

# Divergent Selection for Fiber Length and Bundle Strength and Correlated Responses in Cotton

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## ABSTRACT

Cotton (*Gossypium* spp.) breeders must develop cultivars to meet the demand for longer, stronger, and more uniform fibers. In the current study, two cycles of divergent selection for fiber upper-half mean length (UHML) and bundle strength (Str) were conducted within five diverse parental combinations selected based on their potential for the genetic improvement of fiber quality. Realized heritability estimates for UHML and Str were calculated for each cycle, and correlated responses among fiber properties and lint percent were measured as they responded to selection for UHML and Str. The results suggest that early-generation selection for UHML and Str is an effective strategy for the genetic improvement of fiber quality at College Station, TX. Although UHML and Str were consistently negatively correlated with lint percent, the results demonstrate that sufficient variation for fiber quality exists within the Texas A&M AgriLife Research upland cotton germplasm to improve UHML and Str without a concomitant reduction in lint percent. A negative phenotypic correlation between UHML and fiber elongation at break was also observed and was independent of the association between Str and fiber elongation at break in multiple populations. These findings suggest that further investigation into the relationship between UHML and fiber elongation within the Texas A&M AgriLife Research germplasm is warranted.

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**Abbreviations:** Elon, fiber elongation; HVI, high-volume instrument; LP, lint percent; Mic, fiber micronaire; RCBD, randomized complete block design; Str, fiber bundle strength; UHML, upper-half mean fiber length; UI, fiber uniformity index.

**C**OTTON (*Gossypium* spp.) producers in the United States rely heavily on export markets (USDA, 2015). Currently, the global textile market is characterized by demand for cotton fibers that are suitable for the manufacture of finer yarns produced on ring-spinning systems (Faulkner et al., 2012), while rotor (i.e., open-end) and air-jet spinning systems occupy a smaller portion of the total market share. The most important fiber quality parameters affecting yarn quality are fiber upper-half mean length (UHML) and length uniformity for ring-spun yarn, UHML and fineness for air-jet-spun yarn, and fiber bundle strength (Str) on rotor-spun yarn due to higher processing speeds (Bhortakke et al., 1997; Smith and Zhu, 1999; Joy et al., 2010). Plant breeders must therefore develop cultivars to meet the demand for longer, stronger, and more uniform fibers (Cantrell et al., 2000; Smith et al., 2009; Meredith and Nokes, 2011; Bourland and Jones, 2012).

*Gossypium hirsutum* L., also known as upland cotton, accounts for the majority of global production owing to characteristic high yields and broad adaptation. Generally, traditional genetics studies suggest that sufficient genetic variation exists within cultivated upland cotton germplasm to facilitate the improvement

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of fiber quality through breeding (Bowman et al., 1996; Campbell and Meyers, 2015). However, numerous DNA marker-based studies suggest low levels of genetic diversity within cultivated upland cotton, which may restrict further fiber quality improvements to meet the demands of modern spinning and weaving technology (Van Esbroeck and Bowman, 1998; Lacape et al., 2007; Van Deynze et al., 2009; Hinze et al., 2012; Fang et al., 2013). The other cultivated tetraploid cotton, *Gossypium barbadense* L., also known as Sea Island, Pima, or Egyptian cotton, is valued for its superior fiber quality but is characterized by inferior yield and adaptation. Upland cotton and *G. barbadense* readily hybridize, but attempts to introgress fiber quality traits from *G. barbadense* into upland cotton through conventional breeding have been largely unsuccessful due to skewed chromatin transmission and the elimination of donor alleles (Stephens, 1949; Jiang et al., 2000). The negative relationship between fiber quality traits, specifically fiber length and Str, and yield components must also be considered as a limitation to the improvement of fiber quality among cultivated upland germplasm (Al-Jibouri et al., 1958; Miller et al., 1958; Miller and Rawlings, 1967; Meredith, 1984; McCall et al., 1986; Smith and Coyle, 1997; Ulloa, 2006; Hinze et al., 2011). Research suggests that the negative relationship between fiber quality and lint yield is, at least in part, attributable to repulsion phase linkage, suggesting that simultaneous improvement can be achieved through hybridization between germplasm lines with elite fiber quality and high yield, followed by selection of advantageous recombinants (Meredith and Bridge, 1973; Green and Culp, 1990; Culp and Green, 1992; Constable and Bange, 2007; Zeng et al., 2011; Campbell et al., 2012).

