The *Journal of Cotton Science 20:246–252 (2016)*
http://journal.cotton.org, © The Cotton Foundation 2016

MOLECULAR BIOLOGY AND PHYSIOLOGY

The Use of Obsolete and Modern Cultivars to Examine Advances in Yield and Dry Matter Partitioning

Randy Wells*

ABSTRACT

Genetic gain through cotton improvement has been best established by testing obsolete and modern cultivars in the same environments. This review is an examination of the yield and growth analysis studies performed at Stoneville, MS in the 1970s and 80s. There were four yield studies that exhibited a mean increase of approximately 7.4 kg lint ha^{-1} yr^{-1} and a range from 4.8 to 10.2 kg lint ha^{-1} yr^{-1}. The lowest value was observed at a low nitrogen rate of 22 kg N ha^{-1}. Growth analysis showed earlier and more intense flowering rates in the modern cultivars than rates seen in more obsolete cultivars. This maturity difference was supported by significant, negative correlation coefficients for the relationships between the year of cultivar release and various parameters of vegetative growth later in the season. These data indicate that there was greater vegetative mass in the obsolete cultivars at that time. The opposite was true of the reproductive parameters, which were positively related to year of cultivar release. Reproductive-to-vegetative (RVR) dry weight (DW) ratio was significantly related to year of cultivar release at 69, 96, 117 and 142 days after planting (DAP) with coefficients of 0.39*, 0.50, 0.61** and 0.53**, respectively. Further work with advanced breeding lines and present day cultivars indicated that yield increases through partitioning from vegetative to reproductive structures were likely to continue. It is not known if such alterations have been brought forward in today's biotechnologically modified cultivars.**

Upland cotton (*Gossypium hirsutum* L.) is a perennial, which had a tree-like growth habit before it was domesticated by man (Hutchinson et al., 1947). Due to its perennial growth habit, cotton is generally deep rooting and has good drought tolerance, a useful survival adaptation (De Souza and Vieira da Silva, 1987). Through breeding and selection, cotton has been transformed into a more determinate growth habit, which imparts intensive reproductive development with reduced vegetative production. However, defoliation is still required and the annual label is still not totally reflective of its perennial growth habit.

Fiber yields in the United States of upland cotton have increased linearly ($r^2 = 0.91$) since 1935 (Fig. 1) with an average 8.8 kg per hectare increase per year. Average fiber yields in the United States did not increase until just prior to World War II. While our ability to manage the crop from that time to the present has been facilitated by the advent of fertilizer use, pesticide use, growth regulator use, boll weevil eradication, and the like, genetic improvement has certainly been an important factor (Meredith, 2002).

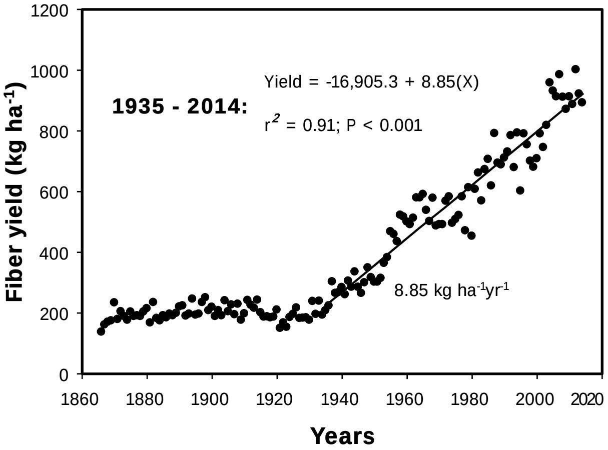

Figure 1. Mean yearly cotton fiber yields in the United States from 1866 to 2014.

Genetic gain through cotton improvement has best been determined by testing obsolete and modern cultivars in the same environments. There is a synopsis of these studies by Schwartz (2005), which has been adapted in Table 1. Fifteen studies covering the range of years of release from 1905 through 2002 were analyzed. The average gain in yield from these studies was 7.0 kg ha^{-1} and the median was 7.2 kg ha^{-1}. The objective of this review is to determine whether these gains were realized through physiological or morphological modifications of new cultivars,

---

R. Wells*, Department of Crop Science, North Carolina State University, Box 7620, Raleigh, NC 27695
*Corresponding author: rwells@ncsu.edu

or multiple external factors such as management or pest control options. This publication will examine the obsolete versus modern studies that were performed at Stoneville, MS from the late 1960s until 1986.

