

Assessing the Breeding Potential of Extra-Long Staple Upland Germplasm in a Cotton Breeding Program

B.T. Campbell,* K.L. Hugie, J. Wu, and D.C. Jones

ABSTRACT

Fiber quality improvement of upland cotton (*Gossypium hirsutum* L.) is essential to increase the value and competitiveness of cotton fiber. The closely related allotetraploid species *G. barbadense* L. has long been targeted as a source of beneficial fiber quality alleles. Although interspecific hybridization between *G. hirsutum* and *G. barbadense* results in fertile offspring, cultivar development programs have seen little success using this approach. In this study, we evaluated the breeding potential of extra-long staple (ELS) upland accessions that presumably contain *G. barbadense* introgressions. As expected, ELS upland accessions produced long fibers with overall excellent mean fiber quality performance. Genetic effects indicated that ELS upland accessions transmitted both additive and nonadditive beneficial alleles for fiber length and micronaire. However, ELS upland accessions also transmitted negative effects for lint percentage, lint yield, and fiber strength. Results suggest that ELS upland accessions are a good source for improving fiber length but also support the idea that linkage drag and skewed chromatin transmission, often seen in progeny derived from interspecific hybridization, may still proliferate in offspring derived from ELS upland accessions.

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Abbreviations: ELS, extra-long staple; HVI, high volume instrument.

IMPROVING fiber quality is critical to increase the value and competitiveness of upland cotton (*Gossypium hirsutum* L.). Genetic improvement of fiber quality is highly dependent on the exploitation and efficient use of available genetic resources. The extensive genetic resources from 50 cotton species have been documented (Campbell et al., 2010), and recent reports have expanded the number of cotton species to 52 with the discovery of *G. ekmanianum* Wittmack (Grover et al., 2015) and *G. stephensii* J. Gallagher, C. Grover, & Wendel (Gallagher et al., 2017). Of the seven tetraploid species within the primary gene pool (which includes upland cotton), *G. barbadense* L., known for outstanding fiber quality, represents an attractive option for introgressing beneficial fiber quality alleles into upland cotton.

As such, introgressing *G. barbadense* fiber quality alleles into upland cotton has long been a breeding objective. This objective has seen limited success, as one of the primary impediments to successful introgression was noted very early when Stephens (1949) observed an underrepresentation of donor alleles in crosses of *G. barbadense* and upland cotton. Although reciprocal introgressions involving *G. barbadense* and upland cotton have been identified (Brubaker and Wendel, 1994; Wendel et al., 1992), their frequency in structured, recombinant populations often falls below Mendelian expectations. Breeding lines with putative *G. barbadense* introgressions are assumed as a key source of historically relevant fiber

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quality improvements in several upland breeding programs including the Pee Dee breeding program (Campbell et al., 2011) and the New Mexico Acala breeding program (Zhang et al., 2005). However, to date, the putative *G. barbadense* chromatin introgressions have not been confirmed. Jiang et al. (2000) studied the genomic architecture of *G. barbadense* introgressions into upland cotton and found skewed chromatin transmission as a result of multilocus epistatic interactions. Subsequently, this skewed chromatin transmission was also identified for *G. tomentosum* Nutt. ex Seem. introgression into upland cotton (Waghmare et al., 2016). Hence, skewed chromatin transmission may be characteristic of the *Gossypium* genus.

Rather than attempting to transfer fiber quality alleles from *G. barbadense* using interspecific crosses with upland cotton, two alternative breeding strategies involve, 1) selection within intraspecific crosses of elite upland genotypes and 2) selection within putative *G. barbadense* introgression line × upland cotton crosses. Smith et al. (2008) demonstrated the effectiveness of selection within intraspecific crosses of upland cotton genotypes. He developed extra-long staple (ELS) upland cotton breeding lines with fiber length exceeding 32 mm. Smith et al. (2009) conducted genetic analyses for fiber length in intraspecific crosses involving these breeding lines and demonstrated transgressive segregants for fiber length. Similarly, Campbell et al. (2016) reported the significant fiber strength increase captured in MD 15 (PI 642769; (Meredith, 2006)) was most likely the result of intraspecific, transgressive segregation.

Breeding schemes directly using putative *G. barbadense* introgression lines crossed with elite upland breeding lines have not been studied in great detail. However, two studies have studied breeding populations derived from an ELS upland genotype developed via transgressive segregation from an intraspecific, upland cross. Hague et al. (2011) studied genetic variation in an ELS upland × medium staple upland cross and identified transgressive segregation for micronaire, fiber length, and fiber strength confounded by differences in heritability across selection environments. Beyer et al. (2014) evaluated the fiber quality of testcross populations derived from crosses involving an ELS upland genotype and a range of upland genotypes and documented poor combining ability. Zhang et al. (2016) evaluated the breeding potential of six *G. barbadense* introgression lines with upland cottons and found they performed well as general combiners for yield and fiber quality improvement.

More information on the use of putative *G. barbadense* introgression lines is needed to determine how they may benefit current upland cotton breeding programs. In this report, we examined the mean performance and genetic effects of breeding populations derived from crosses involving ELS upland accessions obtained from the USDA National Cotton Germplasm Collection and six elite upland

genotypes. The objective of this study was to estimate genetic variance components and predict genetic effects for agronomic and fiber quality traits based on breeding populations derived from elite upland and ELS upland genotypes.

