiting branch. Segregation revealed the complex characteristic of node of first fruiting branch. Interval and multiple QTL mapping were used to determine QTLs contributing to node of first fruiting branch. Significant QTLs were mapped to chromosome 16, 21, and 25, with two suggestive QTLs on chromosome 15 and 16. Results from this study suggested that at least three chromosomes contained factors associated with flowering time, with some epistatic interactions between chromosomes. Guo et al. (2009) conducted QTL studies for two $F_2$ populations of cotton. The populations were developed by crossing the day-neutral cultivar Deltapine 61 with two photoperiodic sensitive primitive *G. hirsutum* accessions, T1107 and T1354. Node of first fruiting branch was determined for the $F_2$ populations and used to measure relative time of flowering. Different flowering time patterns were observed for the two populations. Two QTLs were found across five flowering scoring dates, and they accounted for 28.5 and 15.9% of the phenotypic variation at the last scoring date for the T1107 population; whereas one major QTL was detected across five scoring dates and explained 63% of the phenotypic variation at the last scoring date for population T1354. Minor QTLs effects appeared at various scoring dates, indicating their roles in regulating flowering at a lower or higher node.

Eleven diverse cotton lines were used as parents to make 55 $F_2$ populations and cycles of random mating ranging from one to four (McCarty et al., 2008a). The parents, $F_2$, and random-mated populations were grown and evaluated in field plots in 2005. The results showed the parents had larger variances and ranges for agronomic and fiber traits measured than the $F_2$ hybrids. The genetic variances among the 55 $F_2$ populations decreased with increased cycles of random mating. The mean for parents showed significant differences from the mean of the populations at different cycles of random mating for most traits measured. High correlations were detected among traits and $F_2$ populations, but correlations among traits decreased with increased cycles of random mating. Thus, a random-mated population should provide a useful genetic resource for cotton breeding.

McCarty et al. (2008b) measured genetic association of cotton yield with its component traits using 14 day-neutral lines with desirable fiber quality derived from primitive accessions that were top-crossed to five cultivars. Lint yield and three component traits (boll number, lint percentage, and boll weight) were measured and analyzed by the additive, dominance, additive-by-additive genetic model with the mixed model based conditional approach. Results showed that boll number or boll number and lint percentages or boll weight contributed to the majority of the phenotypic variance components for lint yield. The combination of boll number and boll weight greatly increased their contribution to lint yield. Results suggested a balanced selection of

boll weight and boll number is necessary to obtain high yielding hybrids or pure lines. Wu et al. (2008) investigated the genetic structures of lint yield with component traits (lint percentage, boll number, and boll weight) in cotton chromosome substitution (CS-B) lines. The CS-B lines contained a chromosome or chromosome arm substituted from *G. barbadense* into *G. hirsutum* TM-1. Yield and yield component data were collected for the 14 CS-B lines and their $F_2$ hybrids with TM-1. Analyses showed that boll number or boll number combined with boll weight reduced the conditional variance components and phenotypic variance for lint yield and, thus, indicated that boll number played a more important role in lint yield than the other two component traits. CS-B16, CS-B18, and CS-B4sh were demonstrated to be associated with reduced lint yield. CS-B14sh (short arm), CS-B22sh, and CS-B22Lo (long arm) were associated with reduced additive effects for lint yield through the component boll weight.

Genetic variance components and genetic effects among 11 Upland cotton lines and their $F_2$ hybrids were determined (Jenkins et al., 2009). Ten diverse cultivars and one breeding line were crossed in a half diallel. The parents and $F_2$ hybrids were grown and evaluated for yield and fiber quality traits. Data were analyzed by an additive-dominance model using the mixed linear model approach. Several parents were associated with desirable additive effects for fiber quality and/or yield. Acala Ultima, FiberMax 966, and Coker 315 were good general combiners for fiber length, and Acala Ultima and FiberMax 966 were good combiners for fiber strength. Tamcot Pyramid and M-240 were poor combiners for agronomic and fiber quality traits. Some hybrids had desirable heterozygous dominance effects that could be used for hybrid development.

**Gene Expression and Molecular Marker Studies.** The *Ltp3* gene from cotton along with its 5′ and 3′ flanking regions was cloned using a polymerase chain reaction-based genomics walking method (Liu et al., 2000a). The 5′ flanking region was subsequently analyzed with *Esherichia coli*-GUS gene. The histochemical and fluorgenic GUS assays indicated that the 5′ flanking region of the *Ltp3* gene contains *cis*-elements conferring the trichome specific activity of *Ltp3* promotor.

Two cotton genes, *ghprp1* and *ghprp2*, encoding cell wall proline-rich proteins were cloned and characterized (Tan et al., 2001). The *ghprp1* gene is predominately expressed in fiber during the fiber elongation stage of development. It was also expressed in root tissue, whereas *ghprp2* was only expressed in root tissue.

SSR markers were linked to the Ligon lintless (*Li1*) mutant in cotton (Karaca et al., 2002). The SSR markers associated with the *Li1* gene were located to chromosome 22. When scanning electron microscopy was used to compare fiber initiation between TM-1 and *Li1*, no apparent differences were seen.

Two cDNAs and their corresponding genes (*GhUBC1* and *GhUBC2*) encoding ubiquitin-conjugating enzymes (E2s) were cloned and characterized from tetraploid cotton (Zhang et al., 2003). Three additional E2 genes were also identified in diploid cotton. Genomic origin analysis indicated that *GhUBC1* and *2* are individually present in the A and D subgenomes of *G. hirsutum*. The transcript levels of *GhUBC1/2* increased significantly in leaves and flowers at senescence.

**Root-knot Nematode Studies.** A full-length cDNA, *MIC-3* (Meloidogyne Induced Cotton-3), was identified in root-knot nematode resistant cotton roots after infection with the nematode (Zhang et al., 2002). *MIC-3* encodes a putative protein of 141 amino acids with an estimated molecular weight of 15,517 Da. The *MIC-3* gene belongs to a novel, multi-gene family containing up to six members. The expression of *MIC-3* is root localized and enhanced in the nematode-induced galls of resistant cotton germplasm line M-249. Its role in resistance response to the root-knot nematode requires additional research. Callahan et al. (2004) developed a polyclonal antibody of the *MIC-3* protein and used it as a probe to further verify the relationship between the *MIC-3* cDNA and the 14 kDa protein. The *MIC* antiserum recognized the 14 kDa protein and made it possible to use the antibody to probe the accumulation of the protein in response to root-knot nematode infection in a large subset of cultivars and breeding lines. The cotton lines displayed a range of resistance to the root-knot nematode. *MIC* accumulation levels were compared with the galling index of the cotton lines tested, and the trend showed that susceptibility to the root-knot nematode increases as *MIC* protein levels decrease. Wubben et al. (2008) further characterized *MIC-3* and its relationship to nematode resistance. A time-course analysis of root-knot nematode infection showed that maximum *MIC* transcript accumulated just prior to the manifestation of resistance. Expression was not induced by mechanical wounding or reniform nematode infection. It was shown that

root-knot nematode infection specifically elicits the induction of *MIC-3* in resistant roots and not in other common defense-signaling pathways. Results from this study suggest the *MIC* gene family represents a group of root-specific defense-related genes in cotton.

Buriev et al. (2010) cloned and sequenced *MIC-3* genes from selected diploid and tetraploid cotton species to reveal sequence differences at the molecular level and identify chromosomal locations of *MIC-3* genes in *Gossypium* species. The sequence analysis and phylogenetic clustering of *MIC-3* genes revealed the presence of multiple *MIC-3* gene members in *Gossypium* species. Deficiency tests of single nucleotide proteins delimited six At-genome members of the *MIC-3* family clustered to chromosome 4 short arm and one Dt-genome member to chromosome 19. Clustering was confirmed by long polymerase chain reaction amplification of the intergenic regions using At-genome-specific *MIC-3* primer pairs.

Bezawada et al. (2003) elucidated the genetics of root-knot nematode resistant Clevewilt 6-1 and searched for DNA markers associated with resistance. Moderately resistant Clevewilt 6-1 was crossed with the susceptible cultivar, Stoneville 213. The $F_1$ and $F_2$ populations and parents were genotyped with 120 SSR primer pairs, which revealed 16 polymorphic markers. The $F_2$ population was phenotyped using gall indices as a measure for resistance, and the Mendelian segregation fit a 3:1 ratio (susceptible:resistant). Results of phenotypic and marker data suggested that Clevewilt 6-1 was likely the source of the recessive gene for resistance to galling. SSR marker BNL 1421 explained 8% of the variation in gall index. MAPMAKER analysis indicated that BNL 1421 and BNL 1669 were linked; however, both markers showed distorted segregation.

The mode of inheritance of root-knot nematode resistance in M-315 RNR (M-315) and M-78 RNR (M-78), a day-neutral version of the race stock T-78 was evaluated by McPherson et al. (2004). These lines were crossed to susceptible M-8 and with each other. The parents, $F_1$, $F_2$, and backcross generations of these crosses were evaluated in the greenhouse for resistance to root-knot nematode. The estimated minimum number of genes controlling resistance in M-315 and M-78 was two and one, respectively. A two-gene model, one dominant and one additive, fit the resistance data for M-315. The data from crosses with M-78 indicated that it had only the dominant gene.

Ynturi et al. (2006) identified SSR markers associated with root-knot nematode resistance in cotton and assigned the markers to specific chromosomes. Near-isogenic lines were developed by crossing resistant Auburn 634 RNR with susceptible cultivar Stoneville 213 and backcrossing four times to Stoneville 213, while selecting resistant and susceptible sister lines. The $F_2$ population from a cross between the resistant and susceptible near-isolines, parents, and a susceptible and resistant check were grown in the greenhouse, inoculated with nematode eggs, and scored for gall index. Genotype analysis was conducted on 86 $F_2$ plants with nine polymorphic SSR markers. BNL 3661, 3644, 3545, and 1231 accounted for 21, 19, 12, and 11% of the variation in gall index, respectively. Two markers, BNL 3661 and 1231, accounted for 31% of the variation in gall index. BNL 3661 had significant additive (0.61) and dominance (0.50) genetic effects, whereas BNL 1231 had only significant additive (0.51) genetic effects. BNL 3661, 3544, and 3645 were linked and located to the short arm of chromosome 14. BNL 1231 is on the long arm of chromosome 11. In the cross studied, the association of two different chromosomes suggest that at least two genes are involved in resistance.

*Agrobacterium rhizogenes*-induced cotton hairy roots were evaluated as a model system for studying molecular cotton-nematode interactions (Wubben et al., 2009). Hairy root cultures were developed from the root-knot nematode resistant line M-315 and from the reniform nematode resistant accession GB713 and compared with a nematode-susceptible culture derived from the cultivar Deltapine 90. M-315, GB713, and Deltapine 90 hairy roots differed significantly in their appearance and growth potential; however, these differences were not correlated with transcript levels of the *A. rhizogenes* T-DNA genes *rolB* and *aux2*, which help regulate hairy root initiation and proliferation. Deltapine 90 hairy roots were found to support both root-knot and reniform nematode reproduction in tissue culture, whereas M-315 and GB713 hairy roots were resistant to root-knot and reniform nematodes, respectively. Hairy roots can be useful in evaluating the effect of manipulated host gene expression on nematode resistance in cotton.