YIELD

The first study was conducted by Drs. Bob Bridge, Bill Meredith, and J.F. Chism, in 1967 and 1968. Thirteen obsolete cultivars and three relatively new cultivars (Stoneville 213, DPL Smooth Leaf, and Coker 413-68) were examined (Bridge et al., 1971). The obsolete cultivars were all formerly important commercial cultivars in the Mississippi Delta. Stoneville 213 and Deltapine Smooth Leaf were bred in the Mississippi Delta, while Coker 413-68 was bred in Hartsville, SC. The relationship of yield to year of cultivar release was significant ($r^2 = 0.58$, $P = 0.0006$) and showed a 10.1 kg ha^{-1} increase in fiber yield per year (Fig. 2A). In their study, lint yield was positively related ($r^2 = 0.86$, $P < 0.0001$) to fiber percentage (Fig. 3). For every percent increase in percent fiber there was an increase in lint yield of approximately 51.5 kg ha^{-1}. These data indicate that there was a shift in intra-boll dry matter partitioning from seed to fiber. Similarly, Snider et al. (2013) found that lint percentage was impacted more by genotype than by environment with 51.5% of variability in lint percentage explained by genotype and 38.8% explained by environment in 33 environments.

Bridge and Meredith (1983) performed another study in 1978 and 1979 to examine whether a perceived yield decline was related to the inherent yielding ability of a cultivar. In this study 17 cultivars representing the period from 1910 until 1978 were examined. Twelve of these were released form 1910 through 1944. Three were from the period of 1959 through 1965 and two were released in 1978. The relationship between fiber yield and year of cultivar release found in 1979 can be seen in Figure 2B. (adapted from Bridge and Meredith, 1983; Table 1). There was a significant relationship ($r^2 = 0.83$, $P < 0.001$), which indicated that the mean annual genetic gain for fiber yield was 9.5 kg ha^{-1}. Interestingly, the percentage of lint in the first of two harvests was also positively related to year of cultivar release ($r^2 = 0.47$, $P = 0.003$), indicating a shift towards earlier maturity (Fig. 4). More recently, Bednarz and Nichols (2005) indicated that selection for (a) the compression of the horizontal flowering interval, (b) the reduction of the boll maturation period, and (c) the elongation of sympodial branches at lower main stem nodes were most useful in breeding for earlier maturity.

Wells and Meredith (1984a,b,c) performed an extensive growth analysis study to determine if alterations to growth patterns had been indirectly brought forth through selection for greater fiber yields. In the study, six cultivars from both the Stoneville (STV) and Deltapine (DPL) lineage released from 1905 through 1978 were grown. Two distinct environments were generated through two planting dates, 26 April and 12 May 1982.

Table 1. Reported genetic gain determined through side-by-side comparisons of commercially grown obsolete and modern upland cotton cultivars

Time span of cultivar release^{Z}	Genetic gain (kg ha^{-1})	Number of Cultivars	Reference
1945-1978	10.5	9	Culp and Green (1992)
1922-1962	10.2	13	Bridge et al. (1971)
1910-1979	9.5	17	Bridge and Meredith (1983)
1937-1965	9.0	8	Meredith et al. (1997)
1939-1979	9.0	9	Bassett and Hyer (1985)
1905-2002	8.7	9	Schwartz and Smith (2008)
1937-1974	7.2	6	Hoskinson and Stewart (1977) Culp and Green (1992)
1905-1978	6.8	12	Wells and Meredith (1984); Meredith et al. (1997)
1918-1982	5.6	12	Bayles et al. (2005)
1938-1993	5.3	38	Meredith (2002)
1983-1999	3.9	23	Meredith (2002)
1918-1982	3.7	12	Bayles et al. (2005)
1984-1993	1.5	8	Meredith et al. (1997)
Mean	7.0		

^{Z}Approximate range of year of release for the cultivars tested. Adapted from Schwartz (2005).

The research estimated that the mean annual genetic gains were 7.1 kg ha^{-1} ($r^2 = 0.69$, $P < 0.001$) and 6.6 kg ha^{-1} ($r^2 = 0.61$, $P < 0.003$) with these two respective planting dates as factors in the study (Fig. 2C).