Joy (2014) reported on the combining ability and inheritance of cotton fiber quality traits, including high-volume instrument (HVI)-measured UHML and Str among several genetically diverse parental lines developed by Texas A&M AgriLife Research. The study detected significant genetic variation for UHML and Str among the parental lines and identified several beneficial lines for the genetic improvement of these traits. The narrow-sense heritability estimates for UHML and Str among the parental combinations were moderate to high, and the majority of the genetic variation for fiber properties was attributable to additive genetic effects. Based on these previous findings, divergent selection for HVI-measured UHML and Str was conducted within selected parental combinations from the research conducted by Joy (2014). Previously, McCall et al. (1986) performed multidirectional selection for Str within an upland cotton population and found that selection for greater Str resulted in reduced lint percent (LP) and increased UHML and length uniformity (UI), as well as earliness. In a similar study, Miller and Rawlings (1967) conducted three cycles of recurrent selection for lint yield and observed variable correlated

responses for UHML, Str, fineness, and fiber elongation (Elon) among cycles. The objectives of the current study were (i) to estimate realized heritability for UHML and Str in five genetically diverse populations, selected from the work of Joy (2014) after being subjected to divergent selection, and (ii) to characterize the correlated responses to selection for UHML and Str with regard to HVI-measured fiber properties, including UHML, Str, Elon, UI, and micronaire (Mic), as well as LP.

## MATERIALS AND METHODS

### Plant Material

Five Texas A&M AgriLife Research experimental populations were selected for the study, based on previous estimates of breeding potential for fiber length and strength (Joy 2014). Four genetically diverse parental lines were crossed to derive the five populations: TAM B182-33 ELS (ELSU33) (Smith et al., 2009; PI 654362), an extra-long staple upland (ELSU) line; 06 WE 62-4 (ESU624), an unreleased, upland experimental line with exceptional Str; 'TAMcot 22' (TAM22) (Thaxton et al., 2005a; PI 635877), an upland commercial cultivar with moderate fiber qualities; and 04 SID 84-2 (SID84), an unreleased, experimental line derived from an interspecific hybridization (*G. hirsutum* × *G. barbadense*). The parental lines of ESU624 were upland commercial cultivars 'Delta and Pine Land (DPL) 491' (PI 618609) and 'DPL 90' (PI 529529), along with 'TAM 96WD-18' (Thaxton et al., 2005b; PI 635879) and 'TAM 91C-95Ls' (Smith, 2001; PI 612326). The experimental line, SID84, was derived from a cross between upland germplasm line TAM 94L-25 (Smith, 2003; PI 631440) and the *G. barbadense* cultivar 'New Mexico Sea Island (NMSI) 1331' (Roberts et al., 1997). The five F<sub>2</sub> populations were derived from the following crosses (ignoring reciprocals): ESU624 × ELSU33, TAM22 × ELSU33, ELSU33 × SID84, ESU624 × TAM22, and TAM22 × SID84. Population development and evaluation from crossing through the F<sub>2</sub> generation was as described by Joy (2014). The HVI-measured fiber properties were obtained on approximately 350 individual F<sub>2</sub> plants for each of the five populations in 2010 and 2011 at College Station, and the remnant F<sub>2,3</sub> seed was utilized for the current study.

### Field Trials and Selection Scheme

Field trials evaluating the populations were conducted at the Texas A&M AgriLife Research Farm near College Station on a Weswood silt loam (fine-silty, mixed, thermic Fluventic Ustochrept) integrated with Ships clay (very fine, mixed, thermic Udic Chromustert). Standard cultural practices for cotton production in central Texas were conducted, including pesticide and herbicide applications and furrow irrigation. Throughout the study, fiber properties, including UHML and Str, were measured at Texas Tech University's Fiber and Biopolymer Research Institute (FBRI) in Lubbock, TX, using the HVI system. A pedigree selection scheme was used to conduct two cycles of divergent selection within each population. The first cycle of divergent selection was conducted by selecting the top and bottom 5% of F<sub>2</sub> individual plants from the study by Joy (2014) based on UHML and Str. The F<sub>2</sub> plant selections

were planted on 12 Apr. 2012 as single  $F_{2,3}$  progeny rows measuring 13.1 by 1 m, and plants within each row were thinned to an approximate density of two to three plants per meter. Eight individual plants were selected at random within each  $F_{2,3}$  progeny row. Boll samples (15 fully-developed bolls) were hand harvested from each of the eight plants within each progeny row in late September 2012, ginned, and fiber properties were measured. The top and bottom 10% of  $F_{2,3}$  individual plants for UHML and Str were selected within each population for the second cycle of divergent selection. The selected  $F_{2,3}$  plants were then planted as single  $F_{2,4}$  progeny rows (13.1 × 1 m) on April 24, 2013, and rows were thinned to an approximate density of two to three plants per meter. Four individual plants were selected at random within each of the  $F_{2,4}$  progeny rows, and boll samples (15 fully-developed bolls) were hand harvested from each selected plant in mid-to-late October 2013, ginned, and fiber properties were measured.

Reselection within the  $F_{2,4}$  progeny rows was conducted by selecting the single  $F_{2,4}$  plant with the highest or lowest UHML or Str within each of the progeny rows, corresponding with the direction of divergent selection. The selected  $F_{2,5}$  strains, along with the parental lines, were then planted as replicated single-row plots (1 × 9 m; 9–12 plants m<sup>-1</sup>) on 6 May 2014. The trial was planted as a randomized complete block design (RCBD) with two replications. Boll samples (30 bolls) were hand harvested from each  $F_{2,5}$  progeny row and parental line in late October, preferentially picking first- and second-position bolls from the middle of the fruiting zone to minimize variation within rows due to environmental factors. Seed cotton samples were processed as described above, and HVI-measured fiber properties were obtained. The data collected on the  $F_{2,5}$  strains were used to evaluate the effectiveness of divergent selection for UHML and Str.