MATERIALS AND METHODS

Development of Topcross Families

A total of 66 topcross families were developed using 11 ELS upland genotypes and six elite, upland genotypes (ELITE) (Table 1). The ELS upland genotypes were Acala Messilla Valley 898 (PI 529112), Ewing Long Staple X Tidewater (PI 528726), Greer Wichita-169-1203 Pope 36 (PI 528545), Meade 14-2 (PI 528994), Sealand 1 (PI 528871), Sealand 3 (PI 528872), Sealand 472 (PI 528729), Sealand 883 (PI 528875), D and PL 45-867 (PI 528771), Spears Upland Early Long Staple (PI 529043), and Spears 3 (PI 529037). The ELITE genotypes included cultivar Deltapine 90 (PI 529529), DES 119 (PI 606809), MD 25 (PI 659508), Delta Pearl (PI 614100), PD 94042 (PI 603219), and cultivar UA-48 (PI 660508). In 2011, the ELITE genotypes were each topcrossed as males onto the ELS upland genotypes. The F₁ and parental line seeds were sent to a winter nursery in Tecoman, Mexico, and manually self-pollinated to produce copious amounts of F₂ and parental line seed.

Field Design and Procedures

The 66 F₂ hybrids, 17 parental genotypes, and one commercial check (cultivar Phytogen 72, PI 617043) were evaluated in one environment in 2012 and two environments in 2013. Due to limited seed, the 2012 trial included only 60 F₂ hybrids. The 2012 trial was conducted at the Clemson University Pee Dee Research and Education Center near Florence, SC. In 2013, one trial was conducted at the Clemson University Pee Dee Research and Education Center and the second at the North Carolina State University Sandhills Research Station near Jackson Springs, NC. In each trial, the F₂ hybrids, parental genotypes, and the commercial check were randomly assigned to a replicated, randomized complete block field design. Four and three replicates were used in 2012 and 2013, respectively. In all trials, plots consisted of a single row 10.6 m long with 96-cm row spacing. Trial management followed the established local production practices for rainfed cotton production at each location. Each plot was harvested with a spindle-type mechanical cotton picker, and total seed cotton weight was recorded. A 25-boll sample was hand harvested from each plot before harvest to determine lint percentage and fiber quality properties. All samples from each location were ginned on a common 10-saw laboratory gin, and lint percentage was determined by dividing the weight of the lint sample after ginning by the weight of the seed cotton sample before ginning. Lint yield was calculated by multiplying lint percentage by seed cotton yield. A portion of the lint sample was sent to the Cotton Incorporated Fiber Testing Laboratory (Cary, NC) for determination of high volume instrument (HVI) fiber properties. The fiber properties measured included fiber length, micronaire, fiber uniformity, and fiber strength. Two fiber quality indices (or Q-score) were calculated using a weighted average of HVI fiber properties following the procedure described by Bourland et al. (2010). Quality index 1 included fiber length (50%), micronaire (25%), uniformity index (15%), and fiber strength (10%).

Quality index 2 included fiber length (10%), micronaire (10%), uniformity index (30%), and fiber strength (50%).

Analysis of Phenotypic Data

Phenotypic data were analyzed using a mixed model and the PROC GLM module of SAS 9.2 (SAS Institute, 2008). The RANDOM statement was included to identify random effects and make *F*-tests using the appropriate error term. Initially, individual year-location data were analyzed and homogeneity of variance tests were conducted to determine if a combined ANOVA could be conducted for each trait. After confirming homogenous error variance for each trait, the combined data were analyzed using ANOVA. Block and environment (each year-location) were considered random effects. Genotypes were considered fixed effects. Fisher's protected LSD was calculated and used to make planned comparisons among least square means.

Genetic Analysis

Phenotypic data from each location were analyzed by an additive-dominance genetic model following the procedures described by Jenkins et al. (2006). A mixed linear model approach, minimum norm quadratic unbiased estimation with an initial value of 1.0 called MINQUE1, was used to estimate the variance components (Zhu, 1989). Genetic variances and genetic effects were calculated for each genetic component. The phenotypic variance was partitioned into components for block, additive, dominance, and residual; they were expressed as proportions of the total phenotypic variance (Tang et al.,

1996; Wu et al., 2010). Genetic effects were predicted by the adjusted unbiased prediction approach (Zhu, 1993). Standard errors of variance components and genetic effects were estimated by randomized 10-fold jackknife resampling technique (Zhu, 1993; Wu et al., 2008; Wu et al., 2012). An approximate one-tailed *t* test was used to detect the significance of variance components. A two-tailed *t* test was used to detect the significance of genetic effects (Miller, 1974).

The predicted genetic effects were deviations from the respective population grand mean. A *t* test was used to detect the significance of genetic effects from zero. These effects are measures of the additive or homozygous dominance effects for each of the 17 topcross parents. The 95% confidence intervals for additive and homozygous dominance effects were compared among the ELS upland and ELITE parents. Heterozygous dominance effects were estimated for each F₂ hybrid combination. All of these genetic analyses were conducted using the qgtools package in the minique R package (R Core Team, 2014; Wu, 2014).

RESULTS

Analysis of Variance and Parental Line Comparisons

A combined ANOVA showed highly significant differences for genotypes and genotype × environment interactions for agronomic and fiber quality performance traits (Table 2). Table 3 provides a summary of least square mean trait values for each parent. PD 94042, Delta Pearl, and MD 25 had

Table 1. Description of genotypes used as parents.

Name	PI no.	Type	Reference
Acala Mesilla Valley 898	PI 529112	<i>Gossypium hirsutum</i> (extra-long staple)	–
Ewing Long Staple X Tidewater	PI 528726	<i>Gossypium hirsutum</i> (extra-long staple)	–
Greer Wichita 169-1203 Pope 36	PI 528545	<i>Gossypium hirsutum</i> (extra-long staple)	–
Meade 14-2	PI 528994	<i>Gossypium hirsutum</i> (extra-long staple)	–
Sealand 1	PI 528871	<i>Gossypium hirsutum</i> (extra-long staple)	–
Sealand 3	PI 528872	<i>Gossypium hirsutum</i> (extra-long staple)	–
Sealand 472	PI 528729	<i>Gossypium hirsutum</i> (extra-long staple)	–
Sealand 883	PI 528875	<i>Gossypium hirsutum</i> (extra-long staple)	–
D and PL 45-867	PI 528771	<i>Gossypium hirsutum</i> (extra-long staple)	–
Spears Upland Early Long Staple	PI 529043	<i>Gossypium hirsutum</i> (extra-long staple)	–
Spears 3	PI 529037	<i>Gossypium hirsutum</i> (extra-long staple)	–
Deltapine 90	PI 529529	<i>Gossypium hirsutum</i> (cultivar)	–
DES 119	PI 606809	<i>Gossypium hirsutum</i> (cultivar)	–
MD 25	PI 659508	<i>Gossypium hirsutum</i> (germplasm line)	Meredith and Nokes (2011)
Delta Pearl	PI 614100	<i>Gossypium hirsutum</i> (cultivar)	–
PD 94042	PI 603219	<i>Gossypium hirsutum</i> (germplasm line)	May (1999)
UA-48	PI 660508	<i>Gossypium hirsutum</i> (cultivar)	Bourland and Jones (2012)