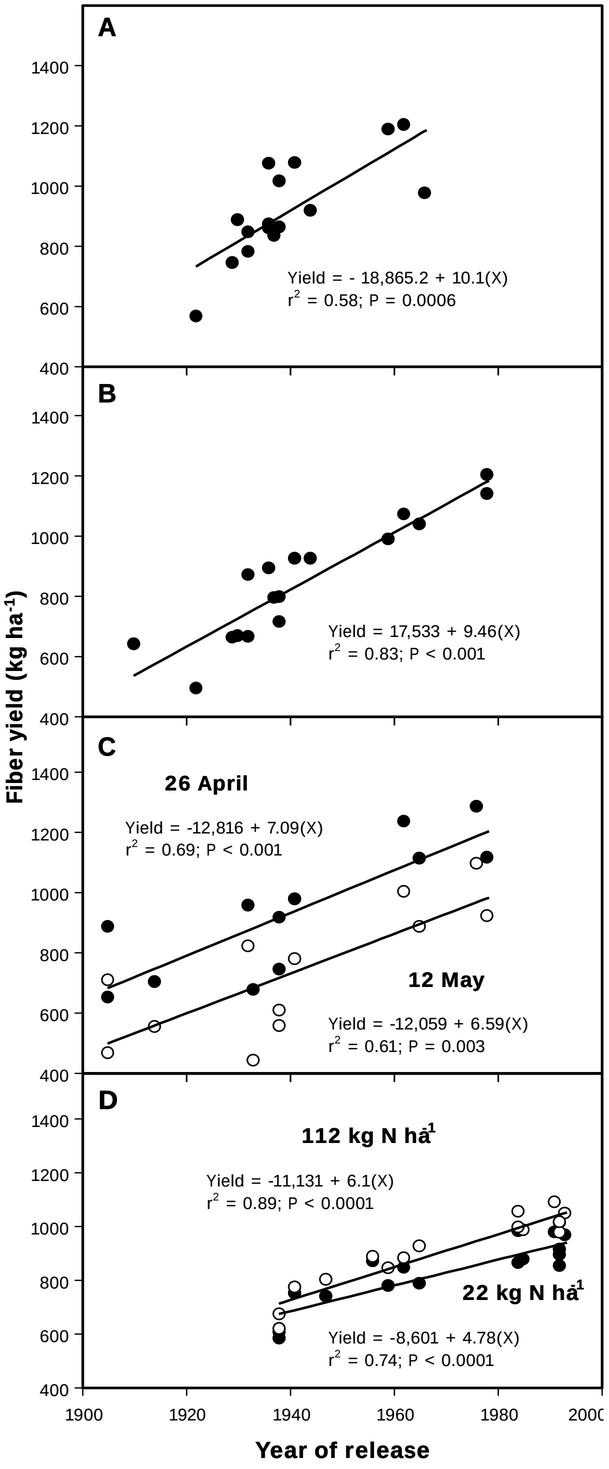

Figure 2. Comparative fiber yield performance of obsolete and modern cultivars from four studies. Adapted from (A) Table 1 of Bridge et al. (1971), (B) Table 1 of Bridge and Meredith (1983), (C) Table 1 of Wells and Meredith (1984c), and (D) Figure 1 of Meredith et al. (1997).

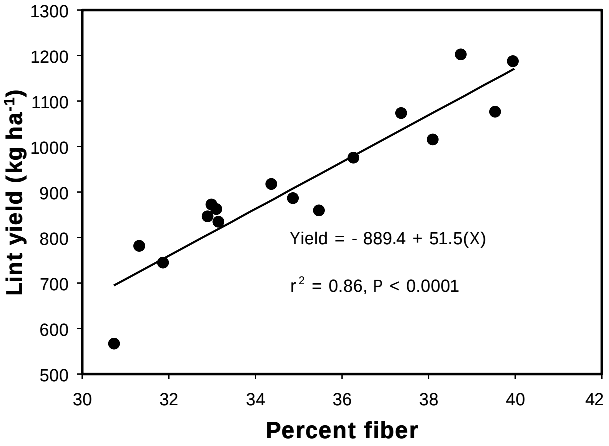

Figure 3. The relationship between lint yield and fiber percentage. Adapted from Table 1 of Bridge et al. (1971).

