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MOLECULAR BIOLOGY AND PHYSIOLOGY

Genotypic Variation in Physiological Strategies For Attaining Cotton Lint Yield Production

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ABSTRACT

The quality and quantity of cotton (*Gossypium hirsutum* L.) lint produced are complex traits controlled by multiple processes. The physiology behind yield and quality variations is not completely understood. Objectives for this research were to document the physiological strategies diverse cotton genotypes take to achieve their yield and fiber quality. The genotypes 'DPL 444BR', 'DPL 555BR', 'FM 800BR', 'MD 9', 'MD 15-OP', 'MD 29', 'MD 51 normal', 'MD 51 okra', 'PM 1218BR', and 'ST 4892BR' were grown in the field from 2005-2008. Dry matter partitioning, leaf photosynthesis, chlorophyll concentration, root hydraulic conductance, lint yield, yield components, and fiber quality data were collected. Lint yields ranged from 1675 to 1119 kg ha^{-1} among the genotypes. The size of the available carbon assimilate pool generated by a genotype appeared to be related to lint yield production. Genotypes used different strategies to generate this carbon assimilate pool, i.e. through improved photosynthetic rates and/or solar radiation interception, and then convert that carbon into lint production. Fiber quality variations, however, could not easily be explained by just variations in the plants ability to produce carbon assimilates. Beyond just the quantity of carbon assimilates, it is the manner in which the plant assembles these carbon skeletons into the cellular matrix that determines the quality of the fiber produced. These research findings can be utilized to meet the challenge of future yield and fiber quality improvements.

Revenue from cotton (*Gossypium hirsutum* L.) production is principally generated through the quantity and quality of the lint produced. Although there has been recent appreciation in cotton prices, in general, input costs have outpaced the income derived from cotton production. This economic climate has placed even more pressure on producers to not only increase both the amount and quality of the lint produced, but to also make the most efficient use of the inputs required. Yield increases occurring over the past few years have been spearheaded by both improved genetics (Meredith, 2000; 2006) and altered production strategies (Pettigrew, 2002).

Genetic gains have come from cotton geneticists and breeders focusing on the broader goal of overall increased lint production while also achieving secondary goals of improved fiber quality (Meredith 2000, 2006a). These yield improvements have come about through alterations in one or more of the multiple yield components (USDA, 2010; and various state Official Variety Trials). Although physiological traits are rarely intentionally targeted in breeding programs, these traits are often impacted through the genetic manipulation to improve yield or achieve other objectives. For instance, the okra and super okra leaf-type isolines of MD 65-11 had 22% and 24% greater CO_2 exchange rates (CER) than their normal leaf-type isoline counterpart (Pettigrew et al., 1993). Rosenthal and Gerik (1991) also reported genotypic differences in radiation use efficiency among upland (*Gossypium hirsutum* L.) cotton normal leaf-type genotypes. Quisenberry et al. (1994) and Pettigrew and Meredith (1994) documented significant genotypic variation in leaf CER among normal leaf-type upland cotton genotypes. Yield increases observed with modern Pima cotton (*Gossypium barbadense* L.) lines were attributed to increased leaf CER and stomatal conductance (Cornish et al., 1991). In follow-up studies, Radin et al. (1994), Lu et al. (1994), and Lu and Zeiger (1994) indicated that yield improvements in modern Pima genotypes were associated with improved heat tolerance due to superior stomatal conductance and smaller leaf size. Furthermore, Wells and Meredith (1984) were able to demonstrate that yield improvements observed in modern cotton genotypes of that era were due to partitioning a higher percentage of the dry matter produced through photosynthesis into reproductive growth rather than vegetative growth.

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Intuitively we know that physiological differences underpin many of the yield and fiber quality differences seen in the multitude of different cotton genotypes, although connecting the physiological differences with the phenotypic expressions of lint yield and fiber quality can be difficult. The problem is that yield and quality development are complicated traits and, as such, are influenced by the availability of resources (i.e. sunlight, water, nutrients, and CO_2) to the plant, the temperature regime to which the plant is exposed during growth, the plant's inherit ability to produce assimilates, the plant's partitioning of the assimilate produced to various growing points, and any loss of, or damage to reproductive structures because of insect predation. Yield and fiber quality improvements often involve slight alterations in multiple processes that, in turn, synergistically operate better or more efficiently.

Although yield and fiber quality are complex traits, it is still important to seek new ways of improving the phenotypic expression of these traits. Understanding physiologically why certain genotypes have superior yields or enhanced fiber quality would be important information for breeders, crop physiologists and agronomists. Breeders could theoretically utilize this information to make targeted crosses that best combine components from the parent lines to improve overall functioning of key physiological processes that impact yield or fiber quality. Crop physiologists and agronomists could use the information to tailor specific production system strategies. Therefore, the objectives of this study were to document genetic variability in certain key physiological traits for a diverse subset of cotton genotypes varying in yield performance and in the quality of the lint produced.