Table 2. Analysis of variance for agronomic and fiber quality performance of 66 F₂ hybrids, 17 parental lines, and one commercial check cultivar combined across three environments in 2012 and 2013.

Source of variation	df	Mean squares							
		Lint percentage	Lint yield	Micronaire	Fiber length	Fiber uniformity	Fiber strength	Quality index 1	Quality index 2
Environment (E)	2	28.0	21,652,636	28.7	488.8	104.3	19,980	50,732	11,748
Replicate (E)	7	10.7**	180,078**	0.4**	8.2**	7.3**	2,091**	688**	381**
Genotype (G)	83	75.6**	239,107**	1.7**	23.8**	8.5**	1,439**	1,771**	629**
G × E	151	5.4**	104,090**	0.1**	2.0**	1.1**	338**	375**	127**
Residual	540	2.3	24,778	0.1	0.9	0.7	142	146	64
CV		4.2	18	7.1	3.0	1.0	4	20	12

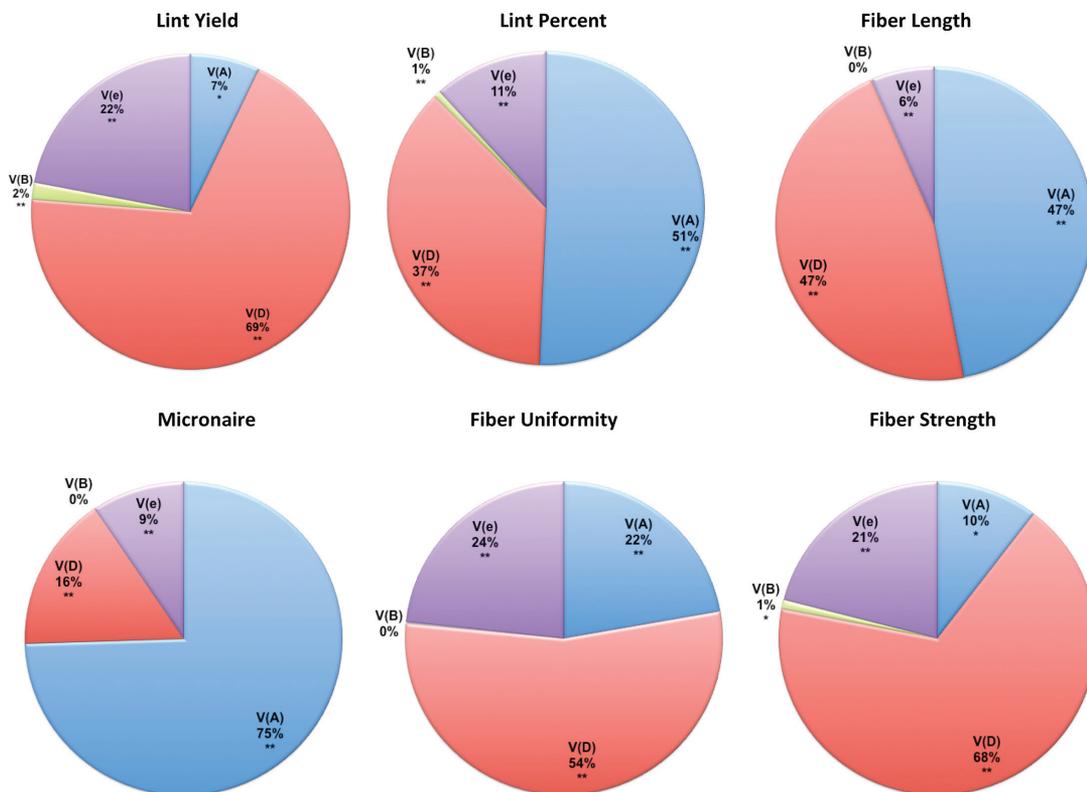
** Significant at the 0.01 probability level.

the highest lint percentage. Among ELS upland parents, PI 528545 had the highest lint percentage and was similar to DP 90, UA-48, and Phytogen 72. UA-48 and MD 25 produced the highest lint yield. Lint yields were comparable among the ELS upland parents, except for PI 528729, which produced the lowest lint yield. PI 529112, PI 528726, and PI

528545 produced lint yields similar to DP 90, PD 94042, Delta Pearl, DES 119, and Phytogen 72. For micronaire, all ELS upland parents, with the exception of PI 528545 and PI 528872, produced fibers with lower micronaire than the ELITE parents. Overall, fibers from PI 528545 and UA-48 had the highest micronaire. Lower micronaire is

Table 3. Mean agronomic and fiber quality performance for eleven extra-long staple upland lines, six elite upland lines, and one commercial check cultivar (Phytogen 72) combined across three environments in 2012 and 2013.