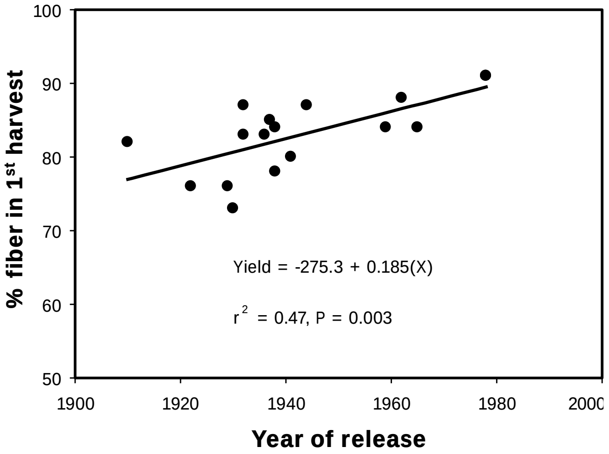

Figure 4. Relationship of percent lint in the first harvest to year of cultivar release. Adapted from Table 1 of Bridge and Meredith (1983).

Meredith et al. (1997) included nitrogen fertilization levels 22 and 112 kg N ha-1, in a study that examined eight obsolete (<1965), seven modern (1984-1995) and one experimental F2 population (MD51ne X STV 6413). They found slightly divergent responses to nitrogen rate with the modern cultivars displaying a significant cultivar X N interaction, which suggests that these modern cultivars responded more to N than many of the older cultivars (Fig.2D). The yield gains due to breeding were 6.1 and 4.78 for the 112 and 22 kg N ha^{-1} treatments, respectively, and represents the lowest gains reported from the Stoneville obsolete versus modern yield studies.

DRY MATTER APPORTIONING

Wells and Meredith (1984a,b,c) performed an extensive growth analysis study as mentioned earlier. Several alterations in dry matter allocation were found due to breeding efforts aimed largely at increasing lint yields. The first alteration was a shift in modern cultivars to earlier reproductive development. Simple correlation coefficients for the relationships between the year of cultivar release and various parameters of vegetative growth (Table 2) showed significant negative relationships at 96, 117 and 142 days after planting (DAP) for the 26 April planting (Wells and Meredith,1984a). There was a significant negative relationship for stem dry weight at 96 and 117 DAP and a significant negative relationship for vegetative DW at 117 DAP. Further, there were significant negative relationships for leaf DW and leaf area index (LAI) at 117 and 142 DAP. The above mentioned Wells and Meredith (1984a,b,c) growth analysis study also found that changes in dry matter allocation were correlated with breeding efforts to increase fiber yield. The modern cultivars also exhibited earlier flowering (Fig. 5A) than either the obsolete or intermediate cultivars in the 26 April planting date (Wells and Meredith, 1984b). Seventy-two percent of white flowers observed in these modern cultivars were found in the first four dates of measurement while the obsolete and intermediate cultivars had 53 and 62%, respectively. Again, these data underscore the shift in the modern cultivars towards earlier maturity.

Correlation coefficients for the relationships between year of cultivar release and various parameters of reproductive development for the 26 April planting date are shown in Table 3 (Wells and Meredith, 1984b). Significant positive correlations were seen for all measurements of reproductive growth and there was a seasonal progression of positive correlations starting early with square number (52 to 96 DAP) and square DW (69 and 96 DAP) to later for mature boll number (117 and 142 DAP), mature boll DW (117 and 142 DAP), total boll number (69 to 142 DAP) and total boll DW (96 to 142 DAP). Conversely, there were sig-

Table 2. Simple correlation coefficients for the relationships between the year of cultivar release and various parameters of vegetative growth measured at different dates from the 26 April 1982 planting date. Adapted from Wells and Meredith (1984a)

Variable	Days after planting					
	38	52	69	96	117	142
	r					
Total Dry Wt.	-0.20	0.01	0.00	0.04	0.01	0.07
Total Vegetative DW	0.20	0.01	0.21	-0.21	-0.39**	-0.22
Stem Dry Wt.	--	-0.12	-0.11	-0.24**	-0.39**	-0.18
Leaf Dry Wt.	0.16	0.10	0.10	-0.11	-0.36**	-0.33**
Leaf Area Index	-0.13	0.07	0.07	-0.08	-0.24*	-0.27*

*, ** Significant at the 0.05 and 0.01 probability level, respectively.