**Chromosome Substitution Studies**. The effect of chromosome substitutions from *G. barbadense* 3-79 into *G. hirsutum* TM-1 on agronomic and fiber traits was determined by Saha et al. (2004). In this study individual chromosomes or arms from TM-1 were replaced with the corresponding chromosome or arm from 3-79 by hypoaneuploid-mediated back-

cross chromosome substitution. Thirteen different chromosome substitutions from *G. barbadense* (CS-B lines), TM-1, and 3-79 were grown and evaluated for agronomic and fiber properties. Compared with TM-1, CS-B lines 16, 18, 14sh, and 22sh had reduced seed cotton and lint yields. CS-B lines 2, 6, 16, 18, 5sh, 22Lo, and 22sh improved lint percentage. CS-B25 had increased fiber length and strength with reduced micronaire. Two lines (14sh and 15sh) had increased fiber length. Most of the CS-B lines produced bolls with lower weight than TM-1 bolls.

Saha et al. (2006) evaluated effects of chromosome-specific introgression in Upland cotton on agronomic and fiber traits. Fourteen CS-B lines, the chromosome *G. barbadense* donor parent 3-79, and *G. hirsutum* recurrent TM-1 were grown in five diverse environments and agronomic and fiber traits were measured. The data were analyzed with an additive-dominance model with genotype and environment interaction. Additive effects were significant for all traits and dominance effects were significant for traits except 2.5% fiber span length. CS-B25 had additive effects for increasing fiber length and strength and reducing micronaire. CS-B16 and CS-B 18 had additive effects related to reduced yields.

McCarty et al. (2006b) evaluated 13 cotton chromosome substitution lines (CS-B) and their specific-$F_2$ hybrids, TM-1, 3-79, and six cultivars for the number of flowers produced during the first 4 weeks of flowering. This period of flowering accounts for the majority of lint yield for most cultivated areas in the southern U.S. CS-B05sh produced more flowers during this period than TM-1 and 3-79, suggesting that a positive genetic association was exhibited for flowering when the short arm of chromosome 5 was substituted into TM-1. The numbers of flowers produced was similar in CS-B05sh and six improved cultivars. Results from the additive-dominance model analyses revealed that dominance genetic effects were more important during the early part of flowering and additive effects were more important during mid-to-late flowering. Wu et al. (2009c) investigated CS-B lines and their chromosome-specific $F_2$ hybrids for genetic changes in plant height and main-stem nodes that were measured weekly for six times following initial flowering. The additive variance component was significant for the two traits at all six dates, whereas significant dominance variance was only detected occasionally. Results revealed that plant height and number of nodes shared some common influence attributed to additive effects during plant development. Chromosomes associated with the genetic changes in plant growth were also detected.

Thirteen chromosome substitution lines (CS-B) with individual 3-79 *G. barbadense* chromosomes or arms substituted into TM-1 *G. hirsutum* were top-crossed with five Upland cultivars (Jenkins et al., 2006). Yield components, lint percentage, boll weight, seed cotton yield, and lint yield were measured over four environments, and additive and dominance effects were determined. Additive effects were greater than dominance for all traits. The cultivars, as expected, had larger additive effects for lint percentage and lint yield than each of the CS-B lines. Several chromosomes or arms were associated with significant negative or dominance effects; however, CS-B22sh and CS-B22Lo showed additive effects for lint yield. When CS-B lines were used in crosses with elite cultivars, alleles for yield components on specific *G. barbadense* chromosomes or arms showed positive interactions with the cultivars. Fiber quality traits, micronaire, elongation, length, and strength were measured in the above study, and additive and dominance effects were determined (Jenkins et al., 2007). The additive proportion of total variance was considerable larger than the dominance or environmental variance for each fiber trait. The cultivar FiberMax 966 had larger additive effects for fiber length than any of the CS-B lines; however, CS-B25 had the greatest additive effects for fiber strength among CS-B lines. Several CS-B lines had negative additive effects on strength, but none were more negative than TM-1. CS-B22sh had the greatest negative effect for fiber length. Among cultivars, Sure-Grow 747 had the greatest negative additive effect for fiber strength. Beneficial alleles for fiber properties were uncovered on chromosomes or arms when CS-B lines were crossed to elite cultivars.

Genetic analysis was conducted for agronomic and fiber traits for four interspecific chromosomes substitution lines (Saha et al., 2008). Agronomic and fiber data were collected at two locations for 2 years and analyzed with an additive-dominance genetic model. CS-B01 and CS-B26Lo had lower boll weight, whereas CS-B12sh had higher weight compared with TM-1. CS-B01 had significant negative additive effects for micronaire, and CS-B11sh had significant additive effects for fiber elongation and strength. Several CS-B lines had homozygous and heterozygous dominance effects for agronomic and fibers traits, suggesting these CS-B lines can be

useful for improving these traits in hybrid cotton.

Thirteen chromosome substitution lines, their donor parent 3-79, their recurrent parent TM-1, and five cultivars were evaluated for seed traits over four environments (Wu et al., 2009b). A mixed linear model approach with the jackknife was used for data analysis. Genotypic effects were more important than genotypic by environment for all seed traits measured. Chromosome associations were detected using the comparative method by comparing the difference between each CS-B line and TM-1. Chromosome 4 of 3-79 in TM-1 background was associated with reduced seed size, embryo percentage, and protein percentage; however, it was associated with increased oil percentage, and seed fiber percentage. Other chromosome associations with seed traits were also observed. Seed index was highly correlated with three seed index traits: seed protein, seed oil, and seed fiber. There were no unfavorable genetic associations between agronomic and seed traits.

## THE 2010S

Breeding and genetic research continued to expand during the 2010s. Limited work continued with tobacco budworm as the *Bacillus thuringiensis* (Bt) transgenic technology remained highly effective in controlling this pest. Nematode research remained an active part of the program, as well as expanding useful genetic diversity for cotton breeding.

**Breeding and Genetic Studies.** A study was conducted to detect QTL or molecular markers associated with yield, fiber, and seed traits within multiple fuzz and fiber loci genetic backgrounds (An et al., 2010a). Two $F_2$ populations were used in the study. Population 1 was a cross between mutant line MD-17 (fuzzless-lintless) by mutant line 181 (fuzzless-linted), and population 2 was a cross between MD-17 and the cultivar FiberMax 966 (fuzzy-linted). The parents and $F_2$ populations were grown in field plots for data collection. Leaf tissue was collected from parents and $F_2$ plants for DNA and marker analysis. A QTL (*qLP-c26-1*) explained 87 and 68% of the phenotypic variation for lint percentages in the MD-17 populations with FiberMax 966 and 181. Single marker regression indicated that STV79-108, on the long arm of chromosome 12, had significant association with lint percentage, lint index, embryo percentage, protein percentage, and micronaire. Multiple QTLs were associated with yield components, seed, and fiber traits within several fuzzless loci genetic backgrounds. This study should help accelerate the genetic dissection of cotton fiber development.

Ligon lintless-2 is a dominant single-gene mutant in cotton that typically produces fuzzy seed with short lint fibers, and most plants express this phenotype. In a field plot of Ligon lintless-2, An et al. (2010b) observed three plants that expressed two seed cotton phenotypes on the same plant. Bolls on one branch of these plants expressed normal seed phenotype (fuzzy seed with normal fiber length), whereas all other branches produced the mutant phenotype (fuzzy seed with short fibers). Bolls from both branch types were harvested and planted the following year. Plants with seed from short lint fibers and plants from seed with long lint fiber each produced short fiber plants, normal fiber plants, and plants with both fiber types on the same plant. The three plants with two fiber phenotypes on the same plant were stubbed below the branch with the normal fibers and transferred to the greenhouse, and regrowth continued to produce two phenotypes on the same plant. The phenomenon observed in the field for 2 years might be due to a lack of consistent expression of the dominant mutant; however, the reoccurrence of the two phenotypes on regrowth of stubbed plants in the greenhouse might suggest a more fundamental mechanism is at work.

A partial diallel among six CS-B lines (CS-B14sh, CS-B16, CS-B17, CS-B22sh, CS-B22Lo, and CS-B25) and TM-1was characterized for lint percentage, boll weight, seed cotton yield, and lint yield across four environments (Saha et al., 2010). Three of the CS-B lines had significantly higher lint percentage values than TM-1. All CS-B lines had boll weights greater than TM-1. TM-1 generally produced more seed cotton and lint cotton than the CS-B lines. Lint percentage contributed a higher proportion to the additive variance compared with the other traits measured. Dominance-by-environment interaction made significant contribution to the variance for boll weight, seed cotton yield, and lint yield. Additive genetic effects were detected for higher lint percentage with CS-B16, CS-B22sh, and CS-B22Lo compared with TM-1. CS-B14sh and CS-B25 had significant negative effects for lint percentage. None of the CS-B lines had greater additive effects for boll weight than TM-1. All CS-B lines had significant homozygous dominance effects on seed cotton yield and lint yield, except for CS-B17. Additive-by-additive epistatic effects were detected for all CS-B lines and their

hybrids for the traits studied. The effects ranged from negative to positive, depending on trait. The partial diallel among CS-B lines revealed epistatic interactions for specific chromosome-chromosome combinations and showed that this approach is effective as a tool to dissect epistatic genetic effects.

Seed traits, including protein content, oil content, seed hull fiber content, seed index, seed volume, and embryo percentage, for $F_3$ hybrids of 13 cotton chromosome substitution lines crossed with five elite cultivars were measured over four environments (Wu et al., 2010a). Both oil and protein were expressed as a percentage of total seed weight and as an index as grams of product per 100 seeds. An additive-dominance genetic model with cytoplasmic effects was designed, assessed by simulation, and employed for data analyses. Results from simulation showed that the additive-dominance genetic model with cytoplasmic effects model had the lowest residual variances among models evaluated. Cytoplasmic effects, which are contributed by genes in the female cytoplasm, were significant for oil content, seed index, seed volume, and embryo percentage. Additive effects were significant for all traits, except oil content. Dominance effects were detected for oil content, oil index, seed index, and seed volume. Dominance-by-environment interaction effects were significant for all traits, except for oil percentage and seed volume. Genetic effects were predicted in this study, and favorable results suggest that these seed traits can be genetically improved.

Chromosome substitution lines were used as testers or probes to detect favorable genetic factors associated with a target chromosome or chromosome arms in different cotton cultivars (Wu et al., 2010b). A modified additive-dominance genetic model was used to analyze a data set of 13 chromosome substitution lines, their recurrent parent TM-1, five commercial cultivars, and their 70 $F_2$ hybrids. Eight traits (four agronomic and four fiber) were measured in the study. Chromosomes 2, 16, 18, 25, 5sh, 14sh, 22sh, and 22Lo had significant additives variances for traits investigated. CS-B25 was found to be favorably associated with several fiber traits, whereas the cultivar FiberMax 966 was favorably associated with both yield and fiber traits on multiple chromosomes or chromosome arms.

Twelve cotton germplasm lines with diverse yield and fiber traits that were created by three types of introgression (chromosome substitution lines, derived day-neutral lines from primitive accessions, and introduced genes from wild species) and their $F_2$ hybrids were evaluated for agronomic and fiber traits (Wu et al., 2010c). The data were analyzed by the additive-dominance model, and significant additive effects were detected for all traits, except seed cotton yield and fiber elongation. Dominance effects were significant for all traits. MD90ne was a good combiner for yield, whereas MD51ne, MD52ne, MD90ne, and three day-neutral lines were associated with increased additive effects for fiber strength. Some $F_2$ hybrids showed positive middle-parent heterosis for both yield and fiber quality.