## Statistical Analysis

The results of divergent selection were used to estimate the realized heritability of a quantitative trait (Falconer and Mackay 1996; Hill, 1972). The following formula described by Fehr (1987) was used to estimate realized heritability for UHML and Str on a single-plant basis for selection cycle one:

$$h^2 = \frac{\bar{x}_{\text{high}, F_3} - \bar{x}_{\text{low}, F_3}}{\bar{x}_{\text{high}, F_2} - \bar{x}_{\text{low}, F_2}}$$

where  $\bar{x}_{\text{high}, F_3}$  and  $\bar{x}_{\text{low}, F_3}$  represent the mean performance of the  $F_{2,3}$  progeny of the  $F_2$  individual plants selected for the high and low groups, respectively, and  $\bar{x}_{\text{high}, F_2}$  and  $\bar{x}_{\text{low}, F_2}$  represent the mean performance of the  $F_2$  plant selections in the high and low groups, respectively. The same formula was used to obtain realized heritability estimates for cycle two using the mean performance of the selected  $F_{2,3}$  individual plants and the resulting  $F_{2,4}$  progeny.

Predicted and observed responses to selection for each cycle were calculated for each population. The observed responses to selection were calculated by taking the difference between the mean performance of the selected individual plants and the mean performance of the resulting progeny. The following formula, described by Falconer and Mackay (1996), was used to calculate the predicted response to selection for each cycle:

$$R = h^2 S$$

where  $R$  represents the predicted response to selection,  $h^2$  represents the heritability, and  $S$  represents the selection differential, which is the mean difference between the base population and the selected parents. The narrow-sense heritability estimates for each population obtained by Joy (2014) were used in predicting the response to the first cycle of selection for UHML and Str, and the realized heritability estimates from cycle one were used in predicting the response to the second cycle of selection.

Analyses of variance (ANOVA) were conducted within each population on UHML and Str among the  $F_{2,5}$  strains resulting from divergent selection. Data were analyzed as a RCBD with subsampling using the General Linear Models procedure (PROC GLM) in SAS (SAS Institute, 2013). The  $F_{2,5}$  strains were grouped according to the corresponding trait and direction of divergent selection, resulting in a high and low group for both UHML and Str. Groups (i.e., high and low UHML or Str) were analyzed as fixed effects, and replication and group × replication terms were treated as random effects. Analyses of UHML and Str conformed to the assumptions of ordinary least squares estimation, including the normality and homogeneity of residuals. The group × replication mean square error was used to test the significance of replication and group. Mean comparisons between groups were conducted using the MEANS statement in SAS to specify Fisher's protected least significant difference based on the mean square error of the group × replication interaction. Pearson's correlation coefficients among fiber properties and LP within each population (computed on the  $F_{2,5}$  strain means) were calculated using the Correlation procedure in SAS (PROC CORR).

## RESULTS AND DISCUSSION

### Selection for UHML

The mean fiber properties of the parental lines grown at College Station in 2014 are shown in Table 1. The realized heritability estimates for UHML among the five populations were moderate to high, ranging from 0.32 for ESU624 × ELSU33 to 0.89 for TAM22 × ELSU33 (Table 2). Consequently, the observed response to selection was similar to the predicted response for each population (Fig. 1). The results support the findings of Joy (2014) that there is sufficient additive genetic variation among these parental combinations to enable selection for improved UHML. The realized heritability estimates from the second cycle of divergent selection ( $F_{2,3}$  to  $F_{2,4}$ ) were either similar to

**Table 1. Mean fiber properties† and lint percent (LP) of parental lines grown at College Station, TX, in 2014.**

Parental line	UHML	Str	Mic	UI	Elon	LP
	mm	kN m kg <sup>-1</sup>		%		
TAM B182–33 ELS (ELSU33)	33.5	338.5	3.7	84.5	5.2	34.6
06 WE 62–4 (ESU624)	30.2	377.2	4.5	85.2	5.8	37.2
04 SID 84–2 (SID84)	33.7	360.5	3.5	85.6	7.0	30.7
Tamcot 22 (TAM22)	27.9	272.7	4.0	83.5	6.7	36.8
CV, %	8.3	12.9	10.1	1.1	12.9	10.3

† High-volume instrument-measured fiber properties: UHML, upper-half mean length; Str, bundle strength; Mic, micronaire; UI, length uniformity index; Elon, elongation.