MATERIALS AND METHODS

Field studies were conducted on a Dubbs silt loam (fine-silty, mixed, active, thermic Typic Hapludalfs) soil near Stoneville, MS. The study was conducted for four years from 2005 through 2008. Ten cotton genotypes [‘DPL 444BR’, ‘DPL 555BR’. ‘FM 800BR’. ‘MD 9’ (Meredith and Nokes, 2011), ‘MD 15-OP’ (Meredith, 2006b), ‘MD 29’, ‘MD 51 normal’ (Meredith, 1993), ‘MD 51 okra’, ‘PM 1218BR’, and ‘ST 4892BR’] were grown each year of the study. DPL 444BR, DPL 555BR, and PM 1218BR seed were obtained from Delta and Pine Land Co., Scott, MS. Seed for FM 800BR and ST 4892BR were obtained from Bayer CropScience, Research Triangle Park, NC. Genotypes were chosen to represent a range of leaf shapes, crop maturities, fiber quality, and breeding programs (Table 1). Plots were planted on 20 April 2005, 18 April 2006, 27 April 2007, and 1 May 2008. The plots consisted of six rows, 9.14-m in length with a 1-m spacing between rows. Plots were initially over-seeded and then hand thinned to a final plant population density of approximately 97,000 plants ha^{-1}. The overall experimental design was a randomized complete block with six replications. Each year the experimental area received 112 kg N ha^{-1} in a preplant application. Recommended insect and weed control measures were employed as needed throughout each growing season.

Table 1. Relative crop maturity and leaf shape of the genotypes grown.

Genotype	Maturity	Leaf shape
DPL 444BR	Early	Normal
DPL 555BR	Late	Normal
FM 800BR	Mid-Late	Okra
MD 9	Mid	Normal
MD 15-OP	Mid-Late	Okra
MD 29	Mid	Normal
MD 51 normal	Mid	Normal
MD 51 okra	Early-Mid	Okra
PM 1218BR	Early	Normal
ST 4892BR	Early	Normal

Dry matter harvests were taken at 65 and 103 days after planting (DAP) in 2005, at 62 and 104 DAP in 2006, 52 and 94 DAP in 2007, 46 and 88 DAP in 2008. The early harvest date corresponds to a squaring or early bloom stage of growth and the late harvest date corresponds to the cutout stage of growth. Cutout refers to a period of slowing vegetative growth and flowering due to a demand for assimilates by the existing boll load. One of the inner plot rows was designated for use in the dry matter harvests. On each harvest date, the above ground portions of plants from 0.3 m of row were cut and separated into their component parts (leaves, stems and petioles, squares, and blooms and bolls). The leaves were then passed through a LI-3100 (LI-COR, Lincoln, NE) leaf area meter to determine leaf area. The number of main stem nodes on each plant were counted. Samples were dried for at least 48 h at 60°C, and dry weights were recorded.

The percentage of incoming photosynthetic photon flux density (PPFD) intercepted by the cotton canopies were determined by use of a LI 190SB point quantum sensor (LI-COR) positioned above the canopy and a 1-m-long LI 191SB line quantum sensor positioned on the ground perpendicular to, and centered on the row. Two measurements were taken on one of the inner plot rows per plot, and the mean of those two measurements was used for later statistical analyses. These measurements were taken under clear skies between 1230 and 1500 h CDT with the incoming PPFD level at least 1700 µmol m^{-2} s^{-1} on 61 and 98 DAP in 2005, 64 and 107 DAP in 2006, 55 and 83 DAP in 2007, and 49 and 85 in 2008. Canopy PPFD extinction coefficients were estimated according to Beer's law as a function of measured LAI and the PPFD intercepted by the canopy, as described previously (Constable, 1986; Sadras and Wilson, 1997).

Leaf CO_2 exchange rates (CER) were determined on the youngest, fully expanded, fully sunlit, and disease-free main stem leaves in each plot during mid-July when blooming was near it's peak. Measurements were collected utilizing a CI-310 photosynthesis system (CID, Inc., Camas, WA) operating as an open system with a leaf chamber that possessed an 11 cm^2 window area. All measurements were collected between 0900 and 1200 h CDT with individual leaves oriented perpendicular to the sun. During all measurements, the PPFD level reaching the leaf surface was at least 1600 µmol m^{-2} s^{-1}. Two leaves per plot had their CER determined and the average of those two measurements used for later statistical analyses. Following CER measurements, the leaves were collected and transported to the lab on ice for later leaf area, specific leaf weight (SLW), and chlorophyll (Chl) concentration determinations.