McCarty et al. (2011) investigated growth, boll retention, and yield of four cotton cultivars when grown in four-row plots with a two-row skip and four plant spacings within each plot row. The within-row plant spacings were 8, 15, 23, and 30 cm between plants. Data were collected from both interior (solid row) and exterior (next to skip row) rows from each plot. As expected, plants were taller in the exterior rows, and the 8-cm spacing had fewer main-stem nodes. Yields were not different in the interior rows in 2003; however, plant spacings greater than 8 cm resulted in significant yield reductions in the exterior rows. In 2004, yield was affected by plant spacing. The 8-cm within-row plant spacing tended to produce more yield in both internal and external rows compared with other plant spacings.

Six chromosome substitution (CS-B) lines and TM-1 were crossed as a partial diallel, and the parents and $F_2$ hybrids were grown and evaluated for fiber quality traits (Saha et al., 2011). Data were analyzed with an additive-dominance additive-by-additive genetic model. Significant additive, dominance, and additive-by-additive epistatic effects for all fiber quality traits were associated with the substituted chromosome or chromosome arm of the of the CS-B lines. The donor parent for the substitution lines, 3-79, had the highest upper-half mean length, uniformity ratio, strength, elongation, and lowest micronaire among parents and hybrids. CS-B16 and CS-B25 had significant additive effects for all fiber traits measured. The comparative analyses of the double-heterozygous combination (CS-B x CS-B) versus their respective single combination (CS-B x TM-1) demonstrated interspecific epistatic effects between the genes in the chromosomes and played a major role in most fiber traits.

Nine chromosome substitution (CS-B) lines and their parents, TM-1 and 3-79, were top-crossed with five cultivars as parental lines, and their $F_2$ popula-

tions were evaluated for agronomic and fiber traits in four environments (Jenkins et al., 2012a). A wide range of values for agronomic and fiber traits were seen in the CS-B lines and $F_2$ hybrids. For lint percentage, boll weight, and lint yield, both additive and dominance variance components were highly significant, with additive being greater than dominance. The interaction of yield with environment was significant but small relative to additive and dominance components. For the seven fiber traits measured, both additive and dominance variance components were significant. Most of the CS-B lines had significant additive effects for most traits measured. For all traits, except boll weight and lint yield, significant additive effects of one or more chromosomes from 3-79 were greater than the corresponding chromosome from TM-1. Favorable additive effects of individual chromosomes or segments from donor 3-79 relative to the corresponding chromosome or segment were identified as follows for chromosome/segment: lint percentage 10, 16-15; longer fibers 01, 11sh, 26Lo; fiber uniformity 01, 11sh, 10, 17-11; stronger fibers 01, 11sh, 12sh, 26Lo, 17-11; fiber elongation 01, 11sh, 26Lo, 10, 17-11; reduced micronaire 01, 12sh, 4-15, 16-15, 17-11; fibers with greater reflectance 10, 4-15, 16-15, 17-11; and fibers with less yellowness 4-15, 17-11. Based on this study, favorable fiber quality alleles can be introgressed into Upland cotton using CS-B lines.

Saha et al. (2013) determined the chromosomal effects on agronomic traits from a partial diallel among seven selected CS-B lines and extended previous studies on intercrossing by including two new lines, CS-B09 and CS-B10. Agronomic trait data for lint percentage, boll weight, seed cotton yield, and lint yield were collected and analyzed with an additive-dominance genetic model. The donor chromosome parent 3-79 had the lowest additive effects for all traits measured. All CS-B lines had significant positive additive effects for boll weight, and most lines had additive effects for the other traits. CS-B10 had the highest additive effects for lint percentage, seed cotton yield, and lint yield among lines evaluated. CS-B09 had additive effects for lint percentage, whereas CB-B06, CS-B10, and CS-B17 had greater additive effects for seed cotton and lint yield compared with TM-1. Dominance and dominance-by-environment interaction were major contributors to the variance components. Line 3-79 had the highest dominance effects for boll weight, whereas CS-B10 had the lowest dominance effects for this trait.

Islam et al. (2014) developed more than 2,000 single nucleotide protein markers using genotyping by sequencing and validated their utility using diverse Upland cotton germplasm. Eleven diverse cotton cultivars and their random-mated recombinant inbred progeny were used for single nucleotide protein marker development. The developed single nucleotide proteins were filtered, and their sequences were aligned to the diploid *Gossypium raimondii* Ulbrich reference genome. Homologous single nucleotide proteins were used to assign 1,071 single nucleotide protein loci to the $A_t$-subgenome and 1,223 to the $D_t$-subgenome. One hundred eleven (111) single nucleotide proteins were tested in 154 diverse Upland cotton lines. The single nucleotide proteins were identified in the 11 cultivars and present in the 154 cotton lines, and no two cultivars had identical genotypes. Results showed that genotyping by sequencing can be used to discover single nucleotide proteins in Upland cotton that can be converted to functional genotypic assays for use in breeding and genetic studies.

Fang et al. (2014) identified stable QTLs related to fiber quality traits in a population of 550 RILs developed from random mating of 11 diverse parents for six generations. The 550 RILs were grown in field plots for 2 years to obtain fiber quality measurements. The 11 parents were screened with 15,538 SSR markers to identify polymorphic markers among the parents. Two hundred seventy-five (275) RILs were genotyped with 1,582 SSR markers that were well-distributed covering 83% of the cotton genome. The software program TASSEL was used to analyze marker-trait association, and 131 fiber QTLs and 37 QTL clusters were identified. Two major QTL clusters were observed on chromosome 7 and 16. The second set of 275 RILs were analyzed and confirmed the marker-trait associations.

Susceptibility of the cotton cultivar Paymaster HS26 (HS26) to the herbicide trifloxysulfuron sodium (commercial formulation Envoke®) was investigated by Thyssen et al. (2014). The sulfonylurea herbicides, including trifloxysulfuron sodium, are acetolactate synthase inhibiting herbicides. The trifloxysulfuron sodium-susceptible HS26 was crossed to Stoneville 474 (resistant to Envoke) to develop an $F_2$ mapping population. The segregation of herbicide resistance in the $F_2$ progeny was consistent with a single dominant gene; however, both cultivars possessed identical and sensitive acetolactate synthase

sequences. Trifloxysulfuron sodium susceptibility in HS26 was closely linked to markers on chromosome 20. Additional studies are needed to characterize the molecular mechanism responsible for trifloxysulfuron sodium tolerance in cotton. In a follow-up study, Thyssen et al. (2018) reported that the P450 gene CYP749A16 (*Gh_D10G1401*) is responsible for the natural tolerance exhibited by most cotton cultivars to the herbicide Envoke. A 1-base-pair frameshift insertion in the third exon of CYP749A16 results in a loss of tolerance to trifloxysulfuron sodium. To further confirm the role of CYP749A16 in cotton, virus-induced gene silencing was used to generate sensitivity in the tolerant cultivar Stoneville 474.

A genome-wide association study was conducted for fiber quality data that were collected over four environments from a multi-parent advanced generation population (Islam et al., 2016). The multi-parent advanced generation population was developed by random mating 11 diverse parents for six generations and subsequent development of 550 RILs. Markers significantly associated with fiber QTLs were identified using a genome-wide association study. One QTL cluster associated with short fiber content, strength, length, and uniformity were identified and confirmed on chromosome A07. Gene expression analysis suggested that a regeneration of bulb biogenesis 1 (*GhRBB1_A07*) gene is a candidate for superior fiber quality in Upland cotton. The DNA marker, *CFBid0004*, designed from an 18 base-pair deletion in the coding sequence of *GhRBBI_A07* in Acala Ultima, was found to be associated with improved fiber quality in the multi-parent advanced generation RILs and 105 additional Upland cultivars.

Jenkins et al. (2017a) compared the genetic effects of chromosome substitution lines for chromosome 1 (CS-B01, CS-T01), 4 (CS-B04, CS-T04), and 18 (CS-B18, CS-T18) from *G. hirsutum, G. barbadense,* and *G. tomentosum* when top-crossed with five Upland cultivars and TM-1, the recurrent parent of the chromosome substitution lines. Agronomic and fiber data were collected from $F_2$ and $F_3$ hybrids and analyzed using an additive-dominance model. Additive genetics effects were greater than dominance effects for lint percentage, fiber uniformity, strength, and elongation, whereas dominance effects were greater than additive for boll weight, lint yield, fiber length, and micronaire. All additive-by-environmental interaction effects were small, whereas dominance-by-environment effects were only significant for boll weight, lint yield, and micronaire. Chromosome B04 and B18 from *G. barbadense* and T01 from *G. tomentosum* had greater additive effects for lint percentage than homologs. Compared with cultivars, chromosomes from the three species generally showed negative additive effects on lint yield. The magnitude of additive effects on agronomic and fiber quality traits indicated that *G. barbadense* and *G. tomentosum* harbor useful alleles for Upland cotton breeding. Jenkins et al. (2017b) reported the genotypic mean effects comparisons for the above study. The predicted hybrid mean effects for the chromosomes from each species were different for several agronomic and fiber traits across cultivars. No single chromosome or species was found to be superior for all traits in crosses. With a few exceptions, the predicted genotypic mean effects for the $F_2$ and $F_3$ generally agreed with the results of the additive-dominance genetic effects analysis.

Boll retention, yield, and yield components of cotton grown with stands reduced by 20 to 40% from the uniform planting pattern of four seeds per 30.5 cm of row were investigated (McCarty et al., 2017a). Treatments with 20% stand reductions did not result in lower total yields; however, each plant in these treatments had to produce two additional bolls to maintain yield. Treatments that had at least 61-cm skips and 40% stand reduction resulted in lower yields. Treatments had minor effects on the yield components boll weight and lint percentage. Position one bolls in the uniform planting pattern accounted for 67% of yield, compared with approximately 50% for reduced stands. Reduced stand treatments produced approximately 20% of their yield on monopodial branches compared with10% for the uniform treatment.

Saha et al. (2017a) reported on the chromosomal association of fiber traits using a partial diallel among chromosome substitution lines of *G. tomentosum* (CS-T), a wild species endemic to Hawaii; *G. barbadense* (CS-B), a species with superior fiber quality; and TM-1 (*G. hirsutum*), the recurrent parent of CS lines. Fiber data were analyzed with an additive-dominance statistical model. Fifty-six percent of 16 different significant additive effects associated with the CS-B lines could be used to improve fiber traits in TM-1, whereas 40% of 15 significant additive genetic effects of the CS-T lines had the potential to improve fiber quality traits. Results from this study suggested that chromosome substitution lines can unveil many beneficial alleles harbored in the other additive-dominance genome species.

Eighteen *G. barbadense* chromosome substitution lines were crossed to three *G. hirsutum* cultivars, and a random-mated population was developed (Jenkins et al., 2018). Following five cycles of random mating and one generation of self-pollination for seed increase, the population was grown in field plots. A random sample of 96 plants from the introgression population was assessed with 139 *G. barbadense* chromosome-specific SSR markers. Of the 139 marker loci, 121 were recovered among the 96 plants. The distribution ranged from 10 to 28 alleles in individual plants. Marker loci showed a range of 6 to 14 chromosomes or chromosome arms were present among individual plants. Results showed that a mostly Upland random-mated population had considerable introgression of *G. barbadense* alleles.

McCarty et al. (2018) assessed the genetic diversity and population structure of 1,115 day-neutral conversions of *G. hirsutum* land races. Genotyping was conducted using 134 genome-wide SSR markers, and 192 polymorphic loci were identified. A total of 1,560 alleles were identified across these day-neutral conversions and a set of 14 U.S. cultivars, with 64% being unique to the day-neutral conversions and only 6% to the cultivars. Alleles ranged from 36 on chromosome 13 to 93 on chromosome 07. The relationship analysis indicated that, as a group, the day-neutral conversions were not closely related and resulted in seven distinct groupings, but these were not related to country of origin. Molecular variance analysis revealed that 58% of the variation was due to within-geographic origin groups and only 41% due to diversity among groups. The study identified extensive genetic diversity among day-neutral conversions within *G. hirsutum*.