**Table 2. Realized heritability (RH) estimates for cycles one and two of divergent selection for upper-half mean length (UHML) and strength (Str) within five populations evaluated at College Station, TX, in 2012 and 2013.**

Population	$h^2$ †	RH	
		Cycle 1‡	Cycle 2§
<b>UHML</b>			
ESU624 × ELSU33	0.47	0.32	0.52
TAM22 × ELSU33	0.67	0.71	0.89
ELSU33 × SID84	0.61	0.85	0.85
ESU624 × TAM22	0.56	0.61	0.69
TAM22 × SID84	0.42	0.84	0.83
<b>Str</b>			
ESU624 × ELSU33	0.55	0.14	0.54
TAM22 × ELSU33	0.46	0.46	0.41
ELSU33 × SID84	0.46	0.60	0.60
ESU624 × TAM22	0.58	0.44	0.65
TAM22 × SID84	0.61	0.50	0.72

† Narrow-sense heritability ( $h^2$ ) estimates for each population derived from the generation means analysis conducted by Joy (2014).

‡ Cycle one of divergent selection, where  $F_2$  represents the overall mean UHML of the  $F_2$  populations,  $F_2$  high and  $F_2$  low represent the mean UHML of the high and low selected  $F_2$  plants, and  $F_{2,3}$  high and  $F_{2,3}$  low represent the mean UHML of the  $F_{2,3}$  plants derived from the high and low selected  $F_2$  plants.

§ Cycle two of divergent selection, where  $F_{2,3}$  high and  $F_{2,3}$  low represent the mean UHML of the high and low selected  $F_{2,3}$  plants, and  $F_{2,4}$  high and  $F_{2,4}$  low represent the mean UHML of the  $F_{2,4}$  plants derived from the high and low selected  $F_{2,3}$  plants.

or slightly higher than the estimates from cycle one ( $F_2$  to  $F_{2,3}$ ). One potential explanation for this observation is that further inbreeding allowed for fixation of additional loci associated with UHML, resulting in more effective selection in later generations. Alternatively, it may be that 2012 was a more favorable environment for the expression of UHML compared with 2010 and/or 2011, thus leading to higher realized heritability in cycle two. The highest realized heritability estimates were observed for ELSU33 × SID84, TAM22 × SID84, and TAM22 × ELSU33, while the realized heritability estimates for ESU624 × ELSU33 were substantially lower. Both ESU624 and ELSU33 are products of a long-term selection program for fiber quality and likely have accumulated many of the same beneficial alleles affecting UHML. Even though the mean UHML of the  $F_2$  progeny derived from ELSU33 × SID84 was similar to that of the  $F_2$  progeny derived from ESU624 × ELSU33 (32 mm), greater improvement in UHML was achieved within ELSU33 × SID84, likely attributable to novel favorable alleles contributed by the interspecific parent SID84 (Fig. 1).

Analyses of variance of the two UHML groups, i.e., high and low, considering progeny within each group within each population as subsamples (Compton, 1994), indicated that early-generation divergent selection for UHML was effective in four of the five populations, resulting in a significant difference in mean UHML (Table 3). The exception was divergent selection within ESU624 × TAM22. The mean difference in UHML between the high and low UHML groups derived from ESU624 × TAM22 was 4.3 mm, but the difference was not significant due to relatively large plot error (i.e., replication ×

group interaction) in comparison to genetic (i.e., group) effects. The greatest difference in mean UHML between high and low UHML groups was observed for ELSU33 × SID84 (7.3 mm), and the smallest difference in mean UHML was observed for ESU624 × ELSU33 (3.1 mm). The means of the  $F_{2,5}$  strains selected for high and low UHML were generally similar to the mean UHML of the parental lines, with the exception of  $F_{2,5}$  derived from ELSU33 × SID84, for which the means were well outside the range of either parental line. Despite relatively low realized heritability within ESU624 × ELSU33, the mean of the  $F_{2,5}$  strains selected for high UHML was comparable with the mean of the  $F_{2,5}$  strains selected for high UHML within TAM22 × ELSU33 and TAM22 × SID84. Positive and negative transgressive segregants for UHML were observed in all five populations, but the most extreme transgressive segregation was observed within  $F_{2,5}$  strains derived from ELSU33 × SID84, again suggesting a high level of allele dispersion between the two parents.

The positive relationship between UHML, Str, and UI has been well documented (Tang et al., 1996; Percy et al., 2006; Ulloa, 2006; Jenkins et al., 2009), and correspondingly, there was a strong positive correlation between UHML, Str, and UI among the  $F_{2,5}$  strains selected for high and low UHML (Table 4). This relationship was characteristic of  $F_{2,5}$  strains within each population, with the exception of ESU624 × ELSU33. There was a negative correlation between UHML and Elon across the combined set of  $F_{2,5}$  strains selected for high and low UHML. Within populations, this correlation did not hold for  $F_{2,5}$  strains derived from ESU624 × ELSU33 and TAM22 × SID84. Ng et al. (2014) reported similar observations regarding the negative correlation between UHML and Elon in experimental populations grown at College Station. Fiber micronaire responded negatively to selection for UHML across all populations. None of the parental lines had Mic indices outside of the nondiscount range (3.5 to 4.9), as defined in the 2015 CCC Loan Premium and Discount Schedule for upland cotton (<http://www.cotton.org/econ/govprograms/cccloan/>). Also, only a small number of the  $F_{2,5}$  strains selected for high and low UHML, derived from crosses between the three upland parents, were outside of the nondiscount range. In contrast, 36% of the  $F_{2,5}$  strains selected for high UHML and derived from TAM22 × SID84, and the majority of high UHML  $F_{2,5}$  strains derived from ELSU33 × SID84, had Mic indices below 3.5, likely resulting from the interspecific nature of the SID84 parent. Thus, the negative relationship between UHML and Mic should not impede selection for high UHML among the three upland germplasm lines, but should be a consideration when selecting high UHML among interspecific populations.