In addition to the CER measurements on the youngest fully expanded main stem leaves, CER vs. PPFD response curves were also generated on the subtending leaf to a first position boll on a sympodial branch arising out of the 15th main stem node. CER measurements were taken on this subtending leaf using the CI-310 photosynthesis system coupled with an artificial light source to generate 5 levels of PPFD intensity. The five PPFD intensities utilized in measuring the CER X PPRD response on each leaf were approximately 2000, 1250, 750, 250, and 0 µmol m^{-2} s^{-1}. Measurements started at the highest PPFD intensity before stepping down to the next lowest intensity for the subsequent measurements on each leaf. All leaves were exposed to and allowed to equilibrate to the highest PPFD intensity for approximately 5 minutes before initiating the CER measurements. After the last CER measurement, the leaves were collected and transported to the lab on ice for later leaf area, specific leaf weight (SLW), and chlorophyll (Chl) concentration determinations. Measurements were collected during mid-July when blooming was near peak.

Chlorophyll concentration, SLW, and leaf area determinations were made on the leaves collected after CER measurements on the main stem and subtending leaves. Two 0.4 cm^{-2} leaf disks were cut from each leaf and the Chl was extracted from those leaf disks overnight in darkness at 30 °C in 950 ml L^{-1} ethanol. The Chl concentration of the extract was then spectrophotometrically determined according to the methods of Holden (1976). Leaves were then passed through a LI-3100 leaf area meter to determine the leaf area. Leaves were then dried for 48 h at 60°C and subsequently weighted to determine leaf dry weights. Specific leaf weights were calculated from the leaf area and leaf dry weights of each individual leaf.

In 2005 and 2007, pots (13.8 L volume) were sown with seed from each variety and placed in a greenhouse. The pots were thinned to two plants per pot when the plants had reached approximately the second or third true leaf stage. Pots were arranged on the bench in a randomized complete block design with four replications. Root hydraulic conductance was measured on both plants in each pot using the Dynamax HPFM high-pressure flow meter (Dynamax, Houston, TX) when most of the plants were in the initial stages of blooming. Methodologies used in measuring the root hydraulic conductance were similar to those previously described (Pettigrew et al., 2009). In 2008, plants in the previously described field plots were utilized for the root hydraulic conductance measurements. Five replicates were measured and two plants were measured per plot. In both the greenhouse and field studies, all measurements were collected between 0900 and 1200 h CDT. The means of the two root hydraulic conductance measurements per pot or plot, were used in all subsequent statistical analyses.

Defoliation of the plots was initiated each year when approximately 65% of the bolls of the latest maturing variety had opened, usually early-to-mid September. A mixture of tribufos and ethephon were used to defoliate the crop and open the remaining unopened bolls. Approximately 2 wk after defoliation, a 1-m long section of row was hand harvested from each plot for yield component determinations.

Next, the two inner most rows of each plot were mechanically harvested using a spindle picker equipped with a weighing system to determine seed cotton yields. Boll mass was determined by dividing the seed cotton weight of the hand harvested sample by the number of bolls hand harvested for each plot. The hand-harvested samples from each plot were then ginned on a 10-saw laboratory gin to determine the lint percentage of each plot, which was used to calculate the lint yield from the mechanically harvested seed cotton. Average seed mass was determined from 100 nondelinted seeds per hand-harvested sample and reported as weight per individual seed.

Lint from each ginned sample was sent to Starlab Inc. (Knoxville, TN) for fiber quality analyses. Fiber strength was determined with a stelometer. Span lengths were measured with a digital fibrograph. Length uniformity was determined by HVI instrumentation. Micornaire was determined with a micronaire device. Fiber maturity and perimeter were calculated from arealometer measurements. A second lint sample was also tested for various fiber quality traits using the Advanced Fiber Information System (AFIS) (Zellweger Uster Inc., Knoxville, TN).

Statistical analyses were performed by analysis of variance (Proc Mixed, SAS Institute, 1996). Although significant genotype X year interactions were detected, the f-values for these interactions were small relative to the genotype main effect. Therefore, it was appropriate to average the genotypic means across the years. These means were then separated by the use of a protected LSD at $P \leq 0.05$. Data from the subtending leaf CER measurements at various PPFD intensities were fit to the following equation for each genotype:

$$CER = \beta_0 + \beta_1(\log PPFD)$$

B_0 = intercept

B_1 = rate of change in CER due to PPFD

Genotypic components of the CER vs. PPFD curve equations were also averaged over years and separated by orthogonal contrast statements.

