Chapter 2

GENOTYPIC DIFFERENCES IN COTTON FRUITING

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INTRODUCTION

Upland cotton (*Gossypium hirsutum* L.) is a perennial and started in its long association with man as more of a tree than the growth habit that we presently manage (Hutchinson *et al.*, 1947). The perennial growth habit was a useful survival adaptation due to generally deep rooting and good drought acclimatization (De Souza and Vieira da Silva, 1987). Through breeding selection cotton has been made into “annual types” which have an intensive reproductive development with reduced vegetative production. However, defoliation is still required and the “annual” moniker is still not reflective of its true growth habit.

Fiber yields in the United States of Upland cotton have increased somewhat linearly since 1937 with an average 8.7 kg per hectare (7.8 pounds per acre) increase per year (Fig. 1). Prior to 1937, a long period of little gain in yield was observed starting in 1866, the start of yield recording. Since 1937 two periods of decline or no gain have been witnessed (Table 1.). The first is 1965 to 1980 and was tied to both a narrow genetic breeding base resulting in a lack of new improved cultivars, and the loss of efficacy of available insecticides (Meredith, 2002). The second decline in the 1990s may have been tied to the backcrossing of new molecular genetic modifications into existing cultivars to give herbicide and insect resistance. Backcrossing, while transferring the trait of interest, allows little opportunity for improved yield. There were two periods of yield gain since 1980. The first, from 1981 to 1990, was reportedly due to the introduction of pyrethroid insecticides and new higher yielding cultivars. Presently, there is a gain starting around 2000 showing a yearly gain of 15.2 kg ha^{-1} (13.5 lb/acre).

Genetic gain through cotton improvement has best been determined by testing obsolete and modern cultivars in the same environments. There is a good synopsis of the studies performed by Schwartz (2005) which has been adapted in Table 2. There have been fifteen studies covering the range of years of release from 1905 through 2002. The average gain in yield from these studies was 7.0 kg ha^{-1}. The question is whether these gains were realized through physiological or morphological modifications of new cultivars, or external factors such as pesticide control options.

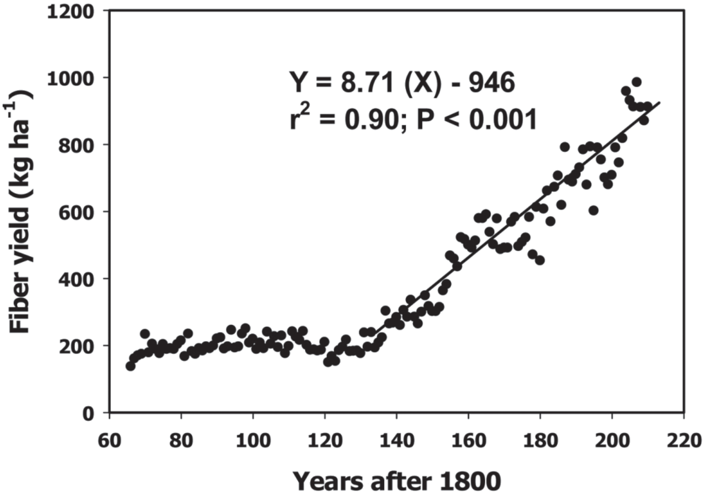

Figure 1. Mean yearly cotton fiber yields in the United States from 1866 to 2010.

Table 1. Regression analysis of yield with year over certain periods of years since 1866.

Period	Regression Equation	r^2	P-value
1866 - 1936	Y = 0.19(X) + 179	0.03	0.175
1937 - 1964	Y = 11.7(X) - 1,348	0.83	<0.001
1965 - 1980	Y = -1.5(X) + 790	0.02	0.59
1981 - 1990	Y = 12.2(X) - 1,583	0.35	0.07
1991 - 2000	Y = -4.6(X) - 1,615	0.05	0.53
2001 - 2010	Y = 15.2(X) - 2,234	0.35	0.07

Table 2. Reported genetic gain determined through comparison of commercially grown obsolete and modern Upland cotton cultivars in the same tests.

Time span of cultivar release†	Genetic Gain (kg ha^{-1} yr^{-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 (2009)
1937-1974	7.2	6	Hoskinson and Stewart (1977); Culp and Green (1992)
1905-1978	6.8	12	Wells and Meredith (1984b); 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		

† Approximate range of years cultivars in the tests were released. Adapted from Schwartz (2005).