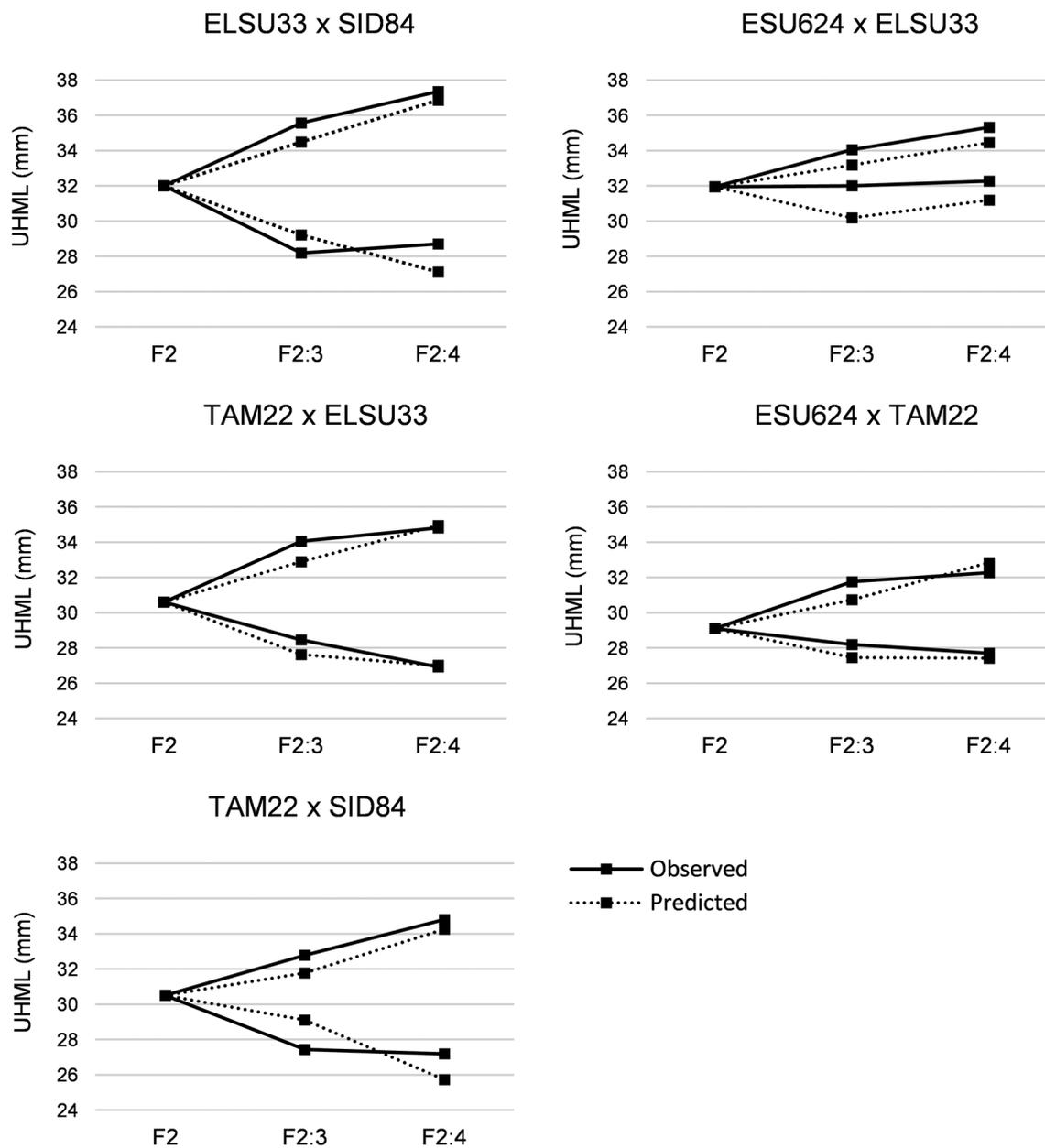


Fig. 1. Comparison of observed and predicted responses to two cycles of divergent selection at College Station, TX, for fiber upper-half mean length (UHML) within five experimental populations. The F<sub>2</sub> progeny derived from each cross were evaluated in 2010 or 2011, and the top and bottom 5% for UHML were selected in cycle one. The F<sub>2:3</sub> progeny derived from the selected F<sub>2</sub> progeny were evaluated in 2012, and the top and bottom 10% for UHML were selected in cycle two. The F<sub>2:4</sub> progeny derived from the F<sub>2:3</sub> selections were evaluated in 2013.