Parental line	Lint percentage	Lint yield	Micronaire	Fiber length	Fiber uniformity	Fiber strength	Quality index 1	Quality index 2
	%	kg ha ⁻¹		mm	%	kN m kg ⁻¹		
PI 529112	34.3	740	3.7	30.4	82.4	308	57	63
PI 528726	31.0	717	3.8	33.7	85.0	313	86	81
PI 528545	38.6	711	5.1	27.0	82.3	287	20	42
PI 528994	30.6	537	3.1	32.5	84.8	307	65	72
PI 528872	29.4	564	4.5	30.2	82.9	316	53	63
PI 528729	25.2	467	2.9	36.1	85.2	325	75	77
PI 528875	30.0	601	3.2	32.5	80.7	305	52	52
PI 528771	31.4	565	3.4	32.0	85.2	310	64	76
PI 529043	33.1	618	3.5	31.1	83.5	315	52	65
PI 529037	33.3	638	3.4	33.3	83.8	333	67	71
DP 90	38.5	917	4.3	29.0	83.3	304	52	59
DES 119	38.8	890	4.3	28.5	82.9	310	41	60
MD 25	39.4	1001	4.2	29.6	84.6	328	54	72
Delta Pearl	40.4	898	4.3	29.2	83.1	307	45	61
PD 94042	41.3	899	4.7	27.9	83.2	290	39	55
UA-48	38.8	1199	4.8	31.3	85.5	345	69	80
Phytogen 72	39.1	904	4.3	29.2	83.4	325	51	68
LSD (0.05)	2.0	211	0.4	1.2	1.1	16	16	11



*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.

Fig. 1. Variance components [V(A), additive; V(D), dominance; V(B), block; V(e), residual] expressed as proportions of the phenotypic variances for agronomic and fiber quality traits collected in Florence 2012.

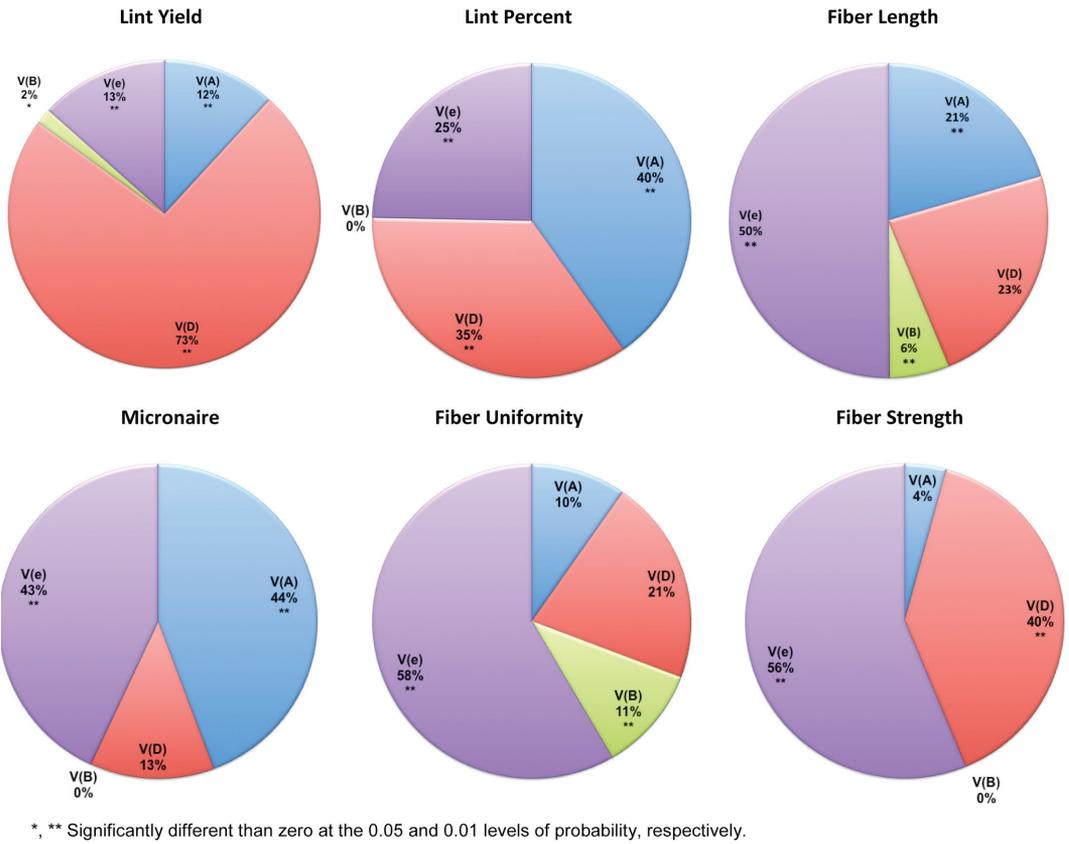


Fig. 2. Variance components [V(A), additive; V(D), dominance; V(B), block; V(e), residual] expressed as proportions of the phenotypic variances for agronomic and fiber quality traits collected in Florence 2013.

