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BREEDING AND GENETICS

History and Current Research in the USDA-ARS Cotton Breeding Program at Stoneville, MS

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ABSTRACT

Cotton breeders have focused mainly on selecting for high yield and early maturity under the impact of the boll weevil (*Anthonomus grandis* Boh.) in the last century. Selection for high fiber quality was once a less important objective in cotton breeding. With the transition of the U.S. cotton industry from a domestic consumer to a major exporter of raw fibers into the global market and the technology advancements in the textile industry since the 1990s, the need for high fiber quality in cotton cultivars has increased. In recent years, genetic improvement in cultivars for insect resistance, disease resistance, and abiotic stress tolerance has become important for maintaining cotton yield. Under strong competition from other major crops, increasing profit in cotton production has become an urgent task for cotton breeders and increasing economic potential in cottonseed and other economic traits can help promote profits for cotton growers. In this paper, the major research projects related to cotton breeding at the USDA-ARS at Stoneville, MS since the 1960s are reviewed. These research projects reflect the changing needs in cotton production during the period and focus on broadening the genetic base of Upland cotton for improving agronomic traits and fiber quality in cotton cultivars by a group of scientists with different scientific disciplines. A comprehensive review of this research can help develop strategies and identify research fields to strengthen to meet challenges in future.

There have been dramatic changes in research objectives for cotton production since the last century when the boll weevil was a major pest. During this period, selection for early maturing cotton cultivars became a long-term breeding objective to escape this pest. Another dramatic change in cotton production during the last century was the invention of the cotton picker and its wide application for harvesting, which had a great impact on cotton breeding for early cultivars. The selection for high fiber quality cultivars was a less important breeding objective. Only 1% of U.S. Upland cotton (*Gossypium hirsutum* L.) produced in 1930 exceeded 28 mm in fiber length (Smith et al., 1999). With advances in technologies of harvesting, ginning, and fiber processing, the need for high fiber quality has increased. From 1935 to 1971, the Pee Dee cotton breeding program of USDA-ARS at Florence, SC has emphasized the development of extra-long staple, high yielding Upland cultivars and introgression of genes from the related species, *G. arboreum* L. and *G. thurberi* Tod. into Upland cotton to improve fiber strength (Culp and Harrell, 1974). The Pee Dee program developed a number of non-Acala–type cotton germplasm lines with high fiber quality including FTA 263 and FTA 266 (Culp and Harrell, 1980). However, utilization of these germplasm lines in the development of cotton cultivars was restricted because of the emphasis on selection for high yield and early maturity, which resulted in a limited number of parents involved in crosses during that time. According to an analysis by Van Esbroeck and Bowman (1998), only 0.03% of the 668 cotton germplasm lines registered during 1972 to 1996 were in the pedigrees of successful cultivars.

The U.S. cotton industry has changed since the 1990s from mainly domestic consumption to a major cotton exporter in the global market. A survey reported that U.S. exports of cotton were estimated to reach 15.0 million bales in 2017 marketing year (National Cotton Council, 2018). This shift from domestic consumption to export has changed the requirements of fiber quality. Foreign customers demand higher fiber quality than domestic market in strength, length, uniformity, and purity of raw fibers. Meanwhile, the surviving domestic textile industry has increased spinning speed through modernization

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of equipment resulting in a need for high quality fiber to withstand the higher spinning speeds. The U.S. cotton breeders have responded well to this challenge and the Upland cotton cultivars released in recent years have improved fiber quality. The U.S. cotton industry and exports have benefited from the improved fiber available in the U.S. and the limited availability of higher quality cotton in global market. However, to remain competitive, fiber quality of U.S. Upland cotton cultivars has to be further improved.

In addition to fiber quality, increasing lint yield is always a top priority breeding objective. Lint yield for U.S. Upland cotton has fluctuated between 600 kg ha^{-1} and 1000 kg ha^{-1} during 1991 through 2014 with an upward trend until 2005 (Fig. 1) (National Cotton Council, 2015). Lint yield has plateaued with yearly yields ranging from 968 kg ha^{-1} in 2007 to 925 kg ha^{-1} in 2014. Meredith (2000) summarized the factors with significant impact on lint yield as yearly variability in weather, changes in field management, pest problems, and variety improvement. Another important factor restricting improvements in lint yield is the negative associations between yield traits and fiber properties (Miller and Rawlings, 1967; Smith and Coyle, 1997). Breeders often have to balance increases in lint yield with improvements in fiber quality. The improvement of cotton lint yield depends on genetic improvement in cultivars through breeding practices and an integration of advancement in different scientific disciplines for factors influencing cotton yield.