A multi-parent advanced generation population developed by random mating of 11 diverse parents and the subsequently development of 550 RILs was used to identify fiber length QTLs and potential genes that contribute to longer fibers (Naoumkina et al., 2019). A cluster of single nucleotide polymorphisms were identified on chromosome D11 associated with fiber length. Further evaluation revealed that 90% of the RILs have a D11 haplotype similar to the TM-1 reference genome (D11-ref), whereas 10% of the RILs inherited an alternate haplotype (D11-alt) from one of the parents, which have fibers that are significantly shorter and contribute to inferior fiber quality. RNAseq analysis of the longest and shortest fiber RILs from the D11-ref and D11-alt RILs helped detect potential genes. Results suggested that low transcriptional activity of the auxin-responsive GH3 gene (*Gh-D11G1989*) in the longest fiber line (RIL 490) can result in greater amounts of indole-3-acetic acid (IAA), which contributes to longer fibers.

Six fiber phenotypes from 12 environments across three locations and 7 years were determined for 550 RILs and 11 cultivar parents (Thyssen et al., 2019). The 550 RILs were whole-genome-sequenced at 3X coverage and the 11 cultivars at 20X coverage. Seven highly significant fiber quality loci were identified from the segregation of 473,517 single nucleotide proteins in the population, including 7,506 non-synonymous mutations. Fourteen genes with non-synonymous single nucleotide proteins were found for the seven fiber quality loci. Additive effects were observed for elongation and micronaire, when the three most significant loci for each trait were examined. Another significant fiber strength locus was unmasked in gene *Gh-D13G1792* on chromosome D13. The loci and candidate causative variant alleles identified in this study will be useful for marker-assisted selection.

**Gene Expression Studies.** Ho et al. (2010) characterized a cotton RING-type ubiquitin ligase E3 gene by isolating a ubiquitin ligase E3 cDNA, *GhRING1*, from developing cotton fiber. Real-time polymerase chain reaction analysis indicated that the gene is expressed in cotton fibers during development. The transcript level of *GhRING1* reaches a maximum in elongating fibers 15 days post-anthesis. The expression pattern of *GhRING1* suggests that protein ubiquitination might be involved in transition to different stages of cotton fiber development.

A ubiquitin ligase E3 gene, *GhRING2*, was identified that is differentially expressed between two *G. hirsutum* lines, TM-1, and chromosome substitution line CS-B25 (Soma et al., 2014). *GhRING*2 was highly expressed in elongating cotton fiber, and GUS expression directed by the *GhRING*2 promoter was found in hypocotyls and young stems of transgenic Arabidopsis plants. GhRING2 was found to interact with a GhFDF1 (Protodermal Factor1) protein. *GhPDF1* was expressed in immature ovules and fiber initials and might play a role in fiber development. The expression and protein interaction data indicate that GhRING2 might be involved in the turnover of GhPDF1 and participation in the transition from initiation to elongation stages during fiber development. Data from this study strongly suggest that the ubiquitin-proteasome pathway might regulate cotton fiber growth and development.

Miao et al. (2017) used an RNAi PHYA line of cotton to identify and characterize microRNAs differentially expressed in fibers of the phytochrome A1 RNAi cotton line compared with the wild type. In this study, a total of 77 conserved miRNAs belonging to 61 families were investigated in the PHYA1 RNAi line and its parent Coker 312 by using multiplex sequencing. Of these miRNAs, seven (miR7503, miR7514, miR399c, miR399d, miR160, miR169b, and miR2950) were differentially expressed in the PHYA1 RNAi line. The target genes of these differentially expressed miRNAs were found to be involved in the metabolism and signaling pathways of phytohormones, which included gibberellin, auxin, and abscisic acid. The expression of several MYB transcription factors were also affected by miRNAs in RNAi cotton. In addition, 35 novel miRNAs (novel miR1 through novel miR35) were identified in fibers for the first time.

Hsu et al. (2018) used deep sequencing to explore the molecular mechanisms underlying improved fiber traits by comparing gene expression in fibers of CS-B25, a chromosome substitution line with improved fiber traits, and TM-1, the recurrent parent line of CS-B25 at 10 days post-anthesis. A total of 1,872 differentially expressed genes were detected between the two lines, with 1,175 up-regulated and 697 down-regulated in CS-B25. Many MYB-type transcription factors observed to regulate plant cell-wall biosynthesis were up-regulated in CS-B25. The results provided new insight into the molecular mechanisms of fiber development during the fiber elongation stage with potential of novel candidate genes that can be useful in cotton fiber quality improvement.

**Nematode Research Studies**. SSR markers linked to root-knot nematode resistance QTLs and markers to specific chromosomes were identified and mapped by Gutierrez et al. (2010). Three RIL populations were developed by single-seed decent from the following crosses: root-knot nematode resistant M-240 RNR x moderately resistant Clevewilt 6; M-240 RNR x susceptible Stoneville 213; and Clevewilt 6 x Stoneville 213. RILs from these populations were grown in the greenhouse, inoculated with root-knot nematode eggs, and scored for root galls, eggs per plant, and eggs per gram of root. Results indicated that at least two major genes were in involved in resistance of M-240 RNR. One gene was linked to marker CIR 316-201 and localized to chromosome 11. The CIR 316-201 allele was also present in Clevewilt 6 but not in Mexico Wild, both of which are parents of the highly resistant Auburn 623 RNR, the source of resistance for M-240 RNR. A second root-knot nematode resistance gene was linked to BNL3545-118 and BNL3661-185 on the short arm of chromosome 14. These two markers were not present in Clevewilt 6 but were present in Mexico Wild. The data collected suggested that the chromosome 11 resistance QTL primarily affects root galling, whereas the QTL on chromosome 14 results in reduced egg production.

The research above led to a study to determine the utility of using marker-assisted selection for root-knot nematode resistance in an applied breeding program (Jenkins et al., 2012b). Two crosses were used in this study: 1. root-knot nematode resistant germplasm M-240 RNR x susceptible cultivar FiberMax 966 and 2. Clevewilt 6 x Mexico Wild-photoperiodic. Cross one is representative of an initial cross in a breeding program to develop root-knot nematode resistant cultivars. Cross two involves the two cotton lines that originally were used to develop the first highly resistant root-knot nematode germplasm (Auburn 623 RNR). The $F_2$ generation for cross one was phenotyped for gall index and number of root-knot nematode eggs per plant, and each plant was genotyped for SSR CIR 316 (chromosome 11) and SSR BNL 3661 (chromosome 14). Results verified that marker-assisted selection was effective, and the QTL on chromosome 14 was primarily associated with a dominant gene affecting reproduction. In cross two, marker-assisted selection was used to identify 11 plants homozygous for the markers on chromosome 11 and 14 in the $F_2$, which also flowered in long days. Progeny of the 11 plants were phenotyped and confirmed to be highly resistant to root-knot nematode. Several generations of root-knot nematode phenotyping and progeny testing were required to develop the original root-knot nematode highly resistant germplasm lines. This study showed the power of these markers for marker-assisted selection. In the $F_2$ of the cross of Clevewilt 6 by Wild Mexican, the use of marker-assisted selection allowed the selection of plants that were homozygous for both genes for nematode resistance. The original research to select plants homozygous for both genes required years of selection and progeny testing and reselection. This study also showed that the markers for these two genes were useful in breeding root-knot nematode resistant cultivars of cotton.

Gutierrez et al. (2011) determined the inheritance of reniform nematode resistance in *G. barbadense* accession GB713, identified SSR markers linked to reniform nematode resistance QTLs and mapped the linked markers to specific chromosomes. GB713 was crossed to Acala Nem-X, and six generations ($P_1$, $P_2$, $F_1$, $F_2$, $BCP_1$, and $BCP_2$) were developed and evaluated for reniform nematode reproduction. Generation means analysis indicated that one or more genes were involved in reniform nematode resistance of GB713. The interspecific $F_2$ population was genotyped with SSR markers, and results showed two QTLs on chromosome 21 and one QTL on chromosome 18 were associated with reniform nematode resistance. One QTL on chromosome 21 was flanked by SSR markers BNL 1551_162 and GH 132_199, and the second QTL was flanked by BNL 4011_155 and BNL 3279_106. One QTL with smaller genetic effects was localized to chromosome 18 and flanked by SSR markers BNL 1721_178 and BNL 569_131. The QTLs on chromosome 21 had significant additive and dominance effects that were approximately equal in magnitude, whereas the QTL on chromosome 18 showed larger additive than dominance effects. It was suggested that the QTLs on chromosome 21 be designated *Ren*$^{barb1}$ and *Ren*$^{barb2}$ and the QTL on chromosome 18 as *Ren*$^{barb3}$.

Wubben et al. (2017) measured reniform nematode reproduction and fecundity for eight *G. hirsutum* near-isolines developed by marker-assisted selection that represented all possible combinations of *Ren*$^{barb}$ (*Ren*$^{barb1}$, *Ren*$^{barb2}$, and *Ren*$^{barb3}$ ) QTL genotypes. Results clearly showed that *Ren*$^{barb1}$–*Ren*$^{barb2}$ QTL interval can be resolved to a single QTL locus. The QTL, *Ren*$^{barb2}$, on chromosome 21 mediates reniform resistance and can be selected for using SSR marker BNL 3279_106. The combination of *Ren*$^{barb2}$ and *Ren*$^{barb3}$ provided resistance equivalent to the GB713 parent; however, *Ren*$^{barb2}$ alone showed approximately 71% reduction of eggs per gram of root compared with the susceptible check. The addition of *Ren*$^{barb1}$ to isolines having only *Ren*$^{barb2}$ or *Ren*$^{barb3}$ did not improve resistance. The number of eggs per egg mass was equivalent across all lines tested, which indicated GB713-derived resistance does not manifest as a reduction in fecundity.

Wubben et al. (2020) assessed root-knot nematode development, egg mass formation, and fecundity in near-isogenic lines that carried chromosome 11 and 14 QTLs separately, together, or not at all. This study showed that chromosome 11 QTL acts early in the resistance response to limit feeding site formation and inhibits the early stages of juvenile development. Chromosome 14 QTL was shown to act on later nematode life stages by delaying the development of mature females and by significantly decreasing female reproductive fitness.

Wubben et al. (2019) used RILs developed from a multi-parent advanced generation population to identify the root-knot nematode resistance gene found on chromosome 14 (D02). Five root-knot nematode resistant RILs were identified, which narrowed the D02-RKN locus to a 30-kb region with four candidate genes. Virus-induced gene silencing was conducted for each of the candidate genes, and results showed that Gh_D02G0276 was required for suppression of root-knot nematode egg production that is conferred by the chromosome 14 gene. A Gh_D02G0276-specific marker for the resistant allele variant was able to identify root-knot nematode resistant germplasm from a collection of 367 cotton accessions.

Two methods were developed for the collection of individual life stages of the reniform nematode (Ganji et al., 2013). A simple method was described for the collection of reniform juvenile and vermiform adult life stages under in vitro conditions and a second method to collect viable sedentary females from host plant roots. For method one, eggs were hatched over a Baermann funnel, and the second-stage juveniles incubated in Petri plates containing sterile water at 30 °C. Development was monitored, and specific times at which each developmental stage predominated were determined. Viable sedentary females were collected from infested roots using a second method that combined blending, sieving, and sucrose flotation.