Table 3. Simple correlation coefficients for the relationships between the year of cultivar release and various parameters of reproductive growth measured at different dates from the 26 April 1982 planting date. Adapted from Wells and Meredith (1984b).

Variable	Days after planting				
	52	69	96	117	142
	r				
Square Number	0.28**	0.43**	-0.36**	-0.22**	--
Immature Boll Number	--	0.22*	0.48**	0.21	-0.12
Mature Boll Number	--	--	--	0.30*	0.40**
Total Boll Number		0.22*	0.48**	0.26*	0.34**
Square DW[Z]	0.15	0.37**	0.27*	--	--
Immature Boll DW	--	0.10	0.48**	0.37**	-0.25**
Mature Boll DW	--	--	--	0.24*	0.48**
Total Boll DW	--	0.10	0.48**	0.40**	0.37**
RVR[Y]	--	0.39*	0.50**	0.61**	0.53**

*, ** Significant at the 0.05 and 0.01 probability level, respectively.

[Z] Dry weight.

[Y] Reproductive-to-vegetative DW ratio.

nificant negative correlations at later dates for square number (96 and 117 DAP) and immature boll dry weight (142 DAP) indicating the delayed reproductive development in older cultivars. Reproductive-to-vegetative DW ratio (RVR) was significantly related to year of cultivar release at 69, 96, 117 and 142 DAP with coefficients of 0.39*, 0.50**, 0.61** and 0.53**, respectively. The data indicate that, in addition to earlier maturity, the newer cultivars allocated greater dry matter to reproductive structures and less to the vegetative portion of the plant. These trends can be seen clearly in the Stoneville background with STV 825 and STV 213 displaying a mean RVR ratio of 0.94 at 142 DAP (Fig. 5B). The intermediate cultivars and Lone Star at 142 DAP had mean RVR ratios of 0.68 and 0.40, respectively. Interestingly, similar results were found in a study of obsolete and modern North Carolina peanut cultivars with RVR ratios positively correlated with the number of breeding cycles with correlations coefficients (r) of 0.46**, 0.53**, and 0.74**, at 71, 104, and 113 DAP over two years (Wells et al., 1991).

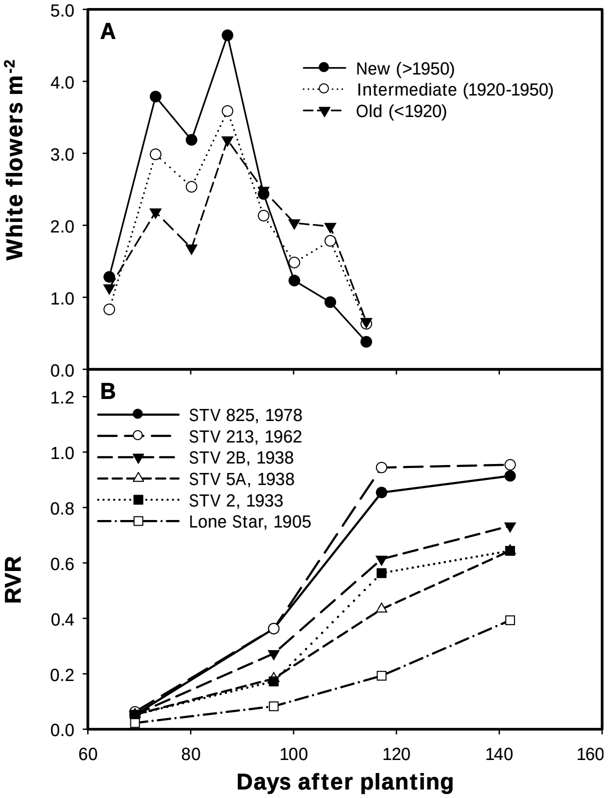

Figure 5. White flower counts (A) and reproductive-to-vegetative ratio (B) at various dates after planting for new, intermediate, and obsolete cultivars for cultivars from the Stoneville background planted 26 April 1982. Adapted from Figure 1 and Table 6 of Wells and Meredith (1984b), respectively.