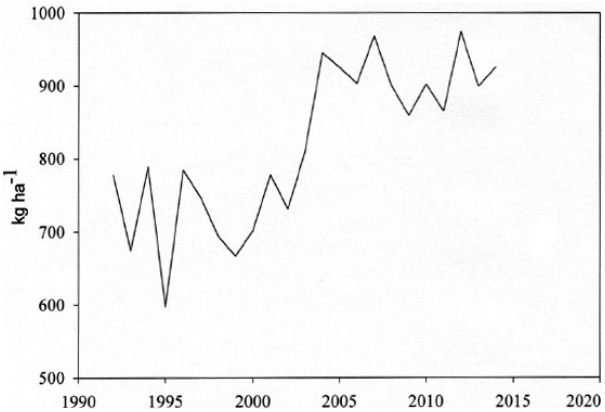

Figure 1. Yearly yield of U.S. Upland cotton between 1991 and 2014 (National Cotton Council, 2015b).

To meet these challenges, USDA-ARS established facilities in the 1960s at Stoneville, MS to conduct cotton research including cotton breeding. The current mission of this breeding program is to (1) expand knowledge of cotton genetics and physiology of cotton fiber development; (2) discover and characterize heritable characteristics that confer resistance or tolerance to adverse environments and pests; (3) coordinate National Cotton Variety Tests; and (4) release germplasm with improved lint yield and fiber quality (www.ars.usda.gov/main/site_main.htm?modecode=60-66-10-00). Research activities at Stoneville have reflected the needs in the U.S. cotton industry. Past research activities have focused on the development of cotton germplasm with improved lint yield, earliness, fiber quality, insect resistance, disease resistance, ginning efficiency, and seed quality. Other research activities include revealing the relationship between leaf types and lint yield and evaluating agronomic potential of nectariless cotton and developing isogenic nectariless lines. Research also extended to expanding knowledge of quantitative genetics to understand interactions of genetic and environmental effects on lint yield and fiber traits and reduce negative associations between yield and fiber quality, and identifying molecular mechanisms of fiber initiation to evaluate molecular basis underlying the critical agronomic phenotype of lint percentage.

IMPACT OF NECTARILESS IN COTTON AND DEVELOPMENT OF ISOGENIC NECTARILESS LINES

With the dominance of Bt cotton and eradication of the boll weevil, the application of insecticides has been reduced and the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), in the mid-south and the western plant bug, *Lygus hesperus* (Knight), have become the most damaging insects in cotton production. Musser et al. (2007) applied nine direct and indirect sampling methods to investigate infestations of hemipterans complex in Upland cotton during the flowering period throughout the mid-south during 2005 and 2006. They reported the tarnished plant bug accounted for 94% of the bug complex during that time. A trial was conducted by Musser et al. (2009) to analyze thresholds of the tarnished plant bug at 19 locations throughout the mid-south during 2006 and 2007 and detected significant yield loss in Upland cotton at eight locations. Meredith and Laster (1975) reported that tarnished plant bug caused damage on cotton plants by decreasing boll number and also caused reduction in lint yield.

Nectariless is a trait in cotton plants where foliar and extrafloral nectaries are absent. The inheritance of the nectariless trait in cotton was

determined by USDA scientists at Stoneville in the early 1960s. The nectariless trait is controlled by two recessive genes, *ne-1* and *ne-2* (Meyer and Meyer, 1961). Although entomologists hypothesized that nectariless in cotton might reduce some insect populations (Lukefahr and Rhyne, 1960), its impact in cotton production was never investigated until Meredith et al. (1973) tested the agronomic potential of nectariless cotton by comparing three nectariless strains to their recurrent parents for lint yield. There was not a strong association between nectariless trait and agronomic performance in cotton detected in that study. Another study by Laster and Meredith (1974) compared Stoneville 7A, Deltapine Smooth Leaf, and Dixie King to their nectariless selections. This study found a significant reduction of tarnished plant bugs in the nectariless lines with no adverse agronomic effects of the nectariless trait and concluded that the nectariless trait might be effective in controlling pest insects in cotton. Meredith (1980) compared nectaried and nectariless hybrid populations and identified larger seed size, boll size, and longer fibers in nectariless cotton plants than nectaried plants. There were no deleterious associations between the nectariless trait and yield in this study. Nine nectariless germplasm lines were developed by Meredith (1977a) by backcrossing to incorporate the nectariless trait into nine cotton cultivars. Most recently, eight isogenic lines were released that had a combination of three traits, sub-okra leaf, smooth leaf, and nectariless (Meredith, 1998a). The nectariless germplasm lines have been used by cotton breeders in private companies to develop six cotton cultivars and one of them, Stoneville 825 was the most planted cultivar in Delta region during the early 80s.

