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Genetic Variation for Fiber Properties in Elite Pee Dee Cotton Populations

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ABSTRACT

Knowledge of heritability and type of genetic variation involved in the expression of fiber traits would facilitate further improvement of cotton fiber properties. A 4 × 4 Design II mating was employed to estimate magnitude and type of genetic variation controlling fiber traits in populations derived from crossing elite Pee Dee cotton (*Gossypium hirsutum* L.) parents. Significant genetic variation was found for 2.5 and 50% span length (SL), fiber length uniformity ratio (UR), fiber strength (T_1), fiber elongation, and micronaire (MIC). Mating design variances from the F_2, F_3, and F_4 generations of the Design II were resolved into estimates of additive, dominance, and additive epistatic variance for the fiber properties. Dominance genetic variance was greater than additive genetic variance for all of the fiber traits. Additive epistatic variance was detected for 2.5% SL, UR, and MIC. Low single-plant heritability for all fiber traits suggested that alternatives to a pedigree generation advance beginning with F_2 plant selection be considered. Evaluation of F_2 bulk populations with a low selection intensity was adequate to identify populations with superior fiber traits. Less than half of the offspring of the top 10% of F_3 lines with highest T_1 were in the 10% of F_4 lines with highest yarn strength (YS). Additionally, the correlation between T_1 and YS among 283 unselected F_4 lines was only 0.25 ($P < 0.05$). Maximum progress in improving YS may require selection for traits in addition to T_1 or for components of YS not measured by the standard fiber properties.

FIBER PROPERTIES of U.S. cotton must continually improve to remain competitive in domestic and world markets and meet the needs of new spinning and weaving methods. A goal of the Pee Dee cotton breeding program is to develop cotton genotypes with improved fiber quality. This goal was recently met with the release of 11 germplasm lines with fiber and yarn properties equal or superior to 'PD-3', which is currently the leading cultivar in the program (Green et al., 1991a,b,c). These 11 germplasm lines represent more than 40 yr of breeding for improved fiber properties. Consequently, further progress in improving fiber properties in populations derived from crossing current Pee Dee germplasm will

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Abbreviations: E_l, fiber elongation; MIC, micronaire; SL, span length; T_l, fiber strength; UR, fiber length uniformity ratio; YS, yarn strength.

depend on the presence of genetic variation or, if necessary, the introduction of new sources of genetic variation. The maintenance of genetic variation for fiber properties in the Pee Dee germplasm is of interest to cotton breeders across the upland belt of the U.S.A. because Pee Dee germplasm has been a source of high fiber quality in many breeding programs (Culp, 1992).

Most studies on the inheritance of fiber traits in cotton have found additive variance or effects to be more important than nonadditive variance in the control of key fiber traits such as fiber length and fiber strength (Miller and Marani, 1963; Ramey and Miller, 1966; Lee et al., 1967; Verhalen and Murray, 1967; Al-Rawi and Kohel, 1969; Meredith and Bridge, 1972; Baker and Verhalen, 1973; Quisenberry, 1975). Thus, pedigree selection schemes have been successful in producing cottons with longer and stronger fiber (Culp, 1982). With the exception of Green and Culp (1990), studies on the nature of genetic control of fiber properties in the Pee Dee germplasm are lacking. In that study, a diallel analysis indicated predominance of general combining ability effects for 2.5% span length (SL), fiber length uniformity ratio (UR), fiber elongation (E_1), and yarn strength (YS). Parents used in the diallel, however, represent the success of past cycles of selection to improve fiber and yarn traits. Knowledge of heritability and magnitude and type of genetic variance controlling fiber traits in current populations would allow a breeder to choose an effective selection scheme when utilizing Pee Dee germplasm.

We conducted this study to (i) estimate genetic variance and heritability of fiber properties in populations derived from elite Pee Dee lines and (ii) determine effect of selection for fiber strength on YS.