RESULTS AND DISCUSSION

Genetic diversity was manifest and documented in most of the traits quantified in this study. This diversity was apparent as early as the late squaring or early bloom dry matter harvest (Table 2). During this early bloom stage DPL 444BR and PM 1218BR, two of the earliest maturing genotypes, were taller than all the others except for DPL 555BR and MD 51 okra. In contrast, the two other okra leaf-type genotypes (FM 800BR and MD 15-OP) were the shortest at this stage. DPL 555BR, the latest maturing genotype in this study had produced the most main stem nodes at this stage while ST 4892BR had produced the fewest (approximately one less). Not surprisingly, the canopies of the okra leaf-type genotypes had lower leaf area indexes (LAI) than the other genotypes and also tended to intercept less of the incoming solar radiation. The extra height and main stem nodes of DPL 444BR, DPL 555BR, and PM 1218BR predominately contributed to their greater total dry matter production, while the high LAI and SLW of ST 4892BR appeared to be responsible for its high total dry matter. Increased reproductive growth at this stage (reflective of earlier maturity) resulted in greater harvest indexes for DPL 444BR, MD 51 okra, and PM 1218BR.

Growth patterns that were observed during the early bloom stage had changed by the time the genotypes had reached late bloom or cutout. The two early maturing genotypes that were tall during early bloom (DPL 444BR and PM1218BR) were now the shortest genotypes with the fewest main stem nodes at this late stage (Table 2). DPL 555BR was taller than any other genotype at this stage and also had more main stem nodes than any variety except for MD 15-OP. Genotypes with the lowest LAI at this stage were the okra leaf-type lines and the two earliest maturing lines. This low LAI of the early varieties may be reflective of an earlier cessation of vegetative growth coupled with an accelerated senescence of some lower leaves due to assimilate remobilization to feed the developing boll load. The low LAI of the okra leaf-type canopies meant that they continued to intercept less solar radiation than canopies of the other genotypes. Maturity and reproductive growth differences among the genotypes were clearly seen in the harvest index differences among the genotypes at the late bloom harvest date. DPL 444BR and PM 1218BR, the earliest genotypes, had clearly partitioned more of their dry matter into reproductive growth at this point than the other genotypes. As the latest maturing genotype, DPL 555BR was still allocating more of its dry matter to vegetative growth rather than reproductive growth at this time compared to the other genotypes. Despite differences among varieties in LAI and canopy light interception, there were no statistical differences in canopy extinction coefficient for either harvest date.

Table 2. Dry matter partitioning and canopy light interception data for various cotton varieties and two stages of growth and averaged across 4 growing season (2005-2008).

Variety	Harvest Date	Height	Main Stem Nodes	Height to Nodes	Leaf Area Index	Specific Leaf Weight	Total Dry Weight	Harvest† Index	% Light Interception	Extinction Coefficient
		cm	nodes $plant^{-1}$	cm $nodes^{-1}$		g m^{-2}	g m^{-2}		%	
DPL 444BR	Early Bloom	47	12.6	3.7	0.90	63.8	108	0.040	42.4	0.7683
DPL 555BR		44	13.6	3.2	1.04	59.2	108	0.021	41.7	0.6683
FM 800BR		35	12.5	2.8	0.87	66.0	98	0.022	37.5	0.6701
MD 9		41	13.2	3.1	0.98	60.7	104	0.023	42.9	0.6793
MD 15-OP		36	13.0	2.7	0.84	64.1	94	0.027	40.4	0.6792
MD 29		42	13.2	3.2	0.94	63.5	104	0.038	40.3	0.6944
MD 51 normal		40	13.1	3.0	0.86	62.2	95	0.026	39.6	0.6562
MD 51 okra		43	13.4	3.2	0.83	63.4	96	0.047	37.3	0.7092
PM 1218BR		46	12.9	3.6	1.03	65.0	122	0.042	44.0	0.7777
ST 4892BR		41	12.4	3.3	0.99	65.0	112	0.029	39.8	0.6783
LSD 0.05		4	0.7	0.3	0.17	3.0	21	0.010	3.5	0.1385 (ns)‡
DPL 444BR	Late Bloom	109	20.3	5.4	3.41	53.7	691	0.330	86.0	1.5027
DPL 555BR		132	25.1	5.3	4.52	44.1	643	0.150	89.9	1.8659
FM 800BR		111	22.5	4.9	3.63	51.5	631	0.253	77.1	1.1676
MD 9		125	23.6	5.3	4.56	44.2	662	0.213	89.2	1.3983
MD 15-OP		112	24.3	4.6	3.82	50.3	595	0.208	82.7	1.2158
MD 29		120	23.3	5.1	4.55	47.0	708	0.269	86.8	1.3760
MD 51 normal		124	23.9	5.2	4.20	45.6	621	0.195	89.2	1.5374
MD 51 okra		112	23.9	4.7	3.23	49.9	625	0.320	79.8	1.6562
PM 1218BR		107	20.7	5.1	3.72	51.3	681	0.340	87.4	1.5815
ST 4892BR		114	22.2	5.1	4.15	47.9	621	0.220	87.6	1.4296
LSD 0.05		7	0.9	0.3	0.59	3.1	94	0.051	4.3	0.4617 (ns)

† Harvest Index = (Reproductive dry weight / Total dry weight).