EFFECTS OF LEAF TYPES ON LINT YIELD IN UPLAND COTTON

There are four leaf types in *G. hirsutum*: broad leaf (also called normal leaf), okra leaf, sub-okra, and super-okra leaf. These leaf types are controlled by a series of lacineate alleles including l_2 for broad leaf, L_2^0 for okra leaf, L_2^u for sub-okra leaf, and L_2^s for super-okra leaf (Percy and Kohel, 1999). The sub-okra leaf type was first found by Green (1953), in a line derived from a tri-species hybrid between *G. hirsutum, G. arboreum,* and *G. thurberi* developed in the Pee Dee germplasm program. Meredith (1984) described the sub-okra leaf type in *G. hirsutum* as a trait with "greater indentation of sinus and more lobing than normal leaf."

The relationship between the enhancement of sub-okra leaf and lint yield in Upland cotton cultivars was not determined until the 1980s. Meredith (1984) developed 48 populations from crosses between eight cultivars of normal leaf type and three mutant leaf types to test for the relationship and showed that lint yield of sub-okra populations was significantly higher (4.8%) than populations of the normal and super-okra leaf types. A study of eight BC_4F_3 populations derived from sub-okra leaf and normal leaf types also showed a 3% yield increase for sub-okra leaf cotton over the normal leaf type, but a significant leaf type × background interaction was detected (Meredith and Wells, 1987). Wells and Meredith (1986) observed a significantly higher canopy apparent photosynthesis in sub-okra than the normal leaf type and concluded that the intermediate leaf isogenic lines are promising as a germplasm for physiological criterion-based selection. Eight sub-okra cotton germplasm lines were released by Meredith (1988) with an average of 3% higher lint yield than their eight recurrent parents and concluded that sub-okra leaf cotton could replace normal leaf cotton in some genetic backgrounds with a lint yield increase from 3 to 5%.

Meredith et al. (1996) hypothesized that pyramiding different beneficial traits in cotton cultivars might increase yield. They developed near isogenic populations of BC_4F_5 by backcrosses of three traits, sub-okra leaf, semi-smooth leaf, and nectariless, into DES 119 from MD 65-11S and these populations were evaluated in 1992 and 1993 at Stoneville. MD 65-11S is a germplasm line descended from 'Deltapine 16' with sub-okra and semi-smooth leaf (Meredith, 1988). The sub-okra leaf type produced significantly higher (4%) lint yield than the normal leaf type and no negative interactions among the three traits were observed in that study. It was concluded that the three traits could be incorporated into one cultivar with no major adverse effects. Eight near-isogenic lines of DES 119 for the three traits, sub-okra, semi-smooth, and nectariless, were released by Meredith (1998a). These lines were used by cotton breeders and physiologists for breeding and physiological research. The sub-okra gene source from ARS germplasm lines has been incorporated into some breeding programs in the U.S. to increase lint yield.

THE NATIONAL COTTON VARIETY TEST PROGRAM

In 1958, a meeting was held in Houston, TX by personnel from across the cotton industry, public agencies, and government research institutes to plan a national program to conduct tests to evaluate experimental varieties for lint yield, fiber quality, and seed quality traits across a wide range of environments of cotton production regions in the U.S. In September 1959, the first meeting of the National Cotton Variety Test (NCVT) program was organized by a USDA-ARS scientist, Charles Lewis, and the first NCVT tests were planted in 1960. The program was managed over the years by ARS scientists at several sites with the majority of those years at Stoneville, MS (1980-current). The program partitioned the Cotton Belt into six regions: East, Delta, Central, Plains, West, and San Joaquin, to facilitate tests for region specific cultivars and identification of the elite cultivars with excellent adaptability across regions. Since the establishment of the program, more than 1,300 cultivars, germplasm lines, and strains have been tested in the program (Suszkiw, 2010). 'DES 56' was tested through the NCVT program in the 1970s and released in 1978 (Bridge and Chism, 1978). This cultivar can be found in the pedigrees of most cultivars developed in the East, Delta, and Central regions. The program also has selected cotton cultivars as national standards in each testing cycle to compare testing lines across regions and years. An archive of data is maintained by the program at Stoneville, MS and available upon request for cotton researchers to analyze genotype × environment interactions and changes in varietal performance over time.