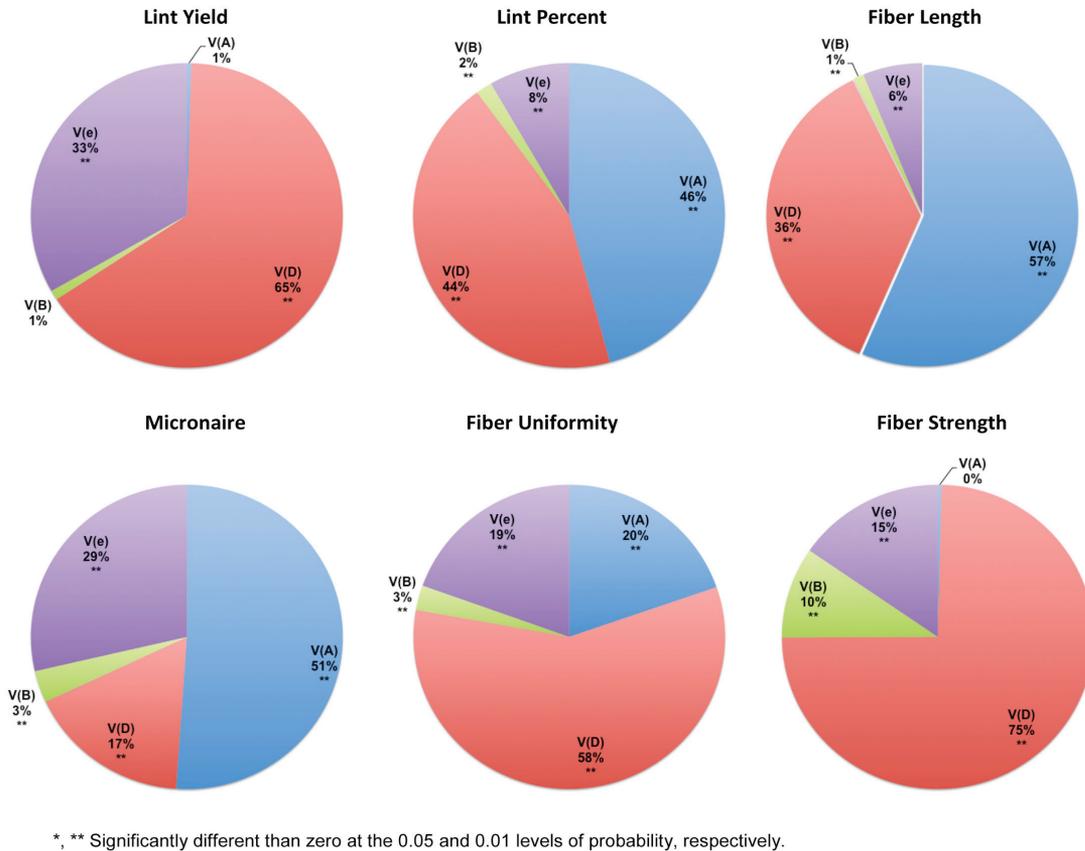
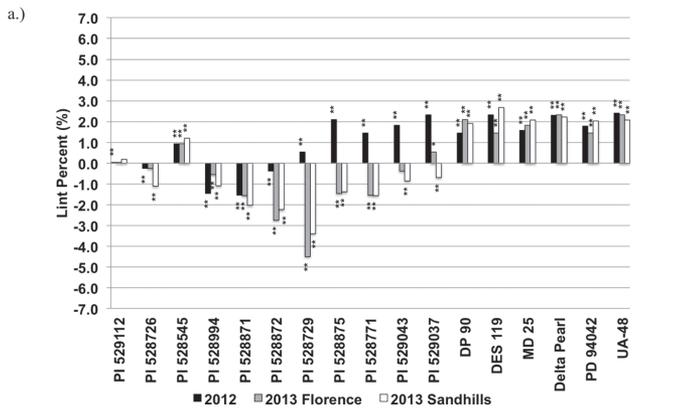


Fig. 3. Variance components [V(A), additive; V(D), dominance; V(B), block; V(e), residual] expressed as proportions of the phenotypic variances for agronomic and fiber quality traits collected in Sandhills 2013.

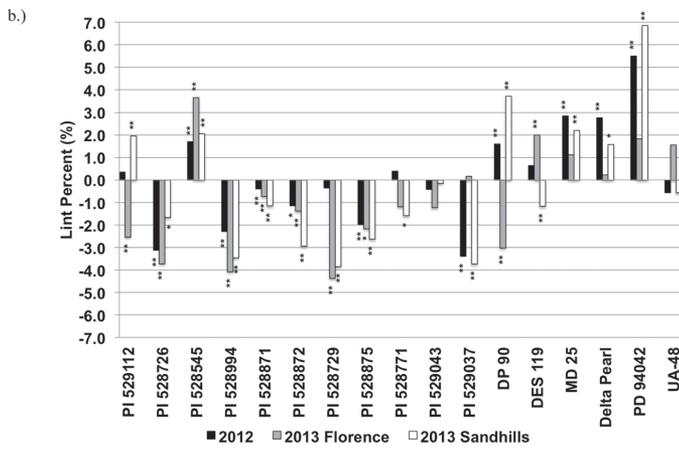
preferred. PI 528729 produced the longest fibers, whereas PI 528726, PI 529037, PI 528994, and PI 528875 produced fibers superior to the longest fiber ELITE parent, UA-48. PI 528729, PI 528771, PI 528726, and PI 528994 had similar fiber uniformity to the highest ELITE parents, UA-48 and MD 25. PI 529037 and UA-48 produced the highest strength, whereas PI 528729, PI 528872, PI 529043, and PI 528726 produced fibers with strength similar to MD 25 and Phytogen 72. PI 528726 and PI 528729 produced the highest value for Quality Index-1, whereas PI 528726, PI 528729, PI 528771, PI 528994, PI 529037, UA-48, and MD 25 produced the highest value for Quality Index-2. Interestingly, although listed as an ELS upland genotype in the USDA-ARS Germplasm Resources Information Network, PI 528545 did not display high-quality characteristics and performed well below other ELS upland and ELITE parents for all fiber quality traits. Collectively, as expected, comparisons among the ELS upland and ELITE parents demonstrate the quality attributes of the ELS upland parents but also highlight some agronomic deficiencies.

Variance Components

Variance components were estimated for individual environments and expressed as proportions of the phenotypic variance (Fig. 1–3). For lint percentage, additive variance accounted for 40 to 51% of the total variation, whereas dominance variance accounted for 35 to 44%. For lint yield, dominance variance accounted for 65 to 73% of the total variation, whereas additive variance accounted for 1 to 12%. For micronaire, additive variance accounted for 44 to 75% of the total variation, whereas dominance variance accounted for 13 to 17%. For fiber length, additive variance accounted for 21 to 57% of the total variation, whereas dominance variance accounted for 23 to 47%. Additive variance accounted for a relatively low percentage of the total variation for fiber uniformity (10–22%) and fiber strength (0–10%). Dominance variance accounted for a larger percentage of the total variation for fiber uniformity (21–58%) and fiber strength (40–75%). Not surprisingly, the proportion of the total variance attributed to each variance component differed across the three environments and from previously conducted studies (Jenkins et al., 2009; Zeng and Wu, 2012). As noted in