‡ ns = not significantly different at the $P \leq 0.05$ level.

Physiological traits measured on the youngest fully expanded main stem leaf also varied (Table 3). CER measured on main stem leaves ranged from 24.0 to 22.1 µmol m^{-2} s^{-1}, with the two highest photosynthesizing genotypes (FM 800BR and MD 51 okra) being okra leaf-type lines. The third okra leaf-type line (MD 15-OP) only exhibited mid-level photosynthetic rates. Greater photosynthesis per unit leaf area for these okra leaf–type lines was similar to that reported earlier (Pettigrew et al., 1993). Much of the CER variation among the genotypes can be explained by the variation in leaf Chl concentrations among the genotypes (r = 0.919 P=0.01). CER of these genotypes was also strongly correlated with SLW (r = 0.679 P=0.03), but it had a negative and non-significant correlation with leaf area (r = -0.415 P=0.23). There was also a strong correlation (r = 0.736 P=0.01) between leaf Chl concentration and SLW. Although it would not be 100% accurate, screening for SLW might also provide an indirect screen for CER differences among cotton lines. This attribute could be important because SLW is a less expensive trait to quantify than CER. No genotypic differences were detected in root hydraulic conductance. In a previous study (Pettigrew et al., 2009), ST 4892BR was reported to have greater root hydraulic conductance than DPL 444BR and DPL 555BR, but that difference was not observed in this current study.

Table 3. Cotton physiological traits of the youngest mature main stem leaf and root hydraulic conductance for various cotton genotypes averaged across four growing seasons (2005-2008).

Genotype	CO_2 Exchange Rate	Chlorophyll Concentration	Chlorophyll A:B Ratio	Leaf Area	Specific Leaf Weight	Root Hydraulic Conductance
	$\mu mol\ m^{-2}\ s^{-1}$	$mg\ m^{-2}$		$cm^2\ leaf^{-1}$	$g\ m^{-2}$	$kg\ s^{-1}\ MPa^{-1}$
DPL 444BR	23.6	400	3.73	156	57.0	4.0×10^{-5}
DPL 555BR	22.3	361	3.64	149	51.0	3.7×10^{-5}
FM 800BR	24.0	423	3.57	133	58.6	3.5×10^{-5}
MD 9	22.1	363	3.74	175	53.6	4.1×10^{-5}
MD 15-OP	22.6	390	3.58	124	57.1	3.4×10^{-5}
MD 29	22.9	375	3.69	154	54.6	6.1×10^{-5}
MD 51 normal	22.3	366	3.80	150	53.1	3.9×10^{-5}
MD 51 okra	23.9	420	3.64	94	55.0	3.9×10^{-5}
PM 1218BR	23.6	390	3.69	162	55.8	3.4×10^{-5}
ST 4892BR	23.2	400	3.66	168	53.9	3.9×10^{-5}
LSD 0.05	1.1	26	0.14	20	2.1	2.1×10^{-5} (ns)[z]

[z] ns = not significantly different at the $P \leq 0.05$ level.

The subtending leaves to the first position fruit on sympodial branches arising out of the 15th main stem node also varied among genotypes for the photosynthetic response to solar radiation (Table 4). These subtending leaves are important because they feed 60% of the fixed carbon to the attached boll (Ashley, 1972). The intercept (β_0) from the CER vs. PPFD response curve equation is indicative of the level of dark respiration occurring in the leaves at that time. The lower the value of β_0, the more dark respiration is occurring. DPL 444BR, PM 1218BR, and ST 4892BR exhibited a greater rate of dark respiration than the other genotypes with the exception of the two okra leaf-type genotypes FM 800BR and MD 51 okra. Interestingly, the rate of change in CER due to the change in PPFD (β_1) was also greater for these genotypes. Genotypes with the lowest rate of change β_1 (DPL 555BR, MD 9, MD 15-OP, and MD 29) also exhibited the lowest saturation CER. There was little correlation between β_0 or β_1 with either leaf chlorophyll concentration (r = 0.19827 P=0.58 and r=-0.1562 P=0.67, respectively) or leaf area (r = 0.17443 P=0.63 and r=-0.1371 P=0.71, respectively). In contrast, there was a strong negative correlation between SLW and β_0 (r = -0.78616 P=0.01) and there was a strong positive correlation between SLW and β_1 (r=0.834093 P=0.01). Similar with the β_1 results, the saturation CER had little correlation with either leaf chlorophyll concentration (r = -0.08825 P=0.81) or leaf area (r=-0.05628 P=0.88), but had a strong positive correlation with SLW (r = 0.819983 P=0.01). The implication being that subtending leaves of genotypes with a greater response to light and a higher saturation CER, also may have had greater levels of the enzymes involved in carbon metabolism (greater dark respiration) and CO_2 fixation than the other varieties. These CO_2 fixation enzymes may be more responsible for the higher photosynthetic rates than chlorophyll concentrations involved in the capture of solar radiation. This aspect of the subtending leaves contrasts with that of the fully sunlit main stem leaves where there was a strong positive correlation between CER and chlorophyll concentration. Previously, it has been documented that during leaf senescence soluble protein is preferentially remobilized before chlorophyll is remobilized (Pettigrew et al., 2000). We speculate that the low photosynthetic potential due to the low light shaded conditions of these intra-canopy subtending leaves may have allowed for some remobilization of the protein N to feed the developing attached boll.