Genotype × Environment Interaction (G × E). Reducing G × E effects is a major breeding objective to improve stability of cultivars. Abou-El-Fittouh et al. (1969a, b) were the first to use NCVT data to evaluate the G × E effect and identify environmental factors contributing to varietal performance. Data from four standard varieties evaluated at 39 locations from 1960 to 1962 were used in those studies. The ratio of the G × E component to the genotype component was 2.3 for lint yield, whereas ratios less than 1.0 were reported for fiber properties. Based on these results, the authors concluded that G × E was important for yield, but less important for fiber properties. The authors also analyzed temperature, elevation, moisture, disease, and insect infection and identified temperature as the most important factor contributing to the G × E effects for yield. Meredith et al. (2012) analyzed G × E effects from 2001 through 2007 in 56 year-location environments in Regional High Quality tests. When variance components were expressed as a percentage of the total variance, the variance components of E, G, and G × E for lint yield were 84.3, 7.4, and 8.4, respectively; whereas the variance components for the fiber quality traits ranged from 25.5 to 73.9 for E, 16.1 to 52 for G, and 9.1 to 22.6 for G × E. They suggested that partitioning the Cotton Belt into regions is still necessary for testing lint yield.

It would be ideal if breeders could identify optimum testing environments so that breeding lines could be tested for agronomic performance in fewer environments (Campbell and Jones, 2005). Because it is difficult to identify the optimum testing environment due to the nature of G × E effects, grouping similar environments using historical data could be another approach to reduce G × E effects and identify suitable testing environments. Zeng et al. (2014) analyzed testing locations using lint yield data from 2003 through 2009 for the testing locations in Florence, SC, Belle Mina, AL, and Jackson, TN for the Eastern region; Keiser, AR, Portageville, MO, and Stoneville, MS for the Delta region; Bossier City, LA and College Station, TX for the Central region; Lubbock, TX for the Plains region; and Las Cruces, NM for the Western region. The testing locations of Lubbock and Las Cruces were distinct from the other testing locations. The daily minimum temperature contributed most to the G × E effects of lint yield in this study. The so called mega-environments that would group similar testing locations for agronomic performance were not identified in this study. However, the environments of Las Cruces, NM and Lubbock, TX appeared unique in these tests for lint yield.

Yearly Changes of Yield. By regression of yield means pooled over 15 testing locations on years from 1960 to 1996 in NCVT tests, two distinct yield trend periods, 1960 to 1981 and 1982 to 1996, were identified with an average higher yield of 193 kg ha^{-1} for the later period (Meredith, 1998b). A yield plateau was identified by the regression of yearly yield over test years within each period as -2.0 and -5.0 kg ha^{-1} $year^{-1}$. Campbell et al. (2014) divided NCVT trials between 1981 and 2011 into two groups, 1981 to 1995 and 1996 to 2011 and used standards in each testing cycle to adjust for environmental effects to estimate genetic gains of lint yield over years. They observed that the rate of genetic gain between 1996

and 2011 was significantly higher than between 1981 and 1995 and the trend paralleled the shift to a transgenic production system. Zeng et al. (2015) analyzed yield data in NCVT tests conducted during 1996 and 2013 and identified significant lint and seed yield increases over testing cycles during that period that also coincided with the increase use of transgenic lines. The number of transgenic varieties ranged from 0 to 2 in the two early cycles between 1996 and 2001, whereas they ranged from 3 to 13 in the next four testing cycles from 2002 to 2013.