Transgenic cotton plants that accumulated high levels of *MIC-3* transcript and protein in root and shoot tissues were developed from the root-knot nematode-susceptible obsolete cultivar Coker 312 (Wubben et al., 2015a). *MIC-3* transcript and protein overexpression were confirmed in root tissues of multiple independent transgenic lines, with each line showing a similar level of increased resistance to root-knot nematode. The overexpression of *MIC-3* in the root-knot-susceptible Coker 312 reduced egg production by approximately 60 to 75 % compared with non-transgenic controls and transgene-null sibling lines. In contrast to egg production, transgenic lines showed root-knot nematode-induced root galling similar to the susceptible controls. No effect

of overexpression of *MIC-3* was seen in reniform nematode reproduction. Transgenic lines did not show obvious difference in plant growth, morphology, or fiber quality traits. The results from this study provided direct evidence that the *MIC* gene family is intimately involved in mediating cotton resistance to root-knot nematode.

*MIC-3* overexpression line 14-7-1, which expresses a high level of *MIC-3*, was crossed to M-240 RNR, and all possible combinations of the chromosomes 11 and 14 QTLs with and without the *MIC-3* overexpression construct were developed (Wubben et al., 2016). Root-knot nematode reproduction and severity of root-knot nematode-induced galling were determined in the different lines. The addition of *MIC-3* overexpression lowered root-knot nematode reproduction in lines lacking both resistance QTLs and in lines having only chromosome 14 QTL, suggesting an additive effect of *MIC-3* with this QTL. In contrast, *MIC-3* overexpression did not improve resistance in lines having the single chromosome 11 QTL or in lines having both resistance QTLs. This suggested there could be an epistatic interaction between the chromosome 11 QTL and the *MIC-3* construct. Overexpression of *MIC-3* did not affect the severity of root-knot nematode-induced root galling, regardless of QTL genotype.

Multiple experiments were conducted to identify reniform nematode genes important for plant infection. Wubben et al. (2010a) performed a transcript analysis of sedentary reniform nematode females and sequenced 2,004 high-quality expressed sequence tags. Among these expressed sequence tags were sequences similar to other plant-parasitic nematode genes that had been shown to be involved in plant parasitism. Extending from this study, multiple reniform nematode genes were analyzed in more detail, including a β-1,4-endoglucanase, C-type lectin gene family, and a series of CLE-motif containing genes (Ganji et al., 2014; Wubben et al., 2010b, 2015b).

**Data Analyses.** Wu et al. (2011) evaluated the performance of available approaches for the efficient construction of large-scale linkage maps. The insertion, seriation, neighbor mapping, and unidirectional growth methods were compared using simulated $F_2$ data with various population sizes and missing genotype rates. Simulation showed that the insertion method outperformed the other three methods. The algorithms were applied to an actual data set, and results showed that the linkage order obtained by the insertion algorithm was superior to the other methods.

A mixed linear model-based multifactor dimensionality reduction approach was developed by Wu et al. (2012) to determine higher-order epistatic effects among markers associated with quantitative traits. The approach was used to analyze a cotton data set that included eight agronomic and fiber traits and 20 DNA markers. Results of the analysis showed that high-order epistatic effects were determined for most of the traits using this multifactor dimensionality reduction approach. Wu et al. (2013) validated the use of an extended additive-dominance model to account for field variations using a data structure with non-replicated plots. Data from simulations were numerically evaluated and used to estimate the variance components. An actual data set was analyzed, and results showed the extended model was comparable to a conventional additive-dominance model. The study provided a general framework to appropriately analyze data from non-replicated designs. Results from a study by Bondalapati et al. (2015), based on simulations, suggested that when there were no row and column effects in the field layout, the conventional and extended models yielded similar results. However, when either field row and/or column were significant, the extended genetic models yielded more unbiased estimates of variances. Actual data analysis by the extended genetic model of lint yield and seed yield from a cotton experiment showed that the residual variances associated with these traits were reduced 65%, compared with the conventional block model. Accordingly, the average heritability estimates increased by approximately 18% for these traits.

## UZBEKISTAN COLLABORATION

The USDA-ARS encourages scientists to build partnerships and collaborations with scientists in other countries in projects of mutual interests so that people of all nations make the transition to sustainable lifestyles. Since 2002, Sukumar Saha has taken a leading role in developing collaborative projects with the scientists of Uzbekistan through ongoing competitive Former Soviet Union projects of USDA-ARS. Approximately $1.7 million in funds from the USDA-ARS office of International Research Engagement and Cooperation has been received for these projects. Cotton is the primary economic source in Uzbekistan. The U.S. State Department's Cooperative Threat Reduction Office provided these

funds to encourage former Soviet researchers to apply their scientific skills to civil-oriented research pursuits of mutual interest. The Former Soviet Union projects created a significant impact on U.S. and Uzbekistan in training young scientists and achieving goals of mutual interest. Former Soviet Union projects have helped establish one of the most advanced molecular biology laboratories in Central Asia and provided an opportunity to train the next generation of public and private Uzbekistan cotton breeders and young scientists. Ten young Uzbekistan scientists received hands-on training in cotton molecular research at USDA-ARS, Mississippi State, MS. The scientists have published more than 30 papers in refereed journals from collaborative Former Soviet Union projects. It should be noted that there were almost no published agriculture research papers in international refereed journals from Uzbekistan prior to the Former Soviet Union projects. Approximately 20 Uzbekistan undergraduate students, 20 M.S. students, and 10 Ph.D. students have completed their degrees through the Former Soviet Union collaborative projects.

In these collaborative projects, the Uzbekistan scientists have developed, for the first time, a unique cotton plant with early flowering, early maturity, high yield, and improved fiber qualities using RNAi technology with an important gene family (phytochrome). They showed this novel strategy will be applicable not only to cotton but to other plant species. Considering the impact of this research and potential benefit to farmers, this technology has been patented (Abdurakhmonov et al., 2014, 2017). Using the RNAi cotton line, scientists in Uzbekistan have developed a series of Porlock cotton lines that have significantly impacted Uzbekistan economy. In 2020, these RNAi Porlock cotton lines were grown on more than 75,000 ha in Uzbekistan. They demonstrated several advantages of genetically engineered RNAi cotton lines over traditional Uzbekistan cotton cultivars. These lines have superior fiber quality (codes 38-41 versus 35-36 codes for traditional Uzbek cultivars, fiber length 38-40 mm versus 29-32 mm for traditional Uzbek cultivars, micronaire 3.9-4.2 versus 4.9-6.0 for traditional Uzbek cultivars). These lines are well adapted to the harsh Uzbekistan environmental conditions (drought, salinization, and heat stress) due to a highly developed root system and early maturity (5-10 days earlier). Recently, seeds of one RNAi line, MS, were exchanged with the USDA-ARS to test its efficacy in crosses with U.S. elite cotton lines.

## GERMPLASM LINES DEVELOPED AND RELEASED

The USDA-ARS cotton host plant resistance/breeding program has made 40 germplasm releases, many of which were made jointly with Mississippi State University or other cooperating institutions. The releases involved 808 germplasm lines and four random-mated populations (Table 1).

**Table 1. Cotton germplasm releases made by the USDA-ARS cotton host plant resistance/breeding program, Mississippi State, MS**

| Year | Germplasm Release |
|---|---|
| 1978 | Release of 81 $F_5$ noncommercial flowering lines of Upland cotton involving 54 *G. hirsutum* race accessions. (Jenkins et al., 1979c, f) |
| 1978 | Release of 16 Fusarium wilt resistant noncommercial stocks of cotton involving *G. hirsutum* race accessions. (Jenkins et al., 1979a, e) |
| 1978 | Release of 1 noncommercial stock of cotton germplasm with resistance to Fusarium wilt and *Lygus lineolaris*; JPM-781-78-3. (Jenkins et al., 1979b, d) |
| 1980 | Release of 68 $BC_1F_4$ noncommercial flowering lines of cotton germplasm involving 68 *G. hirsutum* race accessions. (McCarty et al., 1981a) |
| 1981 | Release of 23 $BC_2F_4$ and 33 $BC_1F_4$ noncommercial flowering lines of cotton germplasm involving *G. hirsutum* race accessions. (McCarty et al., 1981b) |
| 1982 | Release of 6 $BC_2F_4$ and 66 $BC_1F_4$ noncommercial flowering lines of cotton germplasm involving *G. hirsutum* race accessions. (McCarty et al., 1982a) |
| 1982 | Release of 4 semigametic breeding lines of cotton involving the cytoplasms of tetraploid species *G. hirsutum, G. tomentosum,* and *G. barbadense*. (Mahill et al., 1983a) |
| 1982 | Release of 3 semigametic germplasm breeding lines of cotton involving the cytoplasms of tetraploid species *G. hirsutum, G. tomentosum,* and *G. barbadense*. (Mahill et al., 1983a) |
| 1982 | Release of a semigametic germplasm breeding lines of cotton involving the *G. harknessii* species cytoplasm with male sterility. (Mahill et al., 1983a) |
| 1983 | Release of 4 double haploid lines of cotton with resistance to tobacco budworm, *Heliothis virescens*. (Mahill et al., 1984) |