The negative association between LP, which is a primary lint-yield component, and fiber quality traits is a major constraint to cultivar development in upland cotton (Hinze et al., 2011; Meredith, 1984; Miller et al., 1958; Smith and Coyle, 1997). Lint percent responded negatively to selection for UHML across all five populations. However, several strains were identified with improved UHML and LP compared with both parental lines—more specifically, eight F<sub>2:5</sub> strains derived from ESU624 × TAM22, one strain derived from ELSU33 × SID84, and one strain within TAM22 × ELSU33. Simultaneous selection pressure for UHML and LP

would have increased the frequency of recombinants with improved UHML and LP.

### Selection for Fiber Bundle Strength

The realized heritability estimates were moderate to high for Str, ranging from 0.14 for ESU624 × ELSU33 to 0.72 for TAM22 × SID84 (Table 2), suggesting that early-generation selection for Str is effective at College Station. The realized heritability estimate for Str in cycle one within ESU624 × ELSU33 was substantially lower than the narrow-sense heritability estimate from Joy (2014) and the realized heritability estimate from cycle two of divergent selection. This is likely attributable to variation

**Table 3. Analyses of variance and upper-half mean length (UHML) of selected groups (i.e., high and low UHML) composed of F<sub>2:5</sub> strains derived from divergent selection and evaluated at College Station, TX, in 2014.**

Source†	ESU624 × ELSU33		TAM22 × ELSU33		ELSU33 × SID84		ESU624 × TAM22		TAM22 × SID84	
	df	MS‡	df	MS	df	MS	df	MS	df	MS
Replication	1	0.98	1	23.56	1	0.17	1	50.03	1	13.22
Group	1	251.01*	1	1270.8*	1	1306.97*	1	454.34	1	489.86*
Replication × group	1	0.48	1	5.75	1	1.32	1	4.59	1	2.54
Sampling error	101	1.46	119	1.61	96	2.22	98	0.96	86	1.87
<b>Mean UHML§</b>	mm									
High		33.46 a		33.31 a		36.05 a		31.72 a		33.48 a
Low		30.35 b		26.53 b		28.78 b		27.43 a		28.77 b

\* Significant at the 0.05 probability level.

† F<sub>2:5</sub> strains were categorized into two groups for analysis, based on selection for high or low UHML.

‡ MS, mean squares.

§ Least squares means within the same column (i.e., within population) with the same letter are not significantly different according to Fisher's protected LSD at the 0.05 probability level.

**Table 4. Correlated responses† to divergent selection for upper-half mean length (UHML) among high-volume instrument-measured fiber properties‡ and lint percent (LP) of F<sub>2:5</sub> strains evaluated at College Station, TX, in 2014.**

UHML	Str	UI	Elon	Mic	LP
Across populations	0.67***	0.76***	-0.62***	-0.77***	-0.73***
ELSU33 × SID84	0.78***	0.83***	-0.74***	-0.51***	-0.76***
ESU624 × ELSU33	0.03	0.39**	-0.27	-0.73***	-0.51***
ESU624 × TAM22	0.71***	0.74***	-0.59***	-0.76***	-0.60***
TAM22 × ELSU33	0.53***	0.74***	-0.83***	-0.94***	-0.68***
TAM22 × SID84	0.72***	0.87***	0.00	-0.68***	-0.78***

\*\* Significant at the 0.01 probability level; \*\*\* significant at the 0.001 probability level.

† Pearson's phenotypic correlation coefficients.

‡ Str, bundle strength; UI, length uniformity index; Elon, elongation; Mic, micronaire.

due to environmental and/or genotype × environment interaction effects or may suggest the importance of nonadditive genetic effects within this parental combination. The observed responses to selection for Str were similar to the predicted responses, with the exception of ESU624 × ELSU33 (Fig. 2). Effective selection for fiber Str within this parental combination may require additional generations of inbreeding and evaluation across different environments.

Analyses of variance of the two Str groups (i.e., high and low) within each population of F<sub>2:5</sub> strains indicated that divergent selection was effective in four of five populations, resulting in a significant difference in mean Str between strains selected for high and low Str (Table 5). The exception was TAM22 × ELSU33. The mean difference between high and low Str groups within TAM22 × ELSU33 was 59.4 kN m kg<sup>-1</sup>, but the mean difference was not significant due to the large portion of variation in Str attributable to plot error. The greatest difference in mean Str between high and low strength strains was 98.2 kN m kg<sup>-1</sup> within TAM22 × SID84, whereas the smallest difference in mean Str of selected F<sub>2:5</sub> strains was within ESU624 × ELSU33 (40.5 kN m kg<sup>-1</sup>). Despite lower realized heritability

estimates within ESU624 × ELSU33, the mean of the F<sub>2:5</sub> strains selected for high Str was comparable with the mean among F<sub>2:5</sub> strains from ELSU33 × SID84 and ESU624 × TAM22. Positive and negative transgressive segregants for Str were observed within all populations. The most extreme transgressive segregation for Str was observed within F<sub>2:5</sub> strains derived from ELSU33 × SID84 and TAM22 × SID84, suggesting that SID84 also harbors favorable alleles for Str not present in the upland parents.