USE OF EXOTIC GERMPLASM TO REDUCE NEGATIVE ASSOCIATIONS BETWEEN YIELD AND FIBER QUALITY

Meredith (1977b) has shown that the negative association between lint yield and fiber strength can be reduced through introgression of exotic germplasm into Upland cotton. The release of MD51ne by Meredith (1993) is an example for a successful reduction in such negative association. MD51ne was selected from a BC_2F_2 population that originated from a cross between MD65-11ne and 'Deltapine 90'. MD65-11 is a nectariless strain with genetic background of a Pee Dee germplasm line, FTA 263-20. When compared with its parent, Deltapine 90, MD51ne had 6.7% higher lint yield and 11% higher fiber strength. At the time of evaluation (1989-1991), the lint yield of MD51ne was equivalent to the most popular cultivar Deltapine 50. MD51ne has been used in private breeding programs such as Phytogen and public breeding programs to develop cultivars such as Arkot 9608ne (Bourland and Jones, 2008) and TAM 98D-99ne (Thaxton et al., 2005).

Random mating between exotic germplasm and Upland cotton is another method to introgress favorable exotic genes into Upland cotton. The species polycross (SP) population, was initiated by P.A. Miller at North Carolina State University and advanced and maintained at Stoneville. This population underwent random mating among wild tetraploid species including *G. barbadense* L., *G. tomentosum* Nutt. ex Seem., *G. mustelinum* Miers ex Watt., and *G. darwinii* Watt., and Upland cotton in the 1960s and 1970s. The population, John Cotton (JC), was developed by random mating between *G. barbadense* and Acala 1517-type varieties at USDA-ARS in Las Cruces, NM in the 1970s and advanced and maintained at Stoneville. These populations were evaluated at USDA-ARS facilities in Stoneville since the 1990s. Significant genotypic variations for lint yield and fiber properties were identified within populations based on evaluation of 260 SP lines and 200 JC lines in 2005, 2006, and 2007 (Zeng and Meredith, 2009a; Zeng et al., 2007). Nine germplasm lines were selected from the populations showing desirable combinations of lint yield, yield components, and fiber properties and released (Zeng and Meredith, 2009b; Zeng et al., 2010). These germplasm lines have been utilized by the private breeding program of Monsanto and public breeding programs in China and Uzbekistan.

The release of MD 10-5 is a recent example of a germplasm line combining high yield and high fiber strength (Zeng et al., 2016). MD 10-5 was selected from F_5 progenies of a cross between MD 15 and JAJO 1145ne. MD 15 was derived from a cross between 'FiberMax 832' and MD 51ne, and JAJO 1145ne is an unreleased breeding line derived from a cross of JAJO 9596/JAJO 9550 (Jack Jones, JAJO Genetics, Baton Rouge, LA). The mean lint yield of MD 10-5 across nine testing locations in the 2012 Regional High Quality test was 1605 kg ha^{-1}, which was similar to the yield (1607 kg ha^{-1}) of the high yielding check PHY 375WRF, whereas its strength was 329 $kNmkg^{-1}$, significantly higher than the high fiber quality check FM 9058F (316 $kNmkg^{-1}$). In the 2012 and 2013 Regional Breeder's Testing Network trials, MD 10-5 ranked at the top for lint yield and strength compared to the checks. MD 10-5 has been used in major private breeding programs in the U.S. and the public breeding program of the University of Arkansas.

TRANSFERRING NEMATODE RESISTANCE TO UPLAND COTTON

The reniform nematode (*Rotylenchulus reniformis* Linford and Oliveira) occurs in tropical, semitropical, and warm temperate soils (Robinson et al., 2001). Cotton losses in the U.S. to reniform nematode in 2014 were estimated at 3.1% (Lawrence et al., 2015), with higher losses in the mid-southern states of Mississippi, Alabama, and Louisiana, where this species has replaced root-knot nematode (*Meloidogyne incognita* Kofoid & White Chitwood) as the predominant nematode on cotton (Robinson, 2007). Current management strategies rely on nematicides and crop rotation because there are no resistant commercial cotton cultivars available.