**Table 1. continued**

| Year | Germplasm Release |
|---|---|
| 1983 | Release of 54 $BC_2F_4$ and 5 $BC_1F_4$ noncommercial flowering lines of cotton germplasm involving *G. hirsutum* race accessions. (McCarty et al., 1984) |
| 1983 | Release of 15 doubled haploid germplasm lines of Upland cotton with *G. hirsutum* nuclear genes in *G. barbadense* cytoplasm. (Jenkins et al., 1984a) |
| 1983 | Release of MHR-1 a germplasm line of cotton with resistance to tobacco budworm, *Heliothis virescens*. (Jenkins et al., 1984b) |
| 1985 | Release of 8 noncommercial okra leaf-frego bract germplasm lines of Upland cotton, *G. hirsutum*. (Shepherd et al., 1986a) |
| 1985 | Release of 8 noncommercial nectariless-frego bract germplasm lines of Upland cotton, *G. hirsutum*. (Shepherd et al., 1986b) |
| 1985 | Release of 4 $BC_1F_4$, 46 $BC_2F_4$, and 21 $BC_3F_4$ noncommercial flowering lines of cotton germplasm involving *G. hirsutum* race accessions. (McCarty et al., 1985) |
| 1986 | Release of 38 $BC_2F_4$, and 29 $BC_3F_4$ noncommercial flowering lines of cotton germplasm involving *G. hirsutum* race accessions. (McCarty et al., 1986a) |
| 1987 | Release of 3 noncommercial germplasm lines of Upland cotton tolerant to the tobacco budworm – MHR-10, MHR-11 and MHR-12. (Jenkins et al., 1988a) |
| 1987 | Release of 3 noncommercial germplasm lines of Upland cotton tolerant to the tobacco budworm and the tarnished plant bug – MHR-14, MHR-15, and MHR-16. (Jenkins et al., 1988b) |
| 1987 | Release of 2 noncommercial germplasm lines of Upland cotton tolerant to the tobacco budworm – MHR-17, and MHR-18. (Jenkins et al., 1988c) |
| 1987 | Release of 12 root-knot nematode resistant noncommercial flowering lines of Upland cotton involving *G. hirsutum* race accessions. (Shepherd et al., 1988a) |
| 1989 | Release of 9 root-knot nematode resistant germplasm lines of Upland cotton *G. hirsutum*. (Shepherd et al., 1989a, 1996) |
| 1989 | Release of 4 root-knot nematode resistant nectariless germplasm lines of Upland cotton *G. hirsutum*. (Shepherd et al., 1989b) |
| 1990 | Release of 22 $BC_3F_4$, and 10 $BC_4F_4$ noncommercial flowering lines of cotton germplasm involving *G. hirsutum* race accessions. (McCarty et al., 1990) |
| 1992 | Release of 53 $BC_4F_4$ noncommercial flowering germplasm lines of cotton involving *G. hirsutum* race accessions. (McCarty and Jenkins, 1992b) |
| 1993 | Registration of 79 $BC_4$ flowering germplasm lines of cotton involving *G. hirsutum* race accessions, previously released. (McCarty and Jenkins, 1993) |
| 1998 | Release of 18 $BC_4F_4$ noncommercial flowering germplasm lines of cotton involving *G. hirsutum* race accessions. (McCarty and Jenkins, 1998) |
| 2002 | Registration of 16 $BC_4$ flowering germplasm lines of cotton involving *G. hirsutum* race accessions, previously released. (McCarty and Jenkins, 2002) |
| 2004 | Release of 17 germplasm lines of Upland (*Gossypium hirsutum*) cotton, each with a pair of *G. barbadense* chromosomes or arms substituted for the respective *G. hirsutum* chromosome or arms. (Stelly et al., 2004, 2005) |
| 2004 | Release of 21 $BC_4F_4$ noncommercial flowering germplasm lines of cotton involving *G. hirsutum* race accessions. (McCarty and Jenkins, 2005a) |
| 2004 | Release of 14 Upland cotton, *Gossypium hirsutum* primitive derived germplasm lines with improved fiber strength. (McCarty and Jenkins, 2005b) |
| 2006 | Release of 6 root-knot nematode resistant Upland cotton germplasm lines. (Creech et al., 2007) |
| 2007 | Release of RMUP-C5, a random mated population of Upland germplasm. (Jenkins et al., 2008) |
| 2011 | Release of 3 germplasm lines of cotton derived from *Gossypium hirsutum* primitive accession T2468 with moderate resistance to the reniform nematode. (McCarty et al., 2012) |
| 2012 | Release of 3 cotton germplasm lines derived from *Gossypium barbadense* accession GB713 with resistance to the reniform nematode. (McCarty et al., 2013) |
| 2012 | Release RMBUP-C4, a random mated population of Upland cotton germplasm with introgression from *Gossypium barbadense* via chromosome substitution lines. (Jenkins et al., 2013) |
| 2014 | Release of RMPAP-C4, a Upland cotton random mated population between four cultivars and 30 day-neutral lines derived from *Gossypium hirsutum* primitive accessions. (McCarty et al., 2014) |
| 2016 | Release of 6 cotton germplasm lines with resistance to reniform nematode and root-knot nematode. (McCarty et al., 2017b) |
| 2016 | Release of 4 chromosome-specific (*Gossypium barbadense* chromosome 5sh) Upland cotton RILs with improved elongation. (Saha et al., 2017b) |
| 2017 | Release of 2 CS-B17-derived Upland cotton recombinant inbred lines with improved fiber micronaire. (Saha et al., 2018) |
| 2019 | Release of RMBHMTUP-C4 a random-mated population containing alleles from four species. (Jenkins et al., 2019) |
| 2019. | Release of 4 Upland cotton germplasm lines with elevated levels of seed oil oleic acid. (Dowd et al., 2020) |

**Germplasm Releases: 1970s.** Three germplasm releases were made in the late 1970s. The first release was a germplasm line derived from a primitive race accession that carried resistance to fusarium wilt and tarnished plant bug (Jenkins et al., 1979b, 1979d). The second release was 11 germplasm lines derived from primitive race accessions that carried resistance to fusarium wilt (Jenkins et al., 1979a, 1979e). The third release was 77 flowering germplasm lines that involved 53 *G. hirsutum* primitive accessions. Many of the accessions carried resistance to one or more pest (Jenkins et al., 1979c, 1979f).

**Germplasm Releases: 1980s**. During the 1980s, 356 flowering lines of cotton involving *G. hirsutum* race accessions were released (McCarty et al., 1981a, b; 1982a; 1984; 1985; 1986a, b; 1988). These day-neutral lines contained new sources of genetic diversity that can be used in cotton breeding programs. Mahill et al. (1983a) developed and released eight semigametic virescent-7 cotton germplasm lines. The lines are homozygous for the semigamy trait and should produce approximately 50% haploids in their selfed progenies. Each line has tetraploid nuclear genes primarily from the *G. barbadense* recurrent parent. Three have cytoplasms from tetraploid species *G. hirsutum*, *G. tomentosum*, and *G. barbadense*, and five lines have cytoplasms from diploid species *G. herbaceum*, *G. arboreum*, *G. anomalum*, *G. longicalyx* Hutch. and Lee, and *G. harknessii* Brandagee. Fifteen doubled haploid germplasm lines were developed and released with nuclear genes from six *G. hirsutum* parents in the cytoplasm of *G. barbadense* (Jenkins et al., 1984a). The lines were developed via semigamy as paternal haploids that were subsequently doubled. The germplasm lines should provide experimental material for cytological, genetic, and breeding studies.

Mahill et al. (1984) released four doubled haploid cotton germplasm lines with resistance to the tobacco budworm. The lines were developed via semigamy in *G. barbadense* cytoplasm. The paternal parent was a heterozygous line, MOHG, that had resistance to tobacco budworm. Under tobacco budworm infestations, the four germplasm lines yielded 39 to 66% of their yield without budworms compared with checks Stoneville 213 and ST 7A glandless that yielded 28 and 18% of their yield when protected from budworms.

The germplasm line MHR-1, which has resistance to the tobacco budworm, was developed and released (Jenkins et al., 1984b). MHR-1 is a composite of nine lines in the $F_7$ from (DES-24 x MOHG) x MOHG. Resistance in MHR-1 was measured as the ability to yield when artificially infested with 12 first instars of tobacco budworm per foot of row for each of 6 weeks. MHR-1 under infestation obtained 62% of its protected yield, whereas ST 213 attained only 48% of its protected yield. The mechanism of resistance in MHR-1 is not known.

Two cotton germplasm lines, MWR-1 and MWR-2, which carry resistance to the boll weevil, were developed and released (McCarty et al., 1986b). MWR-1 and MWR-2 were derived from the primitive *G. hirsutum* accessions T-326 and T-1180, respectively. The two photoperiodic accessions were converted to day-neutral flowering types, and the $BC_2F_4$ generation was tested for resistance to boll weevil oviposition. Boll weevils oviposited 57 and 54% as many eggs on the day-neutral lines as on Stoneville 213 in a no-choice laboratory test. The resistance was confirmed in field plots in Baton Rouge, LA, where they sustained 65 and 59% as much damage as Stoneville 213 and had 50 and 53% fewer squares that produced weevils.

Eight okra-leaf, frego-bract cotton germplasm lines were developed and released (Shepherd et al., 1986a). The okra-leaf trait reduces boll rot by opening the plant canopy and conferring resistance to the bandedwing whitefly (*Trialeurodes abutiloneus* Haldeman). The frego bract confers resistance to the boll weevil. These germplasm lines have a broad germplasm base that should be useful in enhancement programs to reduce diseases and control insect pest. These germplasm lines have good yield potential and acceptable fiber traits.

Shepherd et al. (1986b) developed and released eight nectariless frego-bract germplasm lines of cotton. These lines offer breeders the advantage of the host-plant resistant traits nectariless and frego-bract in a broad germplasm base. Nectariless reduces populations of tarnished bug, and frego bract offers resistance to the boll weevil. The germplasm lines produced comparable yields to check cultivars. Fiber properties of the germplasm lines were in the range of the check cultivars.

Shepherd et al. (1988a) developed and released 12 root-knot nematode resistant flowering germplasm lines of cotton derived from photoperiodic primitive *G. hirsutum* accessions. These flowering lines constitute a diverse germplasm pool with high resistance to the root-knot nematode, and they are important new sources of resistance.

Three germplasm lines of cotton with tolerance to the tobacco budworm were developed and released (Jenkins et al., 1988a). These lines were developed from a backcross of (MOHG x DES24) x MOHG. The tolerant lines sustained less yield loss when field plots were infested with tobacco budworm larvae compared with the cultivar Stoneville 213.

Jenkins et al. (1988b) developed and released three germplasm lines of cotton with tolerance to tobacco budworm and tarnished plant bug. The lines were developed from a cross of TIMOK 811 x Stoneville 213. TIMOK 811 is an obsolete cultivar (SA 1082) with tolerance to tarnished plant bug. In field plots infested with tobacco budworms in 1984 to 1986, each germplasm line lost significantly less lint yield to the budworm than Stoneville 213. Fiber properties for the germplasm lines were comparable to Stoneville 213, except for length, which was 2 to 3 mm shorter.

Jenkins et al. (1988c) developed and released two cotton germplasm lines with tolerance to tobacco budworm. These lines were developed after extensive selection in JPM-781-69-3. JMP-781-69-3 was derived from the *G. hirsutum* primitive accession and was highly resistant to fusarium wilt. Under infestation with tobacco budworm the germplasm lines produced about twice as much lint as Stoneville 213; when worms were controlled, yields were similar to Stoneville 213.

Shepherd et al. (1989a) developed and released nine germplasm lines in four cultivar backgrounds with resistance to the root-knot nematode. These lines had improved agronomic and fiber traits over previous releases. Also, Shepherd et al. (1989b) developed and released four germplasm lines with high resistance to the root-knot nematode and with the nectariless trait. These germplasms combined, for the first time, root-knot nematode resistance with the nectariless insect resistance trait.

**Germplasm Releases: 1990s.** McCarty et al. (1990) released 22 $BC_3F_4$ and 10 $BC_2F_4$ day-neutral lines derived from primitive accessions and, in 1992, 53 $BC_4F_4$ day-neutral lines were released (McCarty and Jenkins 1992b). Seventy-nine previously released day-neutral germplasm lines derived from photoperiodic primitive *G. hirsutum* accessions were registered (McCarty and Jenkins 1993). These lines represent a broad range of genetic variability.

Shepherd et al. (1996) registered nine cotton germplasm lines with resistance to the root-knot nematode that had previously been released. These nine lines constitute a germplasm pool with high root-knot resistance in a broad genetic base.

McCarty and Jenkins (1998) released 18 $BC_4F_4$ flowering day-neutral germplasm lines of Upland cotton involving *G. hirsutum* race accessions.

**Germplasm Releases: 2000s.** Sixteen $BC_4$ day-neutral flowering germplasm lines previously released were registered (McCarty and Jenkins, 2002). These germplasm lines were derived from different, mostly photoperiodic primitive accessions of *G. hirsutum* and offer new sources of genetic variability. An additional 21 day-neutral germplasm lines derived from primitive accessions were developed and released (McCarty and Jenkins, 2005a).

McCarty and Jenkins (2005b) developed and released 14 germplasm lines with improved fiber strength. These lines were derived from photoperiodic accessions that were converted to day neutrality and selected for improved fiber strength. The germplasm lines generally had lower yields and lint percentages compared with cultivars; however, fiber strength was improved as much as 20% over check cultivars.