MATERIALS AND METHODS

A Design II mating (Comstock and Robinson, 1948) involving eight F_6 Pee Dee germplasm lines was completed in 1987. The eight Pee Dee lines were randomly chosen from a set of 52 elite F_6 Pee Dee lines that were potential parents for a hybridization and selection program to improve fiber properties. The 52 F_6 lines were developed by T.W. Culp from single crosses made in 1981 between commercial cultivars and Pee Dee germplasm lines. Because Pee Dee germplasm has been used in some commercial breeding programs as a source of high fiber quality (Culp, 1992) and the Pee Dee parents of the eight F_6 lines are the result of years of breeding for fiber properties, there may be some degree of relationship among the parents used in the Design II. The objective of this study, however, was to determine whether further progress in improving fiber properties can be made in populations derived from crossing lines that are the result of a long-term program to continually improve fiber properties. The eight lines were randomly allocated to two groups such that four were used as male parents and four as female parents. Subsequently, each male parent was mated to the four females to yield 16 crosses. Following harvest of F_1 seed in 1987, the F_1 was self-pollinated at a winter nursery. The F_2 and F_3 generations of the Design II were evaluated as population bulks for fiber properties at the Pee Dee Research and Education Center at Florence, SC. The F_2 generation was grown in 1988 in a randomized complete-block design with four replications. Each plot was a single row, 10.6 m long with 96 cm spacing between plots. Plots were thinned to two plants per 0.3 m at the two-leaf stage, resulting in approximately 70 plants per plot. Fiber properties were measured on 10 randomly selected plants per plot for a total of 640 observations (10 plants plot^{-1} × 4 reps cross^{-1} × 16 crosses). To represent the F_3 generation, seed from each of the 10 randomly selected F_2 plants was planted in 1989 as a progeny row, generating a total of 640 F_3 rows. The 640 F_3 progeny rows were grown in a replications-in-sets experimental design with 10 replications and four sets. The F_3 progeny rows were not replicated per se because replication is with respect to a Design II cross. Each replication in each set consisted of 16 F_3 progeny rows, with each row representing one of the 16 Design II crosses. Consequently, each set consisted of 160 F_3 progeny rows. Plots consisted of two rows, 10.6 m long with 96-cm row spacing and were thinned to two plants per 0.3 m as previously described. A sample of 25 unweathered open bolls in each F_3 plot was picked from the middle of the plants fruiting zone for fiber testing. Herbicide damage resulted in the loss of 21 F_3 rows in 1989, and thus, fiber properties were measured on 619 F_3 progeny rows. Fiber properties were measured by Starlab, Knoxville, TN, as follows: (i) 50% SL = length (millimeters) at which 50% of the fibers are this length or longer; (ii) 2.5% SL = length (millimeters) at which 2.5% of the fibers are this length or longer; (iii) UR determined as the ratio of 50 and 2.5% SL expressed as a percentage; (iv) fiber strength (T_1) as force (kiloNewton meter per kilogram) necessary to break the fiber bundle with the jaws of the testing instrument (Stelometer) set 3.2 mm apart; (v) E_1 = the percentage elongation at the break of the center 3.2 mm of the fiber bundle measured for T_1 on the Stelometer; (vi) micronaire reading (MIC) = fineness of the fiber measured by the Micronaire and expressed in standard micronaire units.

To assess the effect of selection for T_1 on YS, fiber and yarn properties were determined on bulk F_4 progeny rows selected and unselected for T_1. The selected population was composed of F_4 progeny of the 10% of F_3 lines with highest T_1, giving a population size of 62 F_4 entries (10% of 619). The expense of YS measurement precluded obtaining YS on the remaining F_4 progeny of F_3 lines unselected for T_1. Consequently, the unselected population was represented by 322 F_4 rows, which when combined with the 62 F_4 entries in the selected population, resulted in six F_4 lines per cross per set in 1990. Due to field loss, fiber and yarn properties could be measured on only 283 rows of the unselected population. The selected and unselected F_4 lines from each cross were randomized together in a replications-in-sets experimental design with four sets and six replications. As in the F_3 experiment, progeny rows were not replicated and replication refers to a progeny row being an observation on a Design II cross. Plot size, number of plants per plot, and boll sampling for fiber analysis were indentical to that of the F_3. Fiber properties were measured as previously described. Additionally, YS as force (kiloNewton meter per kilogram) required to break a skein of 27 tex yarn in small-scale, ring-spun tests as described by Landstreet et al. (1959, 1962) was measured on all F_4 progeny.

Standard cultural practices and production recommendations of the Clemson University Cooperative Extension Service were followed for all experiments.

Mating design variance components were calculated for fiber properties in the F_2, F_3, and F_4 generations. In the F_2, eight missing observations were replaced with their least-squares estimate and an analysis of variance (ANOVA) was performed as though the data were balanced. Eight df were subtracted from the within-plot df, and the mean square was recomputed. Subsequently, the experimental error variance was also recomputed. Too many missing observations (21) existed in the F_3

data to replace missing observations with least-squares estimates without causing an upward bias in mating design variances. Mating design variances in the F_3 were thus estimated from unweighted Design II cross means calculated with replications in each set for the 16 crosses. The result was 16 data points in each set, with each data point representing one of the 16 Design II crosses. A similar procedure was employed in the F_4, but then cross means were calculated only using unselected lines in Sets 1 to 3 because Set 4 was comprised mainly of F_4 progeny of F_3 parents selected for T_1. This procedure in the F_3 and F_4 generations resulted in balanced data for a Design II ANOVA, alleviating problems in calculating mating design variances from mean squares with unequal null expectation.

Mating design variances were expressed in terms of genetic components of variance in a genetic model limited to additive (σ^2_a), dominance (σ^2_d), and digenic additive epistatic variance (σ^2_{aa}). Mating design variances from the F_2, F_3, and F_4 generations of the Design II were then resolved into estimates of genetic variance after Stuber (1970). Although the F_2 generation in a self-pollinated crop is frequently considered to be the S_0 despite an inbreeding coefficient of 0.5 (Hallauer and Miranda, 1981), we chose to be consistent with the notation of Stuber (1970) and thus the F_2, F_3, and F_4 generations were defined as the S_1, S_2, and S_3 generations, respectively. Defining the F_2 to be either the S_0 or S_1 generation only affects the magnitude of dominance genetic variance resolved from the male × female variances from two generations of Design II progeny differing in level of inbreeding for the following reason. We would multiply 4/3 the difference in male × female variance components between the F_2 and F_3 generations if F_2 is defined as the S_0, but if the F_2 is defined as the S_1 generation, we would multiply 16/3 the difference in male × female variances between the F_2 and F_3 generations (Stuber, 1970). The parents of the Design II crosses were F_6 lines with an inbreeding coefficient of 0.97. In the resolution of design variances into estimates of genetic variance, the parents were treated as though the inbreeding coefficient was 1.0 to facilitate calculation of estimates of genetic variance. The following equations were solved to estimate genetic variances:

$$\begin{aligned}(\text{i})\ \sigma^2_d &= 16/3[\sigma^2_{m\times f}(F_2) - \sigma^2_{m\times f}(F_3)] \\ &= 16/3[1/4\sigma^2_d + 1/2\sigma^2_{aa}] - [1/16\sigma^2_d + 1/2\sigma^2_{aa}] \\ &= 16/3[3/16\sigma^2_d] \text{ and } \sigma^2_d = 64/3[\sigma^2_{m\times f}(F_3) \\ &\quad - \sigma^2_{m\times f}(F_4)] = 64/3[1/16\sigma^2_d + 1/2\sigma^2_{aa}] \\ &\quad - [1/64\sigma^2_d] + 1/2\sigma^2_{aa}] = 64/3[3/64\sigma^2_d] \qquad [1]\end{aligned}$$

$$\begin{aligned}(\text{ii})\ \sigma^2_{aa} &= 2/3[4\sigma^2_{m\times f}(F_3) - \sigma^2_{m\times f}(F_2)] \\ &= 2/3[1/4\sigma^2_d + 2\sigma^2_{aa}] - [1/4\sigma^2_d + 1/2\sigma^2_{aa}] \\ &= 2/3[3/2\sigma^2_{aa}] \text{ and } \sigma^2_{aa} = 2/3[4\sigma^2_{m\times f}(F_4) \\ &\quad - \sigma^2_{m\times f}(F_3)] = [1/16\sigma^2_d + 2\sigma^2_{aa}] \\ &\quad - [1/16\sigma^2_d + 1/2\sigma^2_{aa}] = 2/3[3/2\sigma^2_{aa}] \qquad [2]\end{aligned}$$

Estimates of one or both of the male and female variances were negative for most of the fiber properties in the F_2 and F_4 generations, and thus, variances from the F_3 were used to calculate σ^2_a. In our genetic model, male and female variance components each estimate $1/2\sigma^2_a + 1/4\sigma^2_{aa}$, and thus, σ^2_a unconfounded with σ^2_{aa} was estimated as $\sigma^2_m + \sigma^2_f - 1/2\sigma^2_{aa}$, using σ^2_{aa} from the F_2 and F_3 generations. If either σ^2_m or σ^2_f was negative, then twice the positive mating design variance was used to calculate σ^2_a. Standard errors were computed for genetic variances from linear combinations of mean squares used to estimate mating design variances.

Heritability on a single-plant basis was estimated as

(i) narrow $h^2 = \sigma^2_a / [\sigma^2_{\text{within plot}} + \sigma^2_{\text{error}} + \sigma^2_{m\times f} + \sigma^2_f + \sigma^2_m]$;
(ii) broad $h^2 = b$ from the regression of F_3 progeny on F_2 parent;
(iii) broad $h^2 = r$ from the correlation between F_3 progeny and F_2 parent (standard unit; Frey and Horner, 1957).

Heritability for a bulk-F_2 population basis was estimated as

(i) narrow $h^2 = \sigma^2_a / [\sigma^2_{\text{within plot}}/rn + \sigma^2_{\text{error}}/r + \sigma^2_{m\times f} + \sigma^2_m + \sigma^2_f]$, where r and n refer to replicates and plants per plot, respectively;
(ii) broad $h^2 = b$ from regression of F_3-bulk mean on F_2-bulk mean;
(iii) broad $h^2 = r$ from the correlation between F_3- and F_2-bulk mean.

Broad sense heritability on an F_3 progeny row basis was computed as

(i) $\sigma^2 F_3$ lines(cross)/[lines(cross) mean square/sets];
(ii) b from regression of F_4 progeny on F_3 parent;
(iii) r from the correlation between F_4 progeny and F_3 parent.

Linear relationships among response variables were evaluated with simple correlation analysis.

RESULTS AND DISCUSSION

At least one significant