There is no strong resistance to reniform nematode in *G. hirsutum* (Robinson, 2007) so USDA ARS researchers at several locations have been utilizing the resistance available in related *Gossypium* species to develop resistant germplasm. Collaborative research involving the Stoneville team resulted in the release of germplasm line BARBREN-713 (PI671965), with resistance to reniform nematode derived from tetraploid *G. barbadense* accession GB 713 (Bell et al., 2015). However, work at Stoneville has focused primarily on identifying resistance in diploid relatives of Upland cotton and transferring that resistance to Upland cotton. Screening accessions under controlled environment conditions (Stetina and Young, 2006) has resulted in characterization of the levels of resistance in more than 450 accessions of *G. arboreum* and more than 50 accessions of *G. herbaceum* resulting in the identification of more than 120 accessions conferring resistance (Sacks and Robinson, 2009; Stetina and Erpelding, 2016). Two *G. arboreum* accessions with high levels of resistance, A_2-190 (PI 615699; Sacks and Robinson, 2009) and A_2-100 (PI 529728; Erpelding and Stetina, 2013) have been used as the basis for germplasm improvement efforts by Stoneville researchers. High levels of resistance to *R. reniformis* also were reported in *G. aridum* (Rose & Standl.) Skov (Romano et al., 2009; Sacks and Robinson, 2009).

Although high levels of resistance to the nematode exist in these diploid species, transferring resistance to a tetraploid species is limited by barriers to hybridization. Breeding methodology including interspecific crosses with ovule culture and embryo rescue used to recover the hybrid plant followed by chromosome doubling to develop compatible breeding lines has been developed or improved by the USDA ARS research team (Erpelding, 2015; Sacks, 2008). Alternatively, Sacks and Robinson (2009) used the hexaploid bridging line G371 [(*G. hirsutum* x *G. aridum*)^2] (Maréchal, 1983) to develop a tri-species hybrid by crossing it to the *R. reniformis* resistant *G. arboreum* accession A_2-190 (PI 615699). All of the selfed seeds of G371 screened for *R. reniformis* reaction were resistant. Because resistance has not been found in *G. hirsutum*, the resistance was postulated to come from *G. aridum* and this hypothesis was confirmed in an independent test (Fang and Stetina, 2011). Backcrossing usually is required to restore fertility, and multiple generations of backcrossing are often needed to recover the desirable tetraploid phenotype before this tri-species hybrid can be used in cotton breeding.

Identification of molecular markers for resistance is critical for developing resistant lines in a breeding program, as it can speed up selection and increase the numbers of individuals that can be evaluated. Determining the number and location of the genes conferring resistance is necessary for marker identification. The genomic location of a single dominant gene from *G. aridum* conferring *R. reniformis* resistance (Ren^{ari}) was identified, along with associated molecular markers (Romano et al., 2009). The resistance from *G. arboreum* accession A_2-190 (PI 615699) was conferred by a single dominant gene (Sacks and Robinson, 2009). Whereas, resistance in *G. arboreum* accession A_2-100 (PI 529728) was conferred by a single recessive gene (Erpelding and Stetina, 2013); thus presenting an opportunity to utilize unique sources of resistance from this diploid species in future introgression research. Presently, 15 sources of resistance from *G. arboreum* accessions have been introgressed and breeding lines are under development to further evaluate these sources of resistance.

INCREASING THE ECONOMIC POTENTIAL OF SEED

Cotton (*G. hirsutum*) produces a number of toxic terpenoid aldehyde (TA) compounds contained in epidermal glands that help protect the plant from pests and diseases. In the seed, one of these toxic compounds, gossypol, limits the use of the seed to ruminants such as dairy cows. A reduction in seed gossypol content would allow a proportional increase of cottonseed meal in ruminant rations. In addition, lines with low seed gossypol would improve the feeding value of cottonseed and allow it to be included in rations for monogastrics such as fish, pigs, and broiler chickens.

One strategy to remove gossypol has been to completely eliminate all the glands on the plant that contain gossypol. A glandless genetic stock was developed by McMichael (1960), and for the next 20 years, extensive efforts were made to develop glandless cotton cultivars. These glandless cultivars have not been successful commercially because without the glands on the vegetative parts of the plant, the plants suffer increased damage from a number of pests.