Meredith and Wells (1989) addressed the question of whether further advances in reproductive partitioning would be realized in advanced lines that were likely to be released as commercial lines. To test this hypothesis, 25 total genotypes representing three groups: five obsolete cultivars, five current cultivars, and 15 advanced strains were evaluated for yield and growth qualities. The advanced lines came from five breeding programs and had the potential to replace cultivars currently grown. Two dry matter harvests were made at approximately 50 and 102 DAP and lint yield was determined at season's end. For the 20 current and advanced genotypes, there was a significant positive relationship (r = 0.63; P = 0.0027) between lint yield and boll DW-to-total DW ratio (Fig. 6A). In addition, there was a significant positive relationship (r = 0.56; P = 0.01) between lint yield and reproductive-to-vegetative ratio (Fig. 6B). These associations supported the notion that further gains for yield through the use of conventional breeding methods were being realized through increased allocation of dry matter from vegetative to reproductive structures. Additionally, reduction of plant height in the advance lines was negatively associated (r = 0.45; P = 0.045) with yield (Fig. 6C).

One research objective of the Meredith and Wells study (1989) was to determine if continued progress through conventional breeding for yield was likely. The genetic variance component for yield among the 20 modern cultivars (5 current and 15 potential cultivars) was large (28%) when expressed as a percentage of the total genetic components. This large genetic component suggests that continued yield advances through breeding were likely during the mid-1980s. Further, a second objective was to determine if this progress would occur through continued apportioning from vegetative to reproductive structures as had been done in cotton breeding efforts prior to that time. In the 20 modern cultivars there was a positive genetic association (Table 4) of boll DW-to-total DW ratio (r = 0.86) and reproductive-to-vegetative ratio (r = 0.91) and stem DW-to-total DW ratio with yield (r = -0.77). These associations suggested that yield increases realized through selection for further partitioning from vegetative to reproductive structures were likely to continue after 1990.