Generally, there was a positive correlation between Str, UHML, and UI among the F<sub>2:5</sub> strains selected for high and low Str (Table 6). Despite ample variation in Str and UHML within F<sub>2:5</sub> strains derived from ESU624 × ELSU33, there was no correlation between Str and UHML. Fiber uniformity index responded positively to selection for Str, even more so than selection for UHML. Across populations, there was no clear relationship between Elon and Str. There was a negative response in Elon to selection for Str among F<sub>2:5</sub> strains derived from ELSU33 × SID84, a positive response in Elon to selection for Str among F<sub>2:5</sub> strains derived from ESU624 × ELSU33, and no correlated response in Elon to selection for Str among the remaining populations. Fiber micronaire also responded inconsistently to selection for Str across genetic backgrounds. There was a positive response in Mic to selection for Str among F<sub>2:5</sub> progeny derived from crosses involving SID84, while there was a negative response in Mic to selection for Str among ESU624 × TAM22 and TAM22 × ELSU33. Generally, there was a negative response in LP to selection for Str, though not as strong as observed for UHML and LP. Three F<sub>2:5</sub> strains derived from ELSU33 × ESU624 had greater Str and LP compared with either parental line, and three strains derived from TAM22 × SID84 had greater Str and LP than either parent.

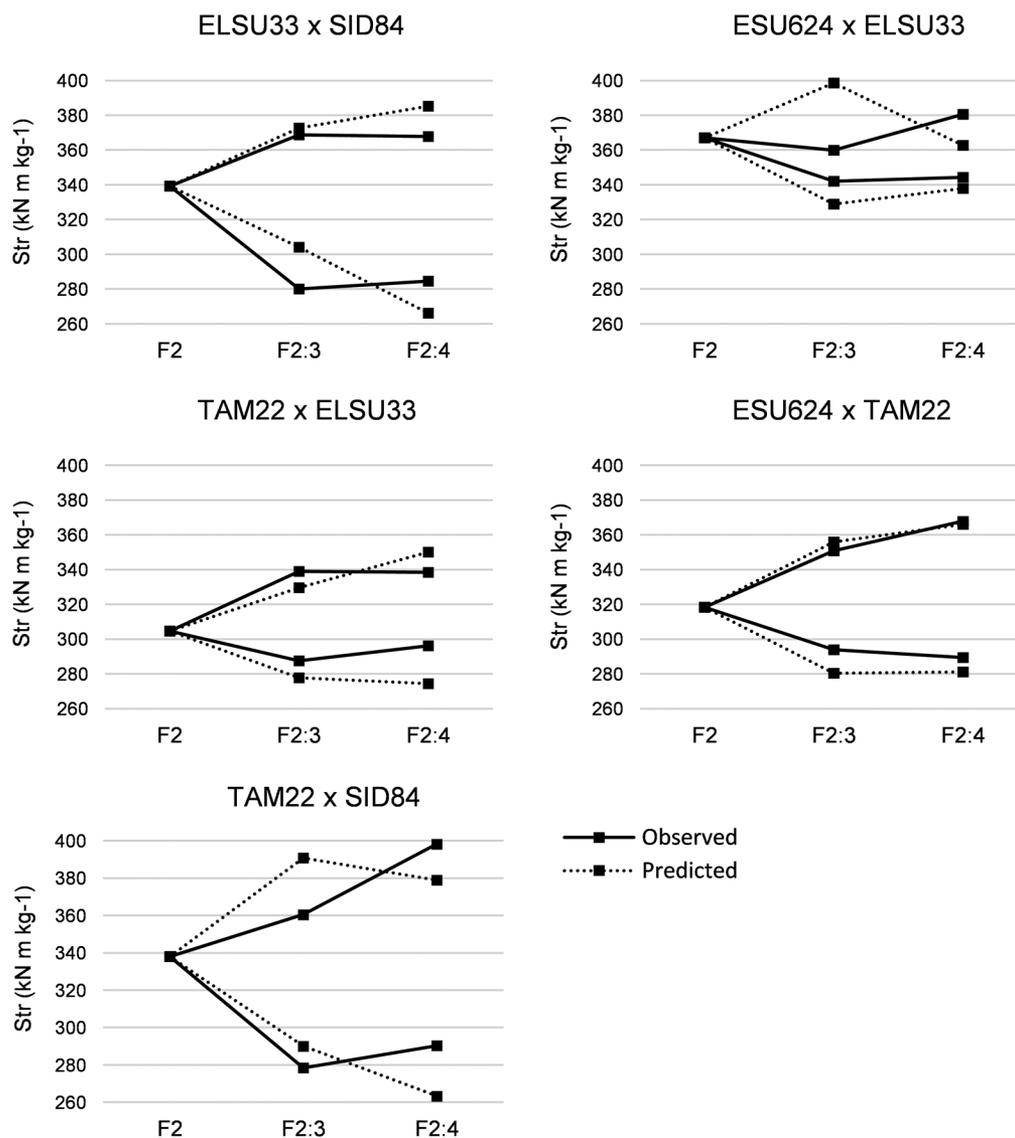


Fig. 2. Comparison of observed and predicted responses to two cycles of divergent selection at College Station, TX, for fiber bundle strength (Str) within five experimental populations. The  $F_2$  progeny derived from each cross were evaluated in 2010 or 2011, and the top and bottom 5% for Str were selected in cycle one. The  $F_{2:3}$  progeny derived from the selected  $F_2$  progeny were evaluated in 2012, and the top and bottom 10% for Str were selected in cycle two. The  $F_{2:4}$  progeny derived from the  $F_{2:3}$  selections were evaluated in 2013.