Glanding in *G. hirsutum* is controlled by two major genes, Gl_2 and Gl_3 (McMichael 1960). Work by Joshua Lee (Lee, 1965, 1977) indicated that the $gl_2gl_2Gl_3Gl_3$ genotype had a greater effect on decreasing seed glanding than $Gl_2Gl_2gl_3gl_3$. Although completely eliminating glands (and gossypol) has not been commercially viable, studies at Stoneville demonstrated that a more moderate strategy could be successful. Studies demonstrated that the number of dominant alleles present affected the density of the glands and although both genes were active in the vegetative and reproductive parts of the cotton plant, it was confirmed that Gl_2 was more highly expressed in the seed, whereas Gl_3 was more active in the non-reproductive plant parts. Because TA compounds are not produced in the above-ground parts of the plant when glands are not present, seed gossypol content is associated with the number of glands present (Scheffler, 2016). Fully glanded plants ($Gl_2Gl_2Gl_3Gl_3$) were crossed to a completely glandless plant ($gl_2gl_2gl_3gl_3$), and selections were made in subsequent generations to obtain lines that minimized seed gossypol content while maintaining near-normal glanding in the remainder of the plant (Romano and Scheffler, 2008). A set of germplasm lines was released based on this research (Scheffler and Romano, 2012).

Although there are breeding techniques and germplasm available to decrease gossypol in the seed, the breeding process also needs to include evaluation of the plant's ability to resist insect pests. Three approaches were tested at Stoneville to assess resistance of cotton to herbivory from bollworm [*Heliocoverpa zea* (Boddie)] and tobacco budworm (*Heliothis virescens* Fabricius): field counts, controlled field antibiosis assays, and laboratory feeding tests of young field-grown leaves. Results indicated that both field and laboratory evaluation could provide an assessment of the cotton host's resistance. Comparing the levels of terpenoid aldehydes in the seed and the leaves confirmed that the levels and types of TAs in the seed were not always good estimators of leaf TAs and that other TAs such as hemigossypolone and heliocides contribute to host plant resistance (Scheffler et al., 2012).

Successful breeding programs optimize the time, labor, and resources needed to produce an improved elite line or variety. When possible, selecting individual plants in the F_2 generation offers the most efficient strategy for selection and development. The genes controlling glanding and gossypol concentration are simply inherited and lend themselves to early generation selection. At Stoneville, we developed rapid and cost effective methods to measure (+) and (-) gossypol in the cotyledon (chalazal) half of a seed by high performance liquid chromatography (HPLC) at a reduced scale. Techniques also were developed to propagate the embryo (micropylar) half of the seed. These techniques were used to develop elite lines with varied gossypol levels. With this strategy, the number of lines needing to be evaluated in later generations was decreased and the lines were produced one year earlier than would have been possible with a more conventional breeding strategy (Scheffler and Romano, 2008; Scheffler et al., 2015).

New technologies are emerging that will allow more targeted and precise methods to modify gossypol in cotton plants. To use these new technologies, a better understanding of gossypol and gland development is needed. Our development study used a VHX-600 Keyence Digital Microscope with a VH-Z20R (20X to 200X) lens to capture developing ovule (seed) images at 14, 16, 18, 20, and 22 days after flowering (DAF) to determine the point in seed development where gossypol glands were initiated and then filled with gossypol. The study revealed empty glands forming as early as 16 DAF and as late as 20 DAF depending on the cotton line evaluated. For most of the varieties, glands were filling with gossypol by 18 DAF, but as early as 16 DAF for special ultra-early varieties from Uzbekistan (Scheffler et al., 2014).

BREEDING ACTIVITIES INTEGRATING MULTIPLE SCIENTIFIC DISCIPLINES

Meredith (2005a) determined that the minimum number of genes controlling fiber strength in a backcross population was 1.1 to 1.3. Two near isogenic lines, MD90ne and MD52ne, were developed with a 10% higher fiber bundle strength in MD 52ne compared to its recurrent parent, MD 90ne (Meredith, 2005b). These two near isogenic lines were used to identify one quantitative trait loci (QTL) for fiber bundle strength, qFBS-c3 on chromosome 3 originating from MD 52ne (Islam et al., 2014).

Reducing cost in cotton production and processing is critical for increasing profit of cotton growers and the industry. Energy consumption during ginning is an important part of the cost and it might be reduced by selection for varieties with lower gin-stand energy consumption. Varieties with