Seventeen germplasm lines developed by hypoaneuploid-based backcross substitution of a different *G. barbadense* chromosome or chromosome segment into *G. hirsutum* genetic background were developed and released by the Texas Agricultural Experiment Station and USDA-ARS (Stelly et al., 2004, 2005). The lines are genetically similar to TM-1, an Upland cotton, and to each other, except that each line differs by the replacement of a specific homologous pair of chromosomes or chromosome segments from the *G. barbadense* donor line 3-79. Evaluation of the CS-B germplasm lines revealed that genetic variation for all measured traits was highly significant among CS-B lines and corresponding TM-1 by CS-B $F_2$ families. Boll weights of all CS-B lines were intermediate to the parents TM-1 and 3-79, except for CS-B06 and CS-B12sh, which produced heavier bolls. Generally, lint percentage was in the same range as the parents. CS-B 25 had reduced micronaire and increased fiber strength relative to TM-l. Fiber length of CS-B14sh, CS-B15sh, and CS-B 25 were longer than TM-1 but were shorter than that of 3-79. CS-B06 and CS-B15sh produced seed cotton yields equal to TM-1; however, all CS-B lines produced more seed cotton than 3-79. Lint yields of the donor parent 3-79 were less than half that of TM-1, and lint yields of CS-B lines are also lower than TM-1. CS-B01 and CS-B26Lo had unexpectedly high fiber elongation, compared with TM-1, indicating possible transgressive segregation. These CS-B lines are useful as new sources of genetic

variation for improvement of Upland cotton through breeding and fundamental genetic research.

Creech et al. (2007) developed and released six germplasm lines with resistance to the root-knot nematode. The source of resistance in these lines is Auburn 634 RNR. All six lines were developed using M-240 RNR as the resistant nematode parental line and crossing it one or more times with different commercial cultivars or released breeding lines followed by selection. In greenhouse evaluation, the root-knot nematode gall index for the six lines ranged from 2.0 to 2.7, whereas the resistant check was 1.8, the susceptible check 4.0, and the resistant cultivar check Acala Nem-X was 2.5. Each of the six lines had significantly fewer wilted plants (2-12%) than the Rowden (48-63%) susceptible check, at the National Fusarium Wilt Nursery in Tallassee, AL, in 2005. Yield and yield components on the six lines were equal to the check cultivar Stoneville 474 following 2 years of field tests. Four lines had significantly heavier bolls than Stoneville 474. Lint percentages for the lines were significantly lower than the check; however, no line was significantly different in yield from Stoneville 474. Fiber properties were equal to or superior to Stoneville 474. All lines had significantly lower micronaire and fiber length equivalent to Stoneville 474.

A population of Upland cotton, RMUP-C5, that was random mated for six cycles, beginning with a half diallel of 11 diverse parents, was developed and released in 2007 (Jenkins et al., 2008). The 11 parents (eight from different breeding company programs, two from Agricultural Experiment Stations, and one from USDA-ARS) were crossed in a half diallel to produce 55 half-sib families. Random mating of the $F_1$ from the half diallel was designated Cycle 0 ($C_0$). These 55 families were planted and cross bolls harvested as separate half-sib families during the breeding process. Random mating was accomplished by mixing pollen from an equal number of protected blooms from each of the 55 families each day of pollination and using the bulked pollen to pollinate 10 emasculated and protected flowers on each of the 55 families. This process was repeated each day until approximately 100 emasculated flowers were pollinated on each half-sib family. After each cycle of random mating, a random sample of crossed seed from each family was planted in a field plot, and the next cycle of random mating was made. After six cycles ($C_5$), an equal number of selfed seeds from each of the 55 families were bulked for release. Comparisons among Pearson correlation coefficients between traits of parents, $C_0$ and $C_5$, showed that linkage blocks were broken up and/or recombined by the random mating process. Correlations between length and uniformity, as well as micronaire and seed cotton yield, were positive in parents and nonsignificant in $C_5$. Correlations between fiber strength and lint yield were negative in parents and nonsignificant in $C_5$. The RMUPC-5 population has recombination that should be useful to breeders for selection and cultivar development. A group of 550 RILs was developed by single-seed descent from this population.

**Germplasm Releases: 2010s.** Three germplasm lines that are moderately resistant to the reniform nematode were developed and released (McCarty et al., 2012). The day-neutral germplasm originated from the *G. hirsutum* land race accession T-2468. Reniform nematode reproduction on the germplasm lines is suppressed approximately by one-half of that occurring on susceptible checks. The lines exhibit considerable differences for agronomic and fiber traits.

McCarty et al. (2013) developed and released three germplasm lines resistant to the reniform nematode. The day-neutral germplasm originated from the photoperiodic *G. barbadense* accession GB713. The lines were selected using SSR markers GH 132, BNL 3279, and BNL 569, which are linked to reniform nematode resistance. Egg production of the reniform nematode was suppressed to approximately 90% below that of the susceptible check in greenhouse tests. The germplasm lines exhibited considerable differences for agronomic and fiber quality traits.

A random-mated *G. barbadense* Upland population cycle 4 (RMBUP-C4), with introgression of *G. barbadense* alleles into *G. hirsutum*, was developed and released (Jenkins et al., 2013). The Upland cultivars Sure-Grow 747, PSC 355, and FiberMax 966 were each crossed to 18 chromosome substitutions lines from *G. barbadense* (CS-B). The seed of one cross was lost, resulting in 53 top-cross populations. Random mating began with the intercrossing of the 53 top-crossed $F_1$ lines, which was considered as cycle zero ($C_0$). The bulked-pollen method of pollination was used in development, and there were five cycles of random mating. After each $C_0$ of random mating, $F_1$ lines were combined using the original CS-B parent, producing 18 individual populations. The 18 populations were planted in individual field rows, and bulked-pollen intercrossing was made among population for cycles of crossing. After five cycles ($C_4$) of random mating, the 18 populations were grown and

self-pollinated for one generation. An equal number of self-pollinated seeds ($C_4S_1$) from each of the 18 populations were combined for release. RMBUP-C4 is a unique population with *G. barbadense* introgression. A group of 180 RILs was developed by single-seed descent from this random-mated population.

McCarty et al. (2014) developed and released a random-mated population (RMPAP-C4) involving four cultivars of Upland cotton and 30 day-neutral primitive accessions. The 30 day-neutral primitive accessions were each crossed to the conventional cultivars Sure-Grow 105, DP 393, FM 958, and ST 474 followed by five cycles of random mating. Random mating was facilitated by hand emasculation and bulk-pollen methodology. After five cycles of random mating, the population ($C_4S_1$) was evaluated for agronomic and fiber traits. Mean values for agronomic traits were not significantly different from those of cultivars, except for lint percentages, which were lower. Small, nonsignificant changes occurred for fiber quality traits, except for fiber uniformity, which increased. Morphological diversity is also present in the population. New genetic combinations and genetic diversity can be found in RMPAP-C4. A group of 600 RILs was developed by single-seed descent from this random-mated population.

Six Upland cotton germplasm lines with resistance to root-knot nematode and reniform nematode were developed and released (McCarty et al., 2017b). The source of resistance to root-knot nematode was M-240 RNR, which contains the Auburn 623 RNR source of resistance. The source of resistance to reniform nematode was M713 Ren1, which was derived from *G. barbadense* accession GB713. These two lines were crossed, and plants were selected using marker-assisted selection, with subsequent crosses to Sure-Grow 747 followed by marker-assisted selection. SSR markers CIR 316 and BNL 3661, which are linked to root-knot nematode resistance, and GH 132, BNL 3279, and BNL 569, which are linked to reniform nematode resistance QTLs, were used for marker-assisted selection. Egg production of root-knot and reniform nematodes was suppressed significantly from the susceptible check Sure-Grow 747 in growth-chamber tests. The germplasm lines resistant to both root-knot and reniform nematode should be valuable to cotton breeding programs, not only for their nematode resistance, but also for their variability for agronomic and fiber quality traits.

A chromosome-specific RIL population was created from a cross of TM-1 by CS-B05sh (Saha et al., 2017b). Four (CS-B05shRIL-93, CS-B05shRIL-68, CS-B05shRIL-65, and CS-B05shRIL-10) of the 50 RILs developed were released because of their improved fiber elongation. Fiber elongation, the ability to stretch before breaking, is a critical trait in determining yarn quality. The elongation of the four RILs ranged from 7.37 to 7.84%, compared with the commercial lines DP 393 and PHY 370 WR, which had elongations of 6.86 and 6.25%. Commercial lines performed better for agronomic traits than the four released RILs.

Saha et al. (2018) developed and released two RILs with improved micronaire values. The RILs were developed by inbreeding individual plants, using single-seed descent for six generations from an $F_1$ hybrid between TM-1 and the chromosome substitution line CS-B17. Results from field-plot data showed that CS-B17-59 and CS-B17-98 had micronaire values of 3.96 and 3.86, compared with the commercial lines DP 393 and PHY 370 WR, which had values of 4.52 and 4.58. However, the agronomic traits of the commercial lines were superior to those for the RIL lines.

A random-mated cotton population, RMBHMTUP-C4, was developed and released (Jenkins et al., 2019). The population contains introgression of alleles from 12 *G. barbadense*, 8 *G. mustelinum*, and 12 *G. tomentosum* chromosome substitution lines and 26 chromosomes from 5 *G. hirsutum* cultivars. The population was developed by crossing each of the 32 chromosome substitution lines with one of five (Sure-Grow747, Stoneville 474, PSC 355, Deltapine 90, and FiberMax 966) cultivars followed by random mating for five cycles beginning with the 32 $F_1$ crosses. The average phenotypic and fiber characteristics of the population are much like an Upland cultivar, despite its allelic diversity. This unique population, RMBHMTUP-C4, should facilitate efforts to diversify the genetic base of Upland cotton breeding, as it brings together alleles from four *Gossypium* species into one random-mated population.

Four germplasm lines with elevated levels of seed oil oleic acid were developed and released in 2019 (Dowd et al., 2020). The lines were developed from previously released reniform nematode-resistant germplasm lines that were derived from *G. barbadense* accession GB713. The oleic acid content of seed oil for the developed lines ranged from 33 to 35%, which is approximately double the normal level found in commercial cottonseed oil. A complete list of germplasms can be found in Table 1.

## RESEARCH PERSONNEL

Research personnel assigned to the cotton host plant resistance and breeding program can be found in Table 2. The team leader since its inception has been Johnie N. Jenkins. Fowden G. Maxwell left the research team in 1968 to become head of the Department of Entomology at Mississippi State University. He was department head at the University of Florida from 1975 to 1978 and was appointed department head at Texas A & M University in 1979. In 1993 he stepped down as department head and became director of the Biointensive IPM Center and retired in 1996. Currently, he serves as professor emeritus in the Department of Entomology at Texas A & M University. William L. (Bill) Parrott served as lead entomologist from 1968 until his retirement in 1991. Bill Parrott passed away after a short illness in 2007. Following retirement in 1990, Raymond Shepherd returned to Auburn, AL, and enjoyed retirement until his death in 2015. Following a 25-year career as a chemist at the USDA laboratory, A. C. Thompson retired in 1987 and enjoyed a long retirement until his passing in 2017. Paul A. Hedin retired in 1997 after 40-plus years of government service (died in 2005). Current research scientists include Johnie N. Jenkins, Jack C. McCarty, Sukumar Saha, and Martin Wubben. In additional to the research personnel, one to two support scientists and two to four technicians have been assigned to the research project. In addition to graduate students (see section below), seasonal labor is hired as needed.

Several visiting scientists have spent from a few weeks up to 1 year working with the research team. Post-docs have been associated with the team over the years and two, Osman Gutierrez and Jixiang Wu, spent almost a decade with the team in the early 2000s making many contributions to the overall research program.

## GRADUATE STUDENT TRAINING

Training and working with graduate students have been an integral part of the cotton host-plant resistance/cotton breeding program since its inception in the early 1960s. Because the USDA research program is located adjacent to Mississippi State University, opportunities exist for students to conduct research projects in the cotton program and take courses at the University leading to a graduate degree. Several undergraduate students work in the research program full time during the summer months and part time during the school year when classes are being held.