Table 4. Carbon Dioxide Exchange Rate (CER) vs. Photosynthetic Photon Flux Density (PPFD) response curve components [$CER = \beta_0 + \beta_1(\log PPFD)$] and physiological traits of the subtending leaf to the first fruiting position on a sympodial branch originating out of the 15th main stem node for various cotton genotypes averaged across four growing seasons (2005-2008).

Genotype	B_0 [z]	β_1 [y]	Saturation CER [x]	Chlorophyll Concentration	Chlorophyll A:B Ratio	Leaf Area	Specific Leaf Weight
			$\mu mol\ m^{-2}\ s^{-1}$	$mg\ m^{-2}$		$cm^2\ leaf^{-1}$	$g\ m^{-2}$
DPL 444BR	-8.1614 c	8.4277 ab	19.6 b	497	3.23	89	52.5
DPL 555BR	-3.8840 ab	6.5496 f	17.7 cde	541	3.03	101	45.0
FM 800BR	-6.4947 bc	7.6381 bcd	18.7 bc	534	3.09	70	49.6
MD 9	-4.0661 ab	6.2808 f	16.7 e	485	2.89	105	41.9
MD 15-OP	-3.9059 ab	6.3781 f	17.1 ed	523	2.72	76	47.1
MD 29	-3.3681 a	6.3776 f	17.7 cde	515	3.00	97	46.7
MD 51 normal	-3.7291 a	6.7657 cdef	18.6 bcd	533	3.09	101	47.1
MD 51 okra	-5.9652 abc	7.5188 bcde	18.8 bc	542	2.99	57	51.9
PM 1218BR	-8.7309 c	9.1051 a	21.3 a	501	3.13	99	51.8
ST 4892BR	-6.9066 c	7.7046 bc	18.5 bcd	539	3.16	97	48.2
LSD 0.05	-	-	-	38	0.29 (ns)[v]	2	3.2

[z] β_0 = intercept.

[y] β_1 =rate of change in CER due to PPFD.

[x] CER at PPFD = 2000 $\mu mol\ m^{-2}\ s^{-1}$.

[v] ns = not significantly different at the $P \leq 0.05$ level.

Table 5. Lint yield and yield components for various cotton genotypes averaged across four growing seasons (2005-2008).

Genotype	Lint Yield	Boll Number	Boll Mass	Lint Percentage	Seed Mass	Seed Number	Lint Index
	$kg\ ha^{-1}$	$bolls\ m^{-2}$	$g\ boll^{-1}$	%	$mg\ seed^{-1}$	$seed\ boll^{-1}$	$mg\ seed^{-1}$
DPL 444BR	1619	93	4.18	41.5	93	26.1	67
DPL 555BR	1675	91	3.66	44.6	71	28.5	57
FM 800BR	1566	82	4.80	40.3	99	28.7	67
MD 9	1300	73	4.62	37.8	100	28.5	61
MD 15-OP	1119	77	4.32	37.0	101	26.5	60
MD 29	1388	83	4.17	38.2	94	27.2	58
MD 51 normal	1249	79	4.13	36.6	91	28.1	53
MD 51 okra	1145	87	4.05	36.7	93	27.1	54
PM 1218BR	1593	85	4.90	40.8	105	27.2	72
ST 4892BR	1594	87	4.18	40.8	94	26.0	65
LSD 0.05	177	9	0.44	1.3	5	2.2	6

The diversity among the genotypes was demonstrated with considerable differences in lint yield performance (Table 5). Lint yields ranged from 1675 kg ha^{-1} (DPL 555BR) to 1119 kg ha^{-1} (MD 15-OP). Although the two lowest yielding genotypes were two okra leaf-type lines (MD 15-OP and MD 51 okra), the other okra leaf-type line (FM 800BR) was comparable and not significantly different from the top yielding genotypes. Although differences among genotypes in the number of bolls produced can explain many of the yield differences observed, other yield components can also contribute to yield performance. For instance, DPL 555BR produced a large number of small bolls, but was able to maximize lint production because it had a high lint percentage and small seed mass. The high lint production with PM 1218BR came from a moderate number of larger bolls produced, which contained large seed and consequently produced more lint per individual seed. In contrast, MD 51 okra produced a moderate number of small bolls with a low lint percentage and low amount of lint produced per seed.