reduced fiber-seed attachment force have potential to improve ginning efficiency and consume less energy than conventional varieties. Bechere et al. (2014) defined ginning efficiency as reduction of net gin-stand energy usage and an increase of ginning rate. Two F_3 populations derived from two crosses between parental cultivars with differential ginning energy requirements were evaluated by Bechere et al. (2014) to determine if the lower energy requirement and higher ginning rate can be used as selection criteria for improving ginning efficiency. Average broad-sense heritability over the two populations for fuzz percentage, ginning rate, net ginning energy, and gross ginning energy was 0.61, 0.16, 0.38, and 0.29, respectively. Genotypic correlations between fuzz percentage and net ginning energy and between fuzz percentage and ginning rate were 0.45 and -0.54, respectively, for the cross of JJ 1145ne × Arkot 9608ne. It was concluded that selection for lower fuzz percentage might result in better ginning efficiency. A further study (Bechere et al., 2016) determined that MD 25, a germplasm line with high lint yield and high fiber quality (Meredith and Nokes, 2011), had high general combining ability (GCA) for ginning rate, and Ark 9317-26, an unreleased breeding line with naked seed derived from a cross of N-143-6/'H1330' had significant negative GCA for net ginning energy. These lines can be used in breeding to improve ginning efficiency.

Understanding the genetic mechanisms of fiber initiation and development will aid in the genetic improvement of fiber properties. Genetic mutations have been identified that inhibit both lint and fuzz development. Three loci, N_1 and n_2 (Percy and Kohel, 1999) and *n3* (Turley and Kloth, 2002), have been reported to inhibit fuzz fiber development. The fuzzless seed locus, n_3, also was shown to be associated with the fiberless seed phenotype in a fiberless line, SL1-7-1 (Turley and Kloth, 2008). A fiberless cotton germplasm line, MD 17, was developed resulting from the homozygous expression of two fuzzless loci N_1 and n_2 (Turley, 2002). Two unreleased Ligon lintless NILs were developed and have been used for studies of biochemical and molecular mechanisms of fiber development: Ligon lintless 1 (Gilbert et al., 2013; Naoumkina et al., 2015; Thyssen et al., 2014b, 2015) and Ligon lintless 2 (Gilbert et al., 2013; Hinchliffe et al., 2011; Naoumkina et al., 2013, 2014; Thyssen et al., 2014a). Other near isogenic lines that should be released soon are derived from a virescent leaf with the seed accession number 30 (SA 30, PI528567) and a bronze leaf (SA 31, PI528448).

CONCLUSIONS AND PERSPECTIVES

The breeding efforts of the USDA cotton breeding program at Stoneville, MS have focused on broadening the genetic base of Upland cotton for improving agronomic performance and fiber quality in cotton cultivars by developing germplasm lines with improved lint yield, fiber quality, insect resistance, disease resistance, and differential leaf morphology. The NCVT program has evaluated more than 1,300 cotton varieties across diverse environments of the U.S. Cotton Belt and the data have been used to analyze genotype × environment effects on yield, fiber quality, and seed traits. The integration of multiple scientific disciplines has contributed to our understanding of molecular basis of fiber quality and mechanisms underlying fiber development.

The improved fiber quality measurement techniques, the dominance of the transgenic cotton in production, and the boll weevil eradication program have had a dramatic impact on cotton production and research. It is expected that the recent achievements in biotechnology and bioinformatics such as the release of the genome sequences for *G. raimondii* (Wang et al., 2012), *G. arboretum* (Li et al., 2014), and *G. hirsutum* (Li et al., 2015) will have a great impact on cotton research. Functional candidate genes can be identified that underlie the QTL for cotton yield traits, fiber properties, and pest resistance. These candidate genes can promote understanding of molecular mechanisms of fiber development, and facilitate validation of QTL for marker-assisted breeding, and reduce or break negative associations between lint yield and fiber quality. Another challenge to breeders is to promote profits for cotton growers by increasing yield, reducing cost of production, and developing new cultivars with value-added traits.

Therefore, we should strengthen research on (1) genetic improvement of lint yield and fiber quality, (2) introgression of exotic germplasm into Upland cotton, (3) molecular mechanisms for fiber development, and (4) development of biotechnological tools for marker-assisted breeding. Currently, the following projects are nearly completed in USDA breeding program at Stoneville: (1) identification of QTL for ginning efficiency in collaboration with

molecular biologists in Cotton Fiber Biotechnology Laboratory; (2) development of three sets of NILs for Ligon lintless and two sets of virescent lines; (3) development of germplasm lines with higher fiber strength and extra-long staple derived from wild crosses among *G. arboreum, G. aridum,* and *G. hirsutum*; and (4) release of *G. hirsutum* germplasm lines with improved nematode resistance from related *Gossypium* species.

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DISCLAIMER

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