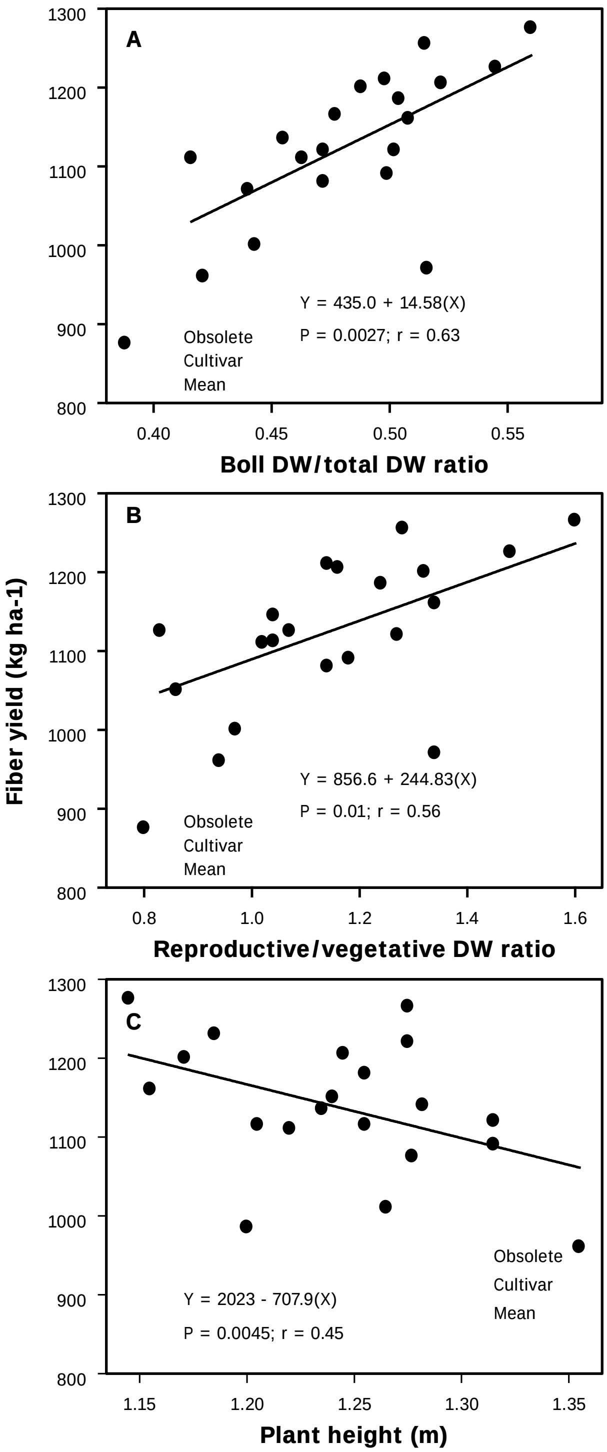

Figure 6. Relationship of fiber yield to (A) boll dry weight (DW)-to-total DW ratio (B) reproductive-to-vegetative DW ratio, and (C) plant height for 20 cultivars (5 current and 15 potential future cultivars). Adapted from Figures 1, 2 and 3 of Meredith and Wells (1989).

Table 4. Genetic and phenotypic correlation coefficients of lint yield with various growth characteristics at approximately 102 days after planting. Adapted from Meredith and Wells (1989)

Yield to Growth Characteristic	102 DAP^{Z}	
	Genetic	Phenotypic
Stem DW-to-Total DW^{Y} Ratio	-0.77	-0.64**
Boll DW-to-Total DW Ratio	0.86	0.70**
Reproductive DW-to-Vegetative DW Ratio	0.91	0.56**

^{Z}DAP= Mean days after planting for sampling for growth characteristics.

*,** Significant at the 0.05 and 0.01 level of probability, respectively.

^{Y}DW = dry weight.

THE BIOTECHNOLOGY AGE

Genetic strategies now involve gene manipulation through modern techniques such as gene guns, electrophoraton, microinjection and *agrobacterium,* (Narusaka et al., 2013) and more recently through transcription activator-like effector nuclease (TALEN) (Jong and Sander, 2013) and clustered regularly interspaced short palindromic repeats (CRISPR) (Yang et al., 2014). These techniques have opened up the possibilities for available traits and have led to herbicide and insect resistant genotypes that are present in over 90% of all cotton grown in the country. With these developments, one must question how the quest for management, stress tolerance or value added driven traits, derived through biotechnological modification, might alter breeding selection benchmarks. Lint yield will remain an important trait to improve, but research should be conducted to determine whether past trends for selection of dry matter have continued. Have the changes in dry matter allocation in response to selection for yield, as seen in the historical studies covered herein, continued to the present day biotechnologically modified cultivars? Pettigrew et al. (2013) examined at low and high plant population densities both conventional and transgenetic genotypes released from 1962 through 2011. Dry-matter partitioning, growth analysis, yield, yield component, and lint quality data were collected yet genotypes did not interact with plant densities for any characteristic.

The movement toward early maturity may be altered by the lessened late-season insect pressure brought about by the development of *Bacillus thuringiensis* containing cotton (BT cotton) and the eradication of the boll weevil. Late-season insect pressure was an integral part of the environments in which breeding selections were being made. Therefore, its effect was confounded within environment and would influence the selection process whether deliberately or inadvertently. The new technologies have effectively eased late-season insect pressure and as a result reduced its influence on breeding decisions. Regardless, new studies are needed to determine the influence of biotechnological modification on the allocation of dry matter and earliness of present-day genotypes.

ACKNOWLEDGEMENT

This paper is in memory of Dr. William (Bill) Ralph Meredith Jr. who was a great collaborator, mentor and friend. He will be missed.

REFERENCES

Bassett, D.M., and A.H. Hyer. 1985. Acala cotton in California: 60 years of varietal improvement. p. 76. In Proc. Beltwide Cotton Prod. Res. Conf., New Orleans, LA.6-11 Jan. 1985. Natl. Cotton Counc. Am., Memphis, TN.

Bayles, M.B., L.M. Verhalen, W.M. Johnson, and B.R. Barnes. 2005. Trends over time among cotton cultivars released by the Oklahoma Agricultural Experiment Station. Crop Sci. 45:966-980.

Bednarz, C.W., and R. L. Nichols. 2005. Phenological and morphological components of cotton crop maturity. Crop Sci. 45:1497–1503.