Many of the highest yielding genotypes also produced lint with less than desirable fiber quality traits (Tables 6 and 7). PM 1218BR produced the weakest fibers, the shortest span length, and largest micronaire of any of the genotypes. DPL 555BR produced weak and short fiber that also exhibited the lowest length uniformity. This low length uniformity of DPL 555BR was confirmed by the greater AFIS short fiber content of that genotype compared to the other genotypes. The length uniformity from HVI measurements appears to be a good inexpensive estimate of the short fiber content trait obtained from AFIS measurements. The thicker diameter fiber for PM 1218BR and ST 4892BR implied from the micronaire and fiber perimeter measurements were reinforced by the greater AFIS fiber fineness means for these genotypes. In contrast, the lowest yielding genotype (MD 15-OP) produced far superior fiber quality compared to the other genotypes. Its fiber was the longest, strongest with the highest level of length uniformity, lowest short fiber content, the smallest perimeter, and the lowest fiber fineness of any of the genotypes. This disconnect between premium fiber quality and lint yield production is not uncommon and has been previously documented and known for some time (Miller and Rawlings, 1967). Breeders are making slow but steady progress in breaking this association between high yields and poor fiber quality (Meredith and Nokes, 2011). Perhaps the best package of high yields and good fiber quality in this particular grouping of genotypes comes from FM 800BR.

Table 6. Fiber quality traits for various cotton genotypes averaged across four growing seasons (2005-2008).

Genotype	Fiber Strength	Fiber Elongation	Span Length		Length Uniformity[z]	Micronaire	Fiber Maturity	Fiber Perimeter
			2.5%	50 %				
	kN m kg^{-1}	%	cm	cm	%		%	µm
DPL 444BR	201	6.72	2.85	1.39	82.7	4.04	80.8	47.3
DPL 555BR	204	6.16	2.82	1.34	81.2	4.23	81.4	49.0
FM 800BR	235	5.97	3.02	1.44	83.7	4.04	85.4	44.4
MD 9	265	6.51	3.00	1.49	84.1	3.81	80.0	46.5
MD 15-OP	317	6.13	3.12	1.55	85.0	3.84	84.8	43.1
MD 29	229	6.32	2.89	1.39	82.2	4.10	79.3	49.6
MD 51 normal	237	6.82	2.95	1.44	83.1	3.97	78.8	48.4
MD 51 okra	223	6.45	2.94	1.39	82.3	3.96	78.5	48.5
PM 1218BR	188	6.41	2.73	1.37	82.4	4.96	85.9	50.8
ST 4892BR	202	7.06	2.82	1.40	83.0	4.52	78.8	52.2
LSD 0.05	14	0.52	0.05	0.03	0.7	0.40	4.6	1.5

[z] Length uniformity was determined by HVI instrumentation.

Table 7. Fiber quality traits means of various cotton genotypes as determined by the Advanced Fiber Information System (AFIS) for 2007 and 2008.

Genotype	Fiber Neps	Seed Coat Fragments	Short Fiber Content	Fiber Fineness	Fiber Maturity Ratio
	no. g^{-1}	no. g^{-1}	% weight	millitex	
DPL 444BR	123	4.5	6.1	165	0.91
DPL 555BR	137	4.2	8.4	161	0.90
FM 800BR	123	5.3	5.2	162	0.94
MD 9	142	3.8	5.1	162	0.93
MD 15-OP	141	5.8	4.3	157	0.95
MD 29	99	2.5	5.8	176	0.94
MD 51 normal	122	2.5	5.4	165	0.92
MD 51 okra	105	2.9	5.6	175	0.94
PM 1218BR	111	4.9	6.1	183	0.93
ST 4892BR	102	5.1	5.4	178	0.93
LSD 0.05	39 (ns) [z]	2.4 (ns)	1.4	8	0.02

[z] ns = not significantly different at the $P \leq 0.05$ level.