**Table 5. Analyses of variance and mean fiber bundle strength (Str) of selected groups (i.e., high and low Str) composed of  $F_{2:5}$  strains derived from divergent selection and evaluated at College Station, TX, in 2014.**

Source	ESU624 × ELSU33		TAM22 × ELSU33		ELSU33 × SID84		ESU624 × TAM22		TAM22 × SID84	
	df	MS†	df	MS	df	MS	df	MS	df	MS
Replication	1	44.3	1	75.8	1	49.6	1	475.5	1	1093.4
Group‡	1	32856.3*	1	77555.2	1	123119.2*	1	163928.1*	1	282418.2*
Replication × group	1	187	1	1124.3	1	342.1	1	746.1	1	840.5
Sampling error	86	593.6	98	185.4	93	609.7	96	327.4	114	625.3
<b>Mean Str§</b>	kN m kg <sup>-1</sup>									
High		371.2 a		333.2 a		377.5 a		365.7 a		391.5 a
Low		330.7 b		273.8 a		296.0 b		284.8 b		293.3 b

\* Significant at the 0.05 probability level.

† MS, mean squares.

‡  $F_{2:5}$  strains were categorized into two groups for analysis, based on selection for high or low Str.

§ Least squares means within the same column (i.e., within population) with the same letter are not significantly different according to Fisher's protected LSD at the 0.05 probability level.

**Table 6. Correlated responses† to divergent selection for fiber bundle strength (Str) among high-volume instrument-measured fiber properties‡ and lint percent (LP) of F<sub>2:5</sub> strains evaluated at College Station, TX, in 2014.**

Str	UHML	UI	Elon	Mic	LP
Across populations	0.64***	0.79***	0.05	-0.03	-0.46***
ELSU33 × SID84	0.83***	0.86***	-0.57***	0.46***	-0.43***
ESU624 × ELSU33	0.29	0.69***	0.57***	-0.20	-0.16
ESU624 × TAM22	0.76***	0.86***	0.16	-0.52***	-0.68***
TAM22 × ELSU33	0.84***	0.90***	0.10	-0.62***	-0.45***
TAM22 × SID84	0.78***	0.89***	0.13	0.25*	-0.56***

\* Significant at the 0.05 probability level; \*\*\* significant at the 0.001 probability level.

† Pearson's phenotypic correlation coefficients.

‡ UHML, upper-half mean length; UI, length uniformity index; Elon, elongation; Mic, micronaire.

## CONCLUSIONS

The results obtained from divergent selection for UHML and Str correspond to those of Joy (2014) and provide further support that there is ample genetic variation for fiber quality among the following parental combinations: ESU624 × ELSU33, TAM22 × ELSU33, ELSU33 × SID84, ESU624 × TAM22, and TAM22 × SID84. Considering that realized heritability provides an estimate of how much of the selection differential imposed was observed as a response in the progeny, these results suggest that early generation selection for UHML and Str is highly effective at College Station, with the exception of progeny derived from ESU624 × ELSU33.

High levels of allele dispersion for UHML and Str were observed between SID84 and the upland parents TAM22 and ELSU33, but negative correlations between agronomic and fiber quality traits still limit the use of SID84 as a parental line. Several F<sub>2:5</sub> strains with improved UHML and/or Str and no associated reduction in LP were identified within each population, providing further evidence that the negative relationship between fiber quality and lint yield is, at least in part, attributable to repulsion phase linkage. The parental combination ESU624 × ELSU33 provided the best opportunity to simultaneously combine beneficial alleles for UHML, Str, and LP, despite comparatively lower realized heritability estimates. Green and Culp (1990) demonstrated that a weak negative genetic correlation exists between Str and Elon. However, only one population included in this study, ELSU33 × SID84, was characterized by a negative phenotypic correlation between Str and Elon, but there was a negative phenotypic correlation between UHML and Elon in three of the populations, ELSU33 × SID84, ESU624 × TAM22, and TAM22 × ELSU33.

The results reported herein suggest that variation for fiber quality exists within the Texas A&M AgriLife Research upland cotton germplasm to improve UHML and Str without a concomitant reduction in LP. The results further suggest that the negative correlation between

UHML and Elon is more than an artifact attributable to the positive correlation between UHML and Str, and combined with the results reported by Ng et al. (2014), suggest that further investigation into the negative relationship between UHML and Elon is warranted.

## Conflict of Interest

The authors declare that there is no conflict of interest.

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