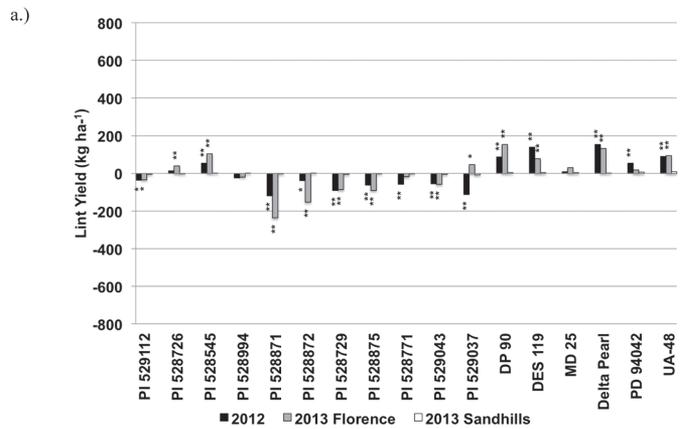


*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.

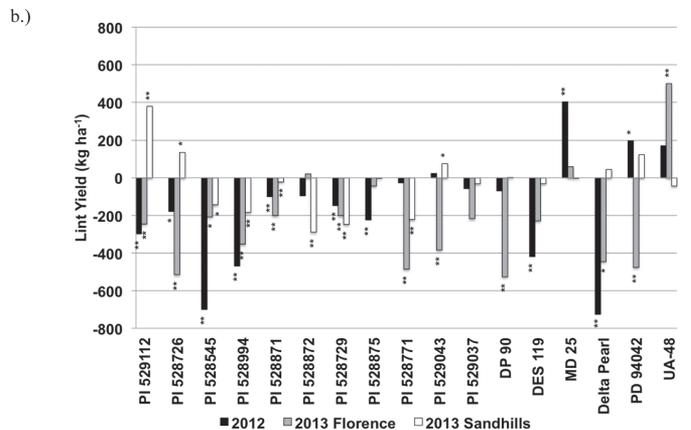


*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.

Fig. 4. Predicted (a) additive and (b) nonadditive effects for lint percentage expressed as deviations from the grand mean for three environments in 2012 and 2013.



*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.



*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.

Fig. 5. Predicted (a) additive and (b) nonadditive effects for lint yield expressed as deviations from the grand mean for three environments in 2012 and 2013.

Zeng et al. (2011), variance component proportions often differ depending on the genotype and environment.

Predicted Genetic Effects

To assess the breeding potential of the 11 ELS upland genotypes used in this study, we predicted additive and dominance effects for each trait. As noted by Jenkins et al. (2009), genetic effect predictions can be translated as follows: (i) additive effects represent general combining ability, (ii) homozygous dominance effects represent inbreeding depression, and (iii) heterozygous dominance effects represent specific combining ability. For each genetic effect, we tested if the effect was different than zero. Predicted genetic effects were also compared between the 11 ELS upland genotypes and the six ELITE parents.

For lint percentage, ELS upland genotypes generally had negative additive and homozygous dominance effects, whereas ELITE genotypes displayed positive additive and homozygous dominance effects (Fig. 4). A similar trend existed for lint yield, with the exception that ELITE genotypes generally displayed negative homozygous

dominance effects for lint yield (Fig. 5). For both lint percentage and lint yield, the only ELS upland genotype showing a different trend was PI 528545, which displayed positive additive and homozygous dominance effects for lint percentage and positive additive effects for lint yield.

As expected, ELS upland genotypes generally displayed positive additive effects for fiber length (Fig. 6). Two ELS upland genotypes (PI 528545 and PI 528872) displayed negative additive effects for fiber length. Four ELS upland genotypes (PI 528726, PI 528871, PI 528729, and PI 529037) displayed positive homozygous dominance effects for fiber length. Collectively, the ELITE genotypes displayed negative additive and homozygous dominance effects for fiber length. The exception was UA-48, which displayed a positive additive effect for fiber length. Figure 7 shows that for micronaire, eight of the ELS upland genotypes displayed negative additive and homozygous dominance effects (preferred), whereas the ELITE genotypes displayed positive additive and homozygous dominance effects (not preferred).