Bridge, R.R., and W.R. Meredith, Jr. 1983. Comparative performance of obsolete and current cotton cultivars. Crop Sci. 23:949-952.

Bridge, R.R., W.R. Meredith, Jr., and J.F. Chism. 1971. Comparative performance of obsolete varieties and current varieties of upland cotton. Crop Sci. 11:29-32.

Culp, T.W., and C.C. Green. 1992. Performance of obsolete and current cultivars and Pee Dee germplasm lines of cotton. Crop Sci. 32:35-41.

De Souza, J.G., and J. Vieira Da Silva. 1987. Partitioning of carbohydrates in annual and perennial cotton (Gossypium hirsutum L.). J. Exp. Bot. 38:1211–1218.

Hoskinson, P.E., and J.M. Stewart. 1977. Field performance of two obsolete cotton cultivars. p. 78-79. In Proc. Beltwide Cotton Prod. Res. Conf., Atlanta, GA. 10-12 Jan. 1977. Natl. Cotton Council. Am., Memphis, TN.

Hutchinson, J.B., R.A. Silow, and S.G. Stephens. 1947. The evolution of Gossypium and the differentiation of the cultivated cottons. Oxford University Press. London.

Jong J.K., and J.D. Sander. 2013. TALENs: a widely applicable technology for targeted genome editing. Nat. Rev. Mol. Cell Biol. 14: 49–55

Meredith, W.R., Jr. 2002. Factors that contribute to lack of genetic progress. 528-532. In D. Richter (ed.) Proc. Beltwide Cotton Prod. Conf. Atlanta, GA. 9-12 January. Natl. Cotton Council, Memphis, TN.

Meredith, W.R., Jr., J.J. Heitholt, W.T. Pettigrew, and S.T. Rayburn, Jr. 1997. Comparison of obsolete and modern cotton cultivars at two nitrogen levels. Crop Sci. 37:1453-1457.

Meredith, W.R., Jr., and R. Wells. 1989. Potential for increasing cotton yields through enhanced partitioning to reproductive structures. Crop Sci. 29:636-639.

Narusaka, Y., M. Narusaka, S. Yamasaki and M. Iwabuchi. 2012. Methods to Transfer Foreign Genes to Plants, In: Transgenic Plants - Advances and Limitations, Yelda Ozden Çiftçi (Ed.), ISBN:978-953-51-0181-9, InTech, Rijeka, Croatia.

Pettigrew, W.T., W.R. Meredith, Jr., and L. Zeng. 2013. Response of obsolete and modern cotton genotypes to varying plant densities. J. Cotton Sci. 17:253–262.

Schwartz, B.M. 2005. Evaluation of the genetic gain in upland cotton during the twentieth century. M.S. Thesis. Texas A and M University, College Station, TX.

Schwartz, B.M., and C.W. Smith. 2008. Genetic gain in yield potential of upland cotton under varying plant densities. Crop Sci. 48:601–605.

Snider, J.L., G.D. Collins, J. Whitaker, and J.W. Davis. 2013. Quantifying Genotypic and Environmental Contributions to Yield and Fiber Quality in Georgia: Data from Seven Commercial Cultivars and 33 Yield Environments. J. of Cotton Sci. 17:285–292.

Wells R., T. Bi, W.F. Anderson, and J.C. Wynne. 1991. Peanut yield as a result of fifty years of breeding. Agron. J. 83:957-961.

Wells, R., and W.R. Meredith, Jr. 1984a. Comparative growth of obsolete and modern cotton cultivars: I. Vegetative dry matter partitioning. Crop Sci. 24:858–862.

Wells, R., and W.R. Meredith, Jr. 1984b. Comparative growth of obsolete and modern cotton cultivars: II. Reproductive dry matter partitioning. Crop Sci. 24:863–868.

Wells, R., and W.R. Meredith, Jr. 1984c. Comparative growth of obsolete and modern cotton cultivars: III. Relationship of yield to observed growth characteristics.Crop Sci. 24:868–872.

Yang L., L. Li, L. Hai-Yang, L. Sen, F. Xing, and L.L. Chen. 2014. CRISPR-P: A web tool for synthetic single-guide RNA design of CRISPR-system in plants. Mol. Plant 7: 1494-1496.