OBSOLETE VS. MODERN APPROACHES

Dry Matter Partitioning

Wells and Meredith (1984a) examined twelve cultivars covering seven decades of breeding effort, six each from the Deltapine and Stoneville breeding programs. They found that modern cultivars partition greater dry matter into reproductive growth than vegetative growth (Fig. 2). At the last harvest date the new, intermediate and old cultivars displayed a mean reproductive-to-vegetative ratio of 1.0, 0.78, and 0.70 kg reproductive weight/kg vegetative weight, respectively. The modern cultivars generally produced a maximal vegetative dry weightwhich was smaller and occurred earlier chronologically than their previously released counterparts. The same trend was found in flowering, with the modern cultivars producing more early white flowers than the obsolete cultivars, which continued producing a greater number of flowers later in the season (Fig. 3). Modern cultivars also generally produced a greater number of smaller bolls with a higher lint percentage (Wells and Meredith, 1984b). In a subsequent study, five obsolete cultivars, five popular and high yielding cultivars from five cotton breeding businesses, and 15 advanced lines from five cotton breeding establishments were examined for growth and yield (Meredith and Wells, 1989). The obsolete cultivars yielded 24% less than the twenty modern genotypes. As before, the obsolete cultivars produced more vegetative mass with respect to reproductive mass with the obsolete, current, and future genotypes displaying reproductive-to-vegetative ratios of 0.80, 1.14, and 1.17, respectively. Regression analysis of the relationship between yield and either boll weight/total dry weight or reproductive/vegetative ratio for the 20 modern cultivars were positive and significant, indicating that alterations in dry matter partitioning continued in ongoing breeding programs. These alterations in dry matter partitioning in more modern genotypes are due to indirect effects from selection for higher yield since no breeding programs use harvest index as a selection criterion.

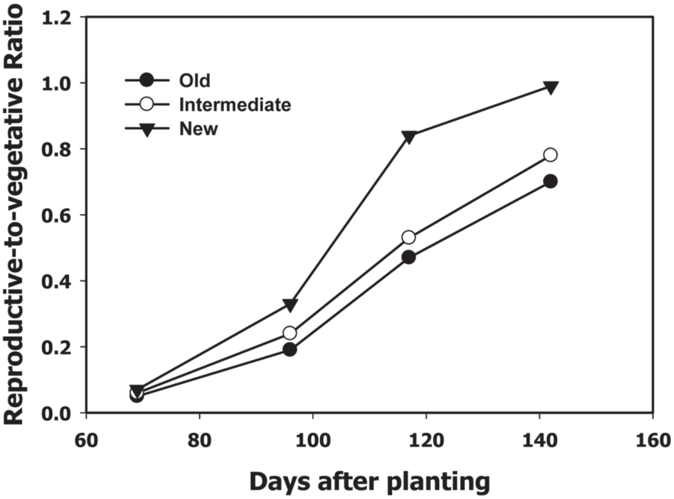

Figure 2. Mean reproductive-to-vegetative ratio occurring at different dates for the cultivars grouped by their year of release and planted on 26 Apr. 1982 (new = 1950 to present; intermediate = 1920 to 1950; old = 1900 to 1920). Adapted from Table 6 of Wells and Meredith (1984b).

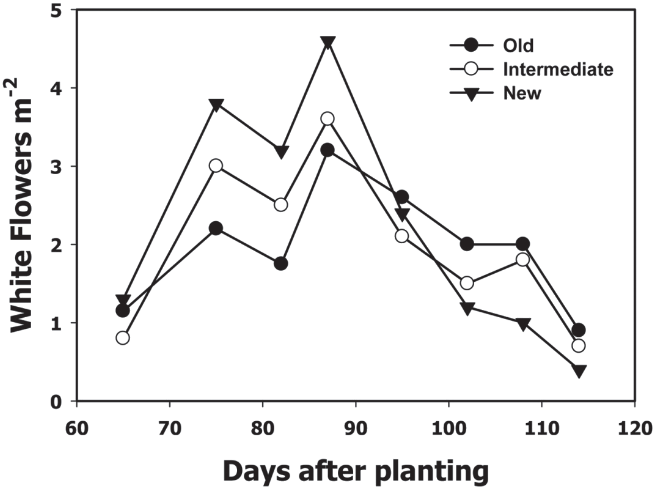

Figure 3. Mean white flower counts determined at various dates for the cultivars grouped by their year of release and planted on 26 April 1982 (new = 1950 to present; intermediate = 1920 to 1950; old = 1900 to 1920). Adapted from Figure 2 of Wells and Meredith (1984a).

Effect of Plant Density

Schwartz and Smith (2008) examined nine current and obsolete cultivars grown at five plant densities. The plants were spaced 3 by 3 m, 2 by 2 m, 1 by 1 m, 1 by 0.3 m, and 1 m by 0.07 to 0.1 m (commercial density). Genetic gain was highest in the commercial, 1 x 0.3m, and 1 x 1m spacing with gains of 8.7, 8.2, and 7.1 kg ha^{-1} yr^{-1}. Lower gains were made in the two largest and least competitive plant interplant distances. They suggest that gain in yield may be due to an increased tolerance to interplant competition and not only yield alone. Their data also support the idea that yield increases have been primarily due to increased boll retention and less from increased lint percentage.

EARLINESS

Movement of the boll weevil (*Amthonomus grandis* Boheman) into the USA occurred in the late 19th century. The goal of cotton management was to hasten crop maturation before boll weevil pressure became too severe (Buie, 1928). Prior to this time, the need for earlier maturity or earliness of cotton was little appreciated or desired. Earliness in a physiological sense has been defined as the percentage of the total fiber yield that is produced by the first harvest. Alternatively, Munro (1971) defined it as the shortest time required to produce an adequate yield. Both definitions are extremely vague on providing an exact length of time for maturation. More recent studies have defined measures of earliness as time to first square, time to first flower, time taken to mature the node of the first boll, and the plant region of greatest fiber production. Bange and Milroy (2004) reported that the attainment of crop maturity (60% open bolls) was related to when the fruit growth rate per unit area was equivalent to the crop growth rate (total dry weight per area per day). They suggested that a key trait related to earliness is the timing of the start of reproductive growth tied with the subsequent development of the demand for dry matter. In another study, they found that earlier maturing cultivars produced more dry matter due to great radiation use efficiency and light interception (Bange and Milroy, 2000). In addition, the greater photosynthetically active radiation (PAR) interception was due to larger canopies and not altered canopy light extinction coefficients.

The industry convention is that each flowering interval occurs at 3 days vertically within the plant and at 6 days horizontally along branches as reported by McClelland (1916). Bednarz and Nichols (2005) found these same respective intervals to be 2.5 and 3.8 days when averaged over nine cultivars and three years. The horizontal flowering interval (HFI) was 2 days shorter than previous reports and different between earlier and later maturing cultivars, suggesting that this attribute has been influenced through the quest for early crop maturity. There was also a difference in boll maturation period and the percentage of bolls produced at lower main-stem nodes. Jenkins *et al.* (1990) reported that newer, earlier maturing cultivars had significantly greater fiber located at nodes 6 through 8 than the older Stoneville 213. Figure 4 is a graph of an early cultivar (STV 213), a more modern cultivar (DPL 50) and the cultivar with the highest yield (DES 119). Both DPL 50 and DES 119 showed greater fiber at lower nodes than STV 213. In addition, DES 119 maintained greater fiber yield through node 13 when compared to STV 213.

Bednarz and Nichols (2005) suggested that the three most viable strategies to attain earlier maturity useful in breeding programs are lessening the horizontal flowering interval, shortening the boll maturation period, and selecting for longer sympodial branches at lower main-stem nodes. Similarly, Hood (1984) found four key components as having an effect on the time required to attain maturity. These were a combination of morphological characteristics affecting plant stature and the initiation of reproductive development, genetic potential for enhanced flowering rate, shorter boll maturation period, and earlier attainment of crop maturity.

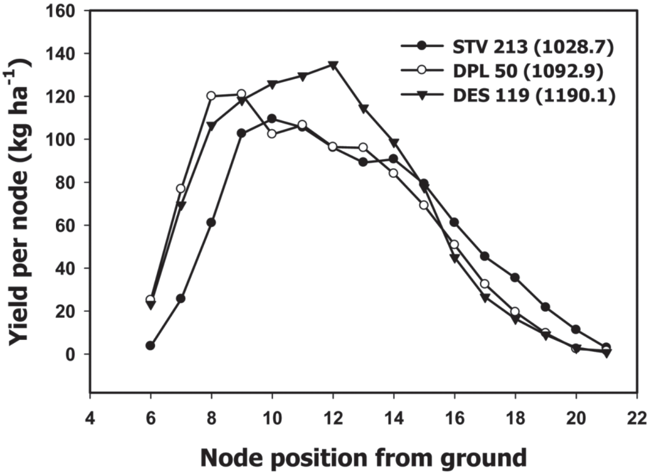

Figure 4. Fiber yield per node for Stoneville 213 (STV 213), Deltapine 50 (DPL 50), and Delta Experiment Station 119 (DES 119) averaged over two years. Adapted from Table 1 of Jenkins *et al.* (1990).

Genetics of Earliness

Godoy and Palomo (1999a) investigated the inheritance of certain phenological and morphological variables contributing to earliness of seven early genotypes. Days to first flower (DFF), days to first open boll (DFOB), node of first fruiting branch (NFFB) and plant height were negatively correlated to vertical flowering index (VFI), total blooms, maturity index, and the percentage of seedcotton at both the first and second harvests (Table 3). Significant dominance effects were noted for NFFB, plant height, VFI, and HFI. Additive effects were greater than dominance effects only for DFF, DFOB, and HFI. The strength of additivity is reflected in the heritability estimates, of which only plant height, DFF, DFOB, and HFI exceeded 0.25. Fiber yield was not correlated with early season measurements of earliness. The general trend found was as maturity became earlier, fiber yield decreased (Godoy and Palomo, 1999b).

The data of Bridge and Meredith (1983) do not show the same trend. Plotting the yield and percent lint in the first harvest from their Table 1 results in the relationships found in Figure 5. The relationship between yield and year of cultivar release showed a 9.46 kg ha^{-1} increase per year. In addition, percent lint at the first harvest was significantly related to year of cultivar release with a 0.18% increase per year ($r^2 = 0.47$; $P = 0.003$). In fact, the relationship between fiber yield and percent of lint in the first harvest was highly significant with nearly 30 kg ha^{-1} increase in yield for every percent increase in first harvest lint ($Y = -1609 + 29.6(X)$; $r^2 = 0.60$**). Guo *et al.*, (2008) utilized molecular markers to locate quantitative trait loci (QTLs) for node of first fruiting branch (NFFB). They found three significant QTLs mapped to chromosomes 16, 21 and 25. Four markers accounted for 33% of the variation in NFB.

Table 3. Phenotypic correlation among various earliness components examined by Godoy and Palomo (1999).

Component	DFF	DFOB	NFFB	Plant height
Days to first square	0.85**	0.71**	0.23**	0.30**
Days to first flower (DFF)	-	0.77**	0.26**	0.37**
Days to first open boll (DFOB)	-	-	0.31**	0.38**
Vertical flowering index	-0.48**	-0.29**	-0.11	-0.30**
Horizontal flowering index	0.08	0.13	0.04	0.26**
Total blooms	-0.59**	-0.52**	-0.27**	-0.28
Maturity index	-0.46**	-0.60**	-0.29**	-0.24**
Boll maturation period	0.20*	0.34	0.17	0.13
Node of First fruiting branch (NFFB)	0.26*	0.31**	-	0.34**
Plant height	0.37*	0.38**	0.34**	-
Percent harvest 1st	-0.58**	-0.72**	-0.34**	-0.27**
Percent harvest 2nd	-0.49**	-0.61**	-0.24**	-0.21**

*,** Significant at 0.05 and 0.01 probability levels, respectively.

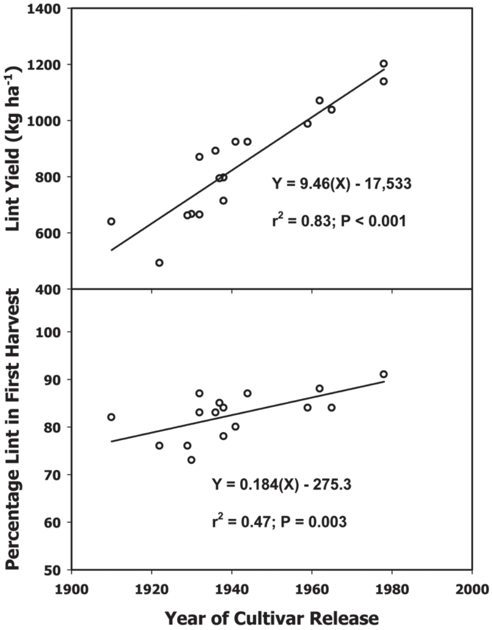

Figure 5. Fiber yield and percentage of fiber present at the first harvest for obsolete and modern cultivars grown in the Mississippi Delta in 1978 and 1979. Adapted from Table 1 of Bridge and Meredith (1983).

PHOTOPERIODISM

While modern cultivars have little or no photoperiod response, any discussion of genetic differences in fruiting would be remiss without mention of its existence. Stephens (1975) found no primitive forms of *G. barbendense* L. or *G. hirsutum* L. that flowered during the long days of summer of temperate latitudes through nearly twenty years of research. In 1960, a collection of perennial forms of *G. hirsutum* L. lines were grown near Cienfuegos, Cuba. Most accessions did not flower until November, when the daylengths were 11.5 h long. Only 18 of 169 accessions flowered before 15 October. The bulk of the accessions showed a classic “short day” flowering response. A majority of the accessions in the USDA cotton germplasm collection are short-day, photoperiodic plants and present a major obstacle to their use in breeding programs.

Zhong *et al.* (2002) used four generations of backcrossed, selected day-neutral flowering plants and compared them with the day-neutral parent and the photoperiodic parent. More of the amplified fragment length polymorphism molecular markers were found from the day-neutral parent than were found from the photoperiodic parent. Day-neutral flowering was developed in the crosses. Their data suggested that after one backcross to the accession parents, day-neutral populations could be selected for use to gain greater genetic diversity in breeding programs. Guo *et al.* (2009) conducted quantitative trait loci (QTL) analysis in two F_2 populations from crosses between day-neutral Deltapine 61 and two photoperiod sensitive *G. hirsutum* L. accessions. Each population had one or two QTLs that explained 15.9 to 63.5% of the phenotypic variation for node of the first fruiting branch (NFB). For photoperiod sensitive accessions in which low NFB is controlled by a relatively small number of QTLs, introgression of day-neutral genes into them should be fairly easy. They did observe linkage drag and suggested that it could be due to the complex nature of flowering initiation. Zhong *et al.* (2002) found that day-neutral derivatives of photoperiodic accessions carried more alleles from the day-neutral parent than from the accession parents.

LEAF MORPHOLOGY AND FRUITING

An extensive genetic survey of New World cottons by Stephens (1945) showed that leaf shape is controlled by a single allelomorphic series having a minimum of four members namely, super okra (L^S), okra (L^O), Sea-Island (L^E) and normal leaf (l). Meredith (1983, 1984, and 1985) reported between 0 and 4% loss in fiber yield due to the okra-leaf trait. Wilson and George (1982) found an 8% reduction due to okra leaf. Landivar *et al.* (1983) reported a 5% yield reduction due to okra leaf and suggested that okra-leaf genotypes do well in more optimal growth environments but perform less well than normal leaf in adverse environments. These lower yields are despite the greater reproductive structures that are found with okra-leaf as compared with normal-leaf (Wells and Meredith, 1986). At peak flowering, the okra-leaf had 48 and 81% more white flowers than the normal-leaf in an early and late planting date, respectively (Fig. 6). There was a positive curvilinear relationship between the maximum number of immature bolls and the percent boll abscission. While no significant leaf type effect was found, the data indicated that producing greater boll numbers led to greater abscission.

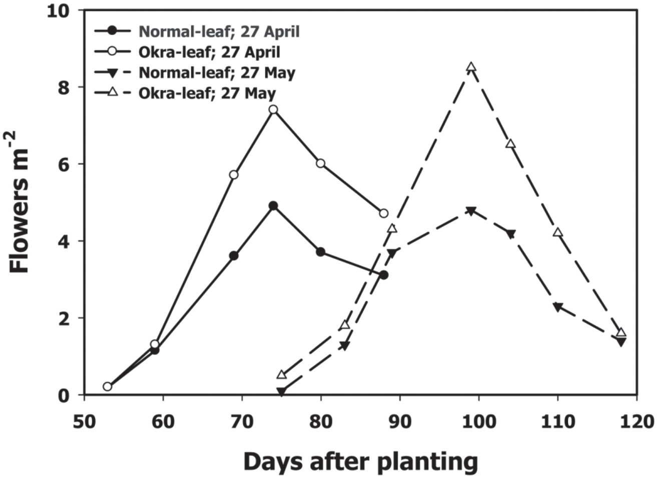

Figure 6. White flowers counted at various dates of normal- and okra-leaf genotypes planted on either 27 April or 27 May 1983

Thomson (1994) reported success of okra leaf commercial cultivars grown in Australia. He utilized a system of breeding involving a wide genetic base with frequent crossing to different types of cotton. His efforts resulted in about 50% of total Australian cotton plantings for the eight-year period of 1986 to 1993. These results indicate that for each mutant trait, there is an identifiable niche where a particular trait has an advantage and can be very successful. When grown in the USA, the Australian okra cultivars were acceptable but not as much as in the Australian management-environment. Meredith (unpublished data) found that the Australian okra-leaf cultivars' leaf area was the same as that for Mid-South cultivars.

Since most okra-leaf cotton genotypes are produced using the backcross method, Meredith and Wells (1986) used a direct selection technique to create okra-leaf and normal-leaf populations. Results from three separate experiments implied that in certain populations there was genetic potential to produce okra-leaf lines with superior yield ability than their normal-leaf counterparts. Similarly, sub-okra lines were shown to yield higher than normal-leaf by 4.8 (Meredith, 1984) and 3.0% (Meredith and Wells, 1987), especially in better growth environments that allow greater plant stature. The sub-okra trait is not expressed at Stoneville, MS until the onset of flowering (~node 10-12). Therefore, during the period prior to canopy closure the normal leaves would be present and lend to greater light interception. Thereafter, sub-okra leaves would be produced and allow greater light penetration to lower canopy positions but nearly attenuated at ground level. Wells *et al.* (1986) found that integrated canopy photosynthesis was negatively associated with light penetration to ground level measure on five different dates over two years. Sub-okra canopies had photosynthesis rates comparable to normal leaf over both years.

YIELD AND YIELD COMPONENTS

Genetic association of yield with yield components and fiber traits has long been described to be due to linkage or pleiotropy (physiology). If linkage was the cause of genetic association, frequent crossing within segregating populations and selection should reduce the negative association. In a review of earlier cotton quantitative genetics, Meredith (1984) reported on four genetic studies where genetic correlations were estimated. More recently, Meredith (unpublished data) determined the genetic correlation involved in 56 year-location environments and 98 genotypes. These tests were conducted from 2001 through 2007. The genetic correlation of yield with lint percentage, fiber length, fiber strength, and micronaire for these two studies may be found in Table 4. Considering that the two studies involve different genotypes grown in different management-time periods, the trends of genetic correlations are very similar. Fiber length and strength are still negatively correlated with yield. The positive genetic correlation for micronaire is not generally desired in the Mid-South as higher micronaire has large discounts. In other regions, such as Texas, higher micronaire is desired as the cotton in that area is frequently discounted for being too low. The search goes on to determine the physiological and genetic casual factors for the negative yield-fiber quality relationships.

Table 4. Genetic correlation of yield with lint percent and three fiber traits.

Fiber trait	Meredith (1984)	Meredith *et al.* (2011)
Lint Percent	0.81	0.587
Fiber Length	-0.25	-0.556
Fiber Strength	-0.51	-0.526
Fiber Micronaire	0.50	0.464

SUMMARY

To the casual eye, today's Upland cotton cultivars probably do not seem too far removed from those of a century ago. The truth is the new cultivars are very different in a number of ways. They yield much more, with new cultivars producing approximately 700 kg/ha more fiber than the cultivars in the 1930s. These new cultivars have realized this increase through earlier crop maturity, greater reproductive dry matter partitioning, and smaller but more efficient vegetative canopies than found in obsolete cultivars. During this period fiber quality has remained high despite negative yield-fiber quality relationships. Photoperiodism has been removed and different leaf morphologies may lead to enhanced light utilization throughout the canopy profile. The question is, what will the next century of crop improvement bring to the new cottons of the future?

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