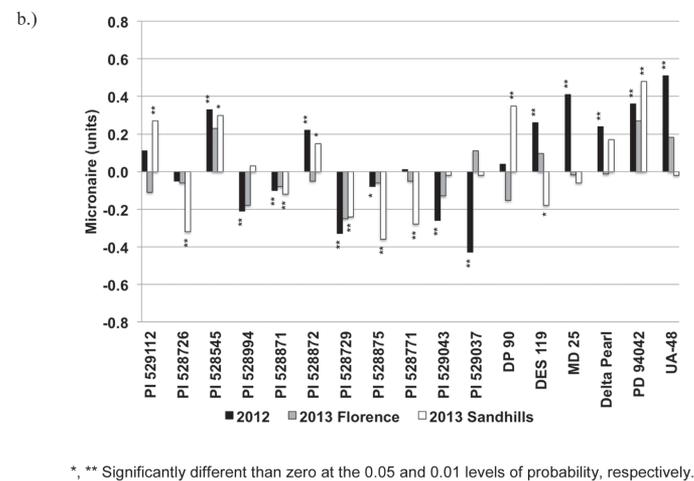
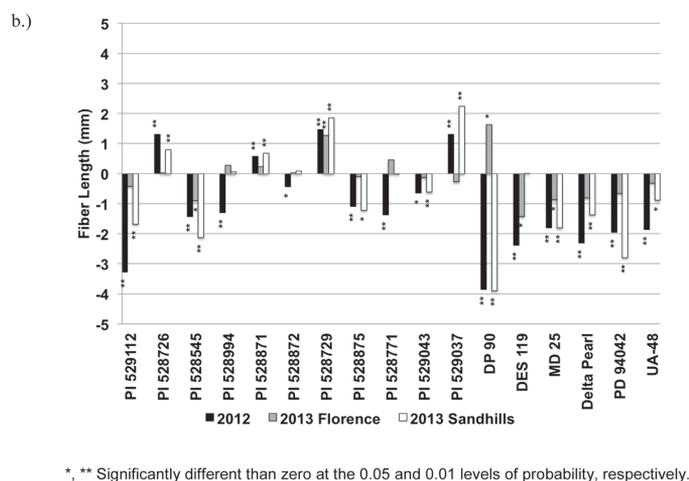
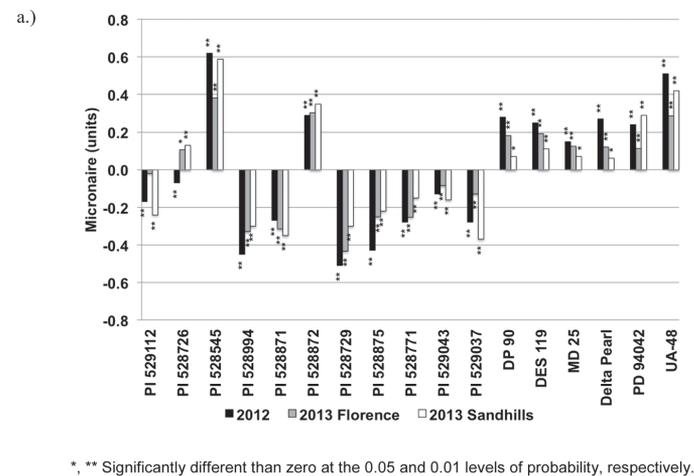
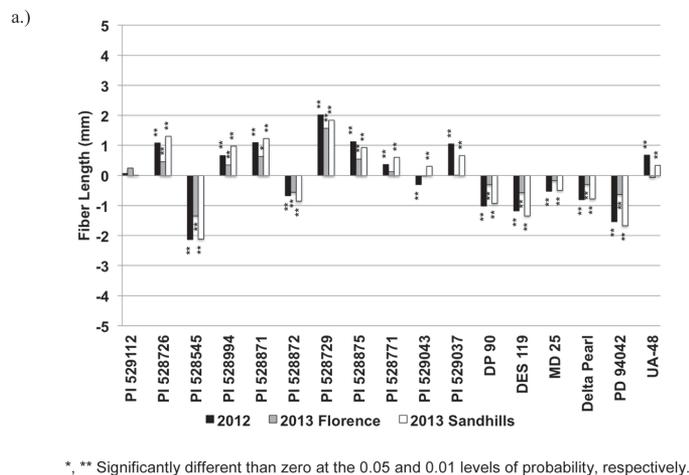
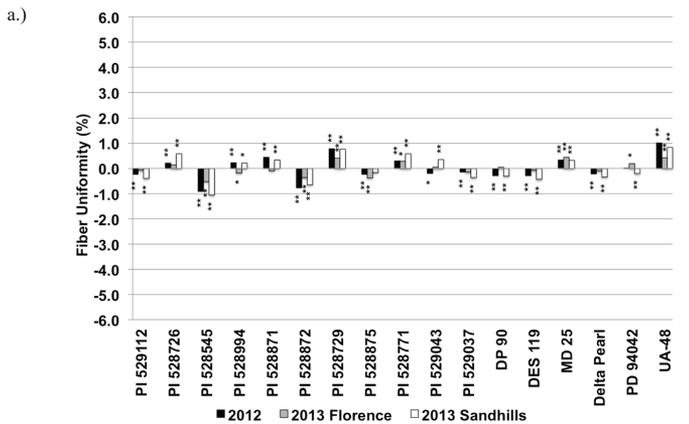
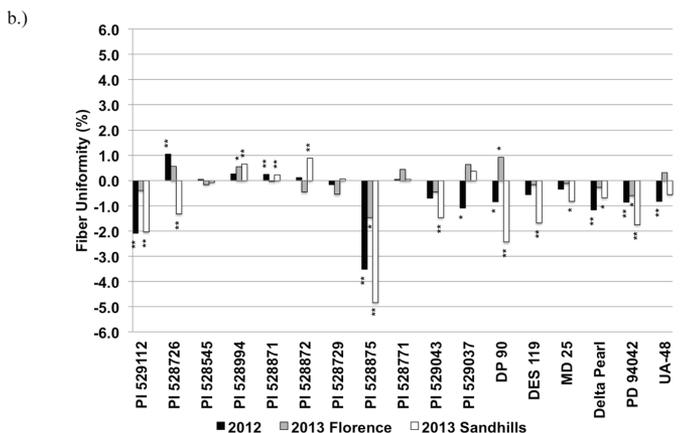


Fig. 6. Predicted (a) additive and (b) nonadditive effects for fiber length expressed as deviations from the grand mean for three environments in 2012 and 2013.

Fig. 7. Predicted (a) additive and (b) nonadditive effects for micronaire expressed as deviations from the grand mean for three environments in 2012 and 2013.



*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.

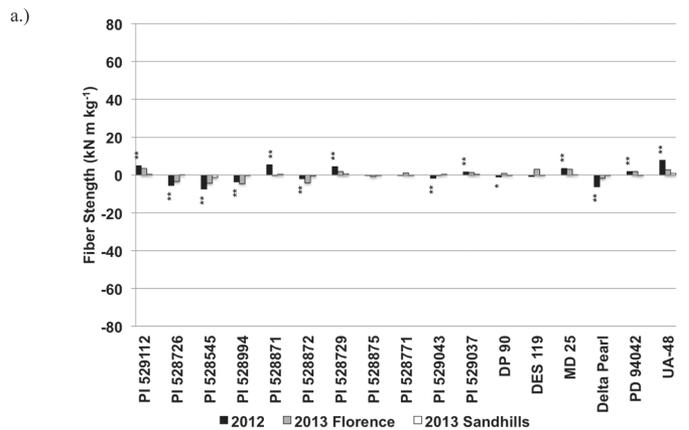


*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.

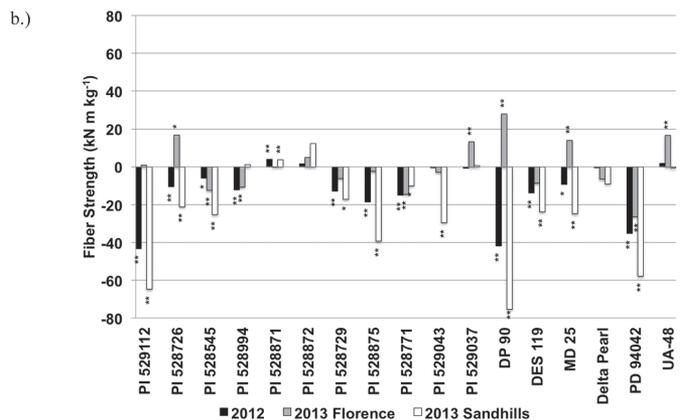
Fig. 8. Predicted (a) additive and (b) nonadditive effects for fiber uniformity expressed as deviations from the grand mean for three environments in 2012 and 2013.

Overall, additive effects for fiber uniformity were negligible for ELS upland and ELITE genotypes (Fig. 8). Significant additive effects resulted in 1% or less increase or decrease in fiber uniformity. Significant homozygous dominance effects for ELITE genotypes were negative, and most ELS upland genotypes displayed negligible homozygous dominance effects with the exception of PI 529112 and PI 528875, which decreased fiber uniformity by >2%. Collectively, additive effects for fiber strength were negligible for ELS upland and ELITE genotypes (Fig. 9). The majority of ELS upland and ELITE genotypes displayed significant negative homozygous dominance effects for fiber strength, especially PI 529112, DP 90, and PD 94042.

For each trait and cross combination, heterozygous dominance effects were predicted and their standard errors estimated. However, no strong trends specific to any of the topcross parents were evident. In general, these results suggested heterozygous dominance effects differed depending on the specific ELS upland × ELITE cross combination.



*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.



*, ** Significantly different than zero at the 0.05 and 0.01 levels of probability, respectively.

Fig. 9. Predicted (a) additive and (b) nonadditive effects for fiber strength expressed as deviations from the grand mean for three environments in 2012 and 2013.

DISCUSSION

Improving fiber quality is paramount to increase the value and competitiveness of cotton fiber for textile manufacturing processes. As expected, ELS upland accessions produced long fibers with overall excellent mean fiber quality performance (Table 3). PI 528545 was the only ELS upland accession that did not display superior ELS-like fiber properties. Agronomic performance of ELS upland accessions was deficient to the ELITE accessions, especially for lint percentage. However, two ELS upland accessions produced lint yields similar to ELITE accessions while also producing excellent fiber properties.

Variance component analysis offered interesting insight into the components of genetic variation for ELS upland × ELITE topcrosses. Genetic variance accounted for a sizeable portion of the overall variance across traits and environments (Fig. 1–3). Genetic variation for lint percentage and fiber length was equally divided between additive and nonadditive effects. Additive effects accounted for greater than half of the total genetic variance for micronaire. Nonadditive effects accounted for a greater

percentage of the total genetic variation for lint yield, fiber uniformity, and fiber strength. Similar to this study, Smith et al. (2009) and Zhang et al. (2016) demonstrated additive variance for fiber length in genetic studies involving an ELS upland cultivar and *G. barbadense* introgression lines, respectively. In contrast with the current study, for traits other than fiber length (yield and other fiber properties), Zhang et al. (2016) documented that additive variance was more prevalent than nonadditive variance.

The presence of additive effects for lint percentage, fiber length, and micronaire suggests that the ELS upland and ELITE germplasm used in the current study contain favorable alleles that can be combined using traditional self-pollinated crop methods of inbreeding. However, the presence of nonadditive effects for lint yield, fiber uniformity, and fiber strength indicate that alternative breeding strategies are needed to accumulate favorable nonadditive genetic variation for those traits.

On average, the genetic effects reported in this study indicated that ELS upland germplasm transmitted positive additive and dominance effects for fiber length and micronaire. This confirms that fiber length and micronaire improvement is probable when using ELS upland germplasm in upland breeding programs. It also suggests that these ELS upland germplasm may transmit beneficial alleles for fiber length and micronaire not present in the high-quality ELITE upland germplasm used in this study. On the contrary, this study also demonstrates that ELS upland germplasm transmit negative additive and dominance effects for lint percentage, lint yield, and fiber strength, which suggests the existence of pleiotropic effects or a preponderance of the linkage drag often associated with interspecific *G. hirsutum* × *G. barbadense* crosses (Jiang et al., 2000). It also suggests that crosses involving ELS upland genotypes suffer from the well-known negative relationship between agronomic performance and fiber quality (Campbell et al., 2012). Overall, these results support the hypothesis of Waghmare et al. (2016) that skewed chromatin transmission is characteristic of the *Gossypium* genus. The transmission of negative (and relatively negligible) genetic effects for fiber strength was surprising. This finding may be a result of skewed chromatin transmission, or it may suggest that the ELITE genotypes used in this study contain fiber strength alleles superior to those present in the ELS upland parents.

Although this study used ELS upland genotypes purportedly containing *G. barbadense* introgressions rather than *G. barbadense* genotypes directly, our results suggest that linkage drag and skewed chromatin transmission likely still proliferates. These negative genetic effects may prohibit the widespread use of ELS upland germplasm as parents in upland breeding programs. However, results of this study highlight a continued need to better understand the genetic architecture of chromatin transmission in *Gossypium*. Advances in this area have great potential to

harness new strategies to simultaneously improve cotton fiber quality and agronomic performance.

Conflict of Interest

The authors declare that there is no conflict of interest.

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