The range of genetic diversity seen among genotypes for yield and fiber quality traits was also observed in many of the physiological traits quantified. These genotypes demonstrated different strategies for yield production. For instance, the high yielding DPL 555BR did not generate an impressive photosynthetic rate for either its youngest mature main stem leaf or the 1st position subtending leaf on the sympodial branch at the 15th main stem node (Tables 2 and 3), but it did produce a greater canopy leaf area than most of the other genotypes allowing it to intercept more of the solar radiation (Table 2). Also being a later maturing variety, it maintained the duration of this leaf area longer than most other genotypes (data not shown). In contrast, two other high yielding and early maturing lines (DPL 444BR and PM 1218BR) demonstrated superior photosynthetic rates for both the main stem and subtending leaves. Both these genotypes produced good early season canopy leaf area development and intercepted high levels of sunlight, but that canopy leaf area had waned by the 2nd dry matter harvest due to the shifting of dry matter allocations toward more reproductive growth as is indicated by their high harvest indexes at this stage. FM 800BR is an okra leaf-type genotype with the typical high leaf photosynthetic rate seen with okra leaf-type lines (Pettigrew et al., 1993) but it also produced sufficient canopy leaf area to support comparably high yield. On the other hand, MD 51 okra showed the high leaf photosynthesis per unit leaf area, but did not produce sufficient leaf area to sustain adequate yield production. MD 15-OP appears to be operating by its own set of rules, as an okra leaf-type line. Rather than producing the typical high CER, its photosynthetic rate was moderate at best. Although it did produce a higher canopy leaf area index than the other okra leaf-type lines, it was not able to overcome this lack of the overall photosynthetic assimilate production resulting in the lowest overall lint yield.

Although many of the yield differences observed could be partially explained by strategic differences in the manner in which these genotypes maximized carbon assimilate production, the connection between carbon assimilation and fiber quality is not as direct or obvious. None of the physiological traits measured that were involved in carbon assimilate production provided much insight into the genetic variability of the various fiber quality traits quantified. This aspect was somewhat surprising because previous research had indicated a connection between the available carbon assimilate supply with fiber strength and micronaire (Pettigrew and Meredith, 1994; Pettigrew, 1995; Pettigrew, 2001). The extraordinarily good fiber quality traits of MD 9 and MD 15-OP are particularly difficult to fit into that model. Neither genotype demonstrated the photosynthetic performance indicative of a superior carbon assimilate supply available to the developing reproductive sinks compared to the other genotypes, although MD 9 did produce a high LAI during bloom. Focusing on the physiology of the subtending leaf to the developing boll, which provides 60% of the carbon assimilates to the attached boll (Ashley, 1972), provided little clarity. Although PM 1218BR was able to combine a high photosynthetic rate per unit leaf area of the subtending leaf with a large subtending leaf area to produce a high fiber micronaire, its fiber strength was comparatively low. On the other hand, MD 15-OP had a lower photosynthetic rate and small leaf area of the subtending leaf, resulting in a low micronaire but high fiber strength. Clearly there is more involved in determining the various fiber quality traits than just the pool of available carbon assimilates.

Fiber quality is undoubtedly determined by the manner in which critical enzymes combine these carbon assimilate and protein substrates into the cellular matrix comprising an individual fiber. Both genetics and the environment play vital roles in determining fiber quality. Genetics contribute to fiber quality through gene expression that impacts enzyme levels and activity. The environment impacts fiber quality through substrate supply and enzyme activity, among other issues.

Although the physiological traits measured did not reveal obvious direct connections with fiber quality, substantial genetic variation within most of the traits was nonetheless clearly established. We also identified different physiological strategies utilized by the various genotypes to produce competitive yields. Utilizing this information, breeding programs may be able to target and pair desired variations in these physiological traits to achieve even further yield improvements. Although the traits we quantified did not appear directly connected with the quality of the fiber produced, we remain confident that physiological variation (perhaps not necessarily in carbon assimilation) underpins the fiber quality differences observed. Future research is needed to elucidate these physiological-fiber quality associations.

In conclusion, genetic variations in many of the physiological traits involved in the production of carbon assimilates were closely related to lint yield production through impacts on critical yield components. However, the fiber quality variations from this diverse group of cotton genotypes were not as easily connected to the carbon assimilate pool. Other elements also make important contributions to the determination of fiber quality. Locating the genes involved in fiber quality determination and identifying the physiological functions of their protein products would be an important step forward. An equally important step would be to research how these enzymes interact with the various environmental influences encountered during a growing season to impart phenotypic expression of the given fiber quality trait. Utilizing this sort of information, geneticists, crop physiologists, and agronomists might be able to match cotton genotypes with appropriate environments and production practices to generate a cropping system package that optimizes both the amount and quality of the lint produced.

DISCLAIMER

Trade names are necessary to report factually on available data, however, the USDA neither guarantees nor warrants the standard of the product or service, and the use of the name by USDA implies no approval of the product or service to the exclusion of others that may also be suitable.

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