Most graduate students get their degrees in the departments of Entomology or Agronomy (currently Plant and Soil Sciences). Their research projects are a part of the overall research that is being conducted. They also have the opportunity to work in all aspects of the research program. Almost 60 students have been trained, with several receiving more than one degree (Table 3). Students have been employed by universities; federal agencies,

**Table 2. USDA-ARS personnel assigned to the Cotton Host Plant Resistance /Genetics/ Sustainable Agriculture Research Unit at Mississippi State, MS**

| Name | Title/position | Year |
|---|---|---|
| Johnie N. Jenkins | Research Geneticist | 1961 – present |
| Fowden G. Maxwell | Research Entomologist | 1961 – 1968 |
| William L. (Bill) Parrott [z] | Research Entomologist | 1961 – 1967 & 1968 – 1991 |
| Jack C. McCarty[y] | Research Agronomist | 1976 – present |
| Raymond L. Shepherd[x] | Research Agronomist | 1984 – 1990 |
| Paul A. Hedin[w] | Research Chemist | 1985 – 1997 |
| A. C. Thompson[w] | Research Chemist | 1985 – 1987 |
| Frank E. Callahan[v] | Research Plant Physiologist | 1989 – 2018 |
| Sukumar Saha | Research Geneticist | 1997 – present |
| Martin J. Wubben | Research Molecular Geneticist | 2005 – present |
| Russell W. Hayes | Agronomist | 1990 – present |
| Dewayne Deng | Geneticist | 2010 – present |

[z] Assigned to Brownsville, TX in 1967 and re-assigned to Mississippi State in 1968.

[y] Worked as a graduate/postgraduate student from 1969-1975.

[x] Cotton genetics research unit was moved from Auburn, Al to Mississippi State in 1984.

[w] Assigned from the Boll Research Unit.

[v] Assigned to a support position in 2004.

such as USDA-ARS, USDA-APHIS, U.S. Department of Energy, Defense Department, Federal Bureau of Investigation; as well as seed breeding, chemical, technology, and other private companies. A few students have gone on to other universities for their Ph.D.s. David Holder went on to Purdue University, receiving a Ph.D. in genetics and plant breeding, and was the lead sugar cane breeder for U.S. Sugar Corporation in Florida for many years until he retired. After receiving his M.S. degree, Clay B. Cole went to North Carolina State University and got his Ph.D., and, since 2018, he has been the lead corn quantitative breeder for Syngenta at Ankeny, IA. Juan Landivar received his M.S. in 1979 in agronomy/breeding; his interest shifted and a few years later, he received his Ph.D. (1987) in plant physiology at Mississippi State University, and currently he is director of the Texas A&M AgriLife Research and Extension Center at Corpus Christi, TX.

**Table 3. Graduate students trained by the USDA-ARS cotton host plant resistance/breeding program, Mississippi State, MS**

| Name | Degree | Employer |
|---|---|---|
| Jack C. Bailey | 1965 M.S., 1967 Ph.D. Entomology | Entomologist USDA-ARS |
| Billy F. Oliver | 1965 M.S., 1968 Ph.D. Entomology | Prof. Louisiana State Univ. |
| William T. Buford | 1966 M.S. Entomology | Tech. USDA-ARS; Private Business |
| David G. Holder[z] | 1967 M.S. Genetics | U.S. Sugar Corp. Clewiston, FL |
| William N. Hudspeth | 1967 M.S. Entomology | Dept. Entomology, Univ. of Georgia |
| William L. Parrott | 1967 Ph.D. Entomology | Entomologist USDA-ARS |
| Jerry M. Coakley | 1969 M.S., 1972 Ph.D. Entomology | Oklahoma State Univ. Extension Service |
| Jack C. McCarty, Jr. | 1971 M.S., 1974 Ph.D. Agronomy | Research Agronomist, USDA-ARS |
| Aubrey T. Earnheart | 1973 M.S. Agronomy | Union Planters National Bank |
| Larry N. Latson | 1972 M.S., 1974 Ph.D. Entomology | Asst. Prof. rice insects, LSU |
| Joel Fallieri | 1975 M.S., 1977 Ph.D. Agronomy | Embrapa, Minas Gerais, Brazil |
| Lavone Lambert | 1977 Ph.D. Entomology | Miss. Extension Service; USDA-ARS |
| Peter K. Hall | 1979 M.S. Entomology | |
| Juan A. Landivar[y] | 1979 M.S. Agronomy | Texas A&M AgriLife |
| Jim R. Nichols, Jr. | 1979 M.S. Agronomy | Delta Branch Exp. Station; Industry |
| Abdel Galil Moahed Eissa | 1981 Ph.D. Agronomy | |
| William M. Thomas III | 1981 M.S., 1985 Ph.D. Entomology | |
| William H. White | 1981 Ph.D. Entomology | Resch Entomologist USDA-ARS Homa LA. |
| Michael R. Milam | 1981 Ph.D. Agronomy | Univ. Missouri Extension Service |
| Joel F. Mahill | 1982 Ph.D. Agronomy | Pima cotton breeder Dow/Phytogen |
| Donald L. Dearing | 1983 M.S. Agronomy | Farm in Arkansas |
| Francisco Ramalho | 1983 Ph.D. Entomology | Embrapa, Brazil |
| Joseph E. Mulrooney | 1984 Ph.D. Entomology | USDA-ARS; USDA Forest Service |
| Charles T. Graham | 1995 M.S. Agronomy | Tech Services Bayer |
| Ching-Hsiang Hsieh | 1985 Ph.D. Agronomy | |
| Barry L. Knight | 1988 M.S. Agronomy | Industry several companies |
| Poomsan Silpisornkosol | 1988 Ph.D. Agronomy | Pioneer – Thailand |
| Thomas F. Wharton | 1988 M.S. Agronomy | |
| David H. Smith | 1989 M.S. Agronomy | Farm near Jackson, MS |
| Tang Bing | 1992 Ph.D. Agronomy | Department of Energy |
| G. Randall McPherson | 1993 Ph.D. Agronomy | Cotton Breeder Dow-Phytogen/Corteva |
| Russell W. Hayes | 1993 M.S., 2004 Ph.D. Agronomy | Support Scientist USDA-ARS |
| Mike Swindle | 1993 M.S. Agronomy | Assistant cotton breeder BASF |
| Zachary W. Shappley | 1994 M.S., 1996 Ph.D. Agronomy | Cotton Breeder Monsanto |

**Table 3. continued**

| Name | Degree | Employer |
|---|---|---|
| Michael R. Robinson | 1994 M.S., 1998 Ph.D. Agronomy | Cotton Breeder Stoneville; Americot |
| Phillip D. Wilcox | 1994 M.S. Entomology | |
| Yang Si | 1996 Ph.D. Agronomy | |
| John B. Creech | 1998 Ph.D. Agronomy | MAFES; US Dept. of Defense |
| Sutirtha Basu | 2000 M.S. Agronomy | |
| Douglas B. Shoemaker | 1998 M.S., 2000 Ph.D. Agronomy | Cotton Breeder Deltapine/Monsanto |
| Xiang-Dong Zhang | 1998 M.S. Agronomy | |
| Christopher L. Cheatham | 1999 M.S., Ph.D. 2001 Agronomy | USDA-ARS; FBI |
| Shannon B. Crawley | 2001 Ph.D. Agronomy | Deltapine/Monsanto |
| Jay F. Standley | 2001 M.S. Agronomy | USDA-APHIS |
| Mehmet Karaca | 2001 Ph.D. Agronomy | Prof., Akdeniz Univ., Antalya, Turkey |
| Ming Zong | 2001 M.S. Agronomy | |
| Chethana Bezawada | 2003 M.S. Agronomy | Resch. Scientist, Corteva, Johnston, IA |
| Mitchell K. Fulton | 2002 M.S. Agronomy | USDA-NRCS |
| Brian H. Maxwell | 2002 M.S. Agronomy | USDA Stoneville |
| Clay B. Cole[x] | 2003 M.S. Agronomy | Corn breeder Syngenta |
| Jixiang Wu | 2003 Ph.D. Agronomy | Professor South Dakota State Univ. |
| Liberty Cash, III | 2005 M.S. Agronomy | Terral Seed, Inc. Lake Providence, LA |
| James M. LaFoe, II | 2005 M.S. Agronomy | Bayer Crop Science |
| Herbert T Miller, IV | 2005 M.S. Agronomy | Dow Agri Science/Corteva |
| Parvathi Ynturi | 2005 M.S. Agronomy | |
| Daniel L. Haire, II | 2006 M.S. Agronomy | Miss. State Univ. Extension Service |
| Yufang Guo | 2007 Ph.D. Agronomy | Res. Associate Michigan State Univ. |
| Chuanfu An | 2008 Ph.D. Agronomy | Senior editor Nature Communications, based in NY |
| Satish Ganji | 2012 Ph.D., Molecular Biology | Return to India |

[x] Ph.D Purdue University

[y] Ph.D Mississippi State University

[x] Ph.D. North Carolina State University

Graduates from the program currently lead two commercial cotton breeding programs. Mustafa McPherson (Ph.D., 1993) currently is the lead cotton breeder for Dow-Phytogen (now Corteva Agriscience). Michael Robinson (Ph.D., 1998) is the lead mid-south cotton breeder for Americot, Inc. Until he retired in 2019, Joel Mahill (Ph.D., 1982) was the lead Pima breeder for Dow-Phytogen located in California. Many former graduates are involved in different parts of the cotton sector.

In addition to the graduate students directly trained in the cotton program, research staff have served on many graduate student advisory committees. Mentoring students, both graduate an undergraduate, remains a vital part of the cotton program.

From a bankers, to schoolteachers, to extension service personnel, to agricultural researchers, to technical support staff, to private business and consultants, graduates trained by Mississippi State University and this cotton research program are making impacts not only in the U.S. but throughout the world.

## BOOK CHAPTERS

During the 1970s, three review articles were written by the host plant resistance team, including topics such as resistance of plants to insects (Maxwell et al., 1972), insect plant attractants, feeding stimulants, repellents, deterrents, and other related factors affecting insect behavior (Hedin et al., 1974), and behavior and developmental factors affecting host plant resistance to insects (Hedin et al., 1977). These reviews are valuable resources for students and scientists.

In the 1980s, seven book chapters were written in the areas of host plant resistance and breeding. These chapters are excellent reviews, not only for students, but researchers working in the field of plant resistance (Hedin et al., 1981, 1983, 1984; Jenkins 1981, 1982, 1989, Namken et al., 1983).

During the 1990's, six book chapters were written. These reviews provide excellent resources for those interested in host plant resistance to insects and nematodes (Creech et al., 1998; Hedin and McCarty, 1994; Jenkins 1993, 1995, 1999; Jenkins and Wilson, 1996).

Four book chapters were written during 2000 to 2009. These reviews provide excellent resources for students with interest in breeding and the utilization of new technologies. These chapters were written by Agrawal et al., 2002; Jenkins et al., 2001; Saha et al., 2001; and Wu et al., 2003.

During 2010 to 2019, three book chapters and one review paper were written. These reviews provide in-depth looks at specific topics and serve as excellent resources for students with interest in plant breeding and new technologies. These chapters were written by Adburakhmonov et al., 2012; Ayubovl et al., 2018; and Saha et al., 2012 and the review paper by Zhang et al., 2014.

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Genetic Improvement of Cotton: Emerging Technologies. J.N. Jenkins and S. Saha (eds.). Science Publishers, Inc., Enfield, NH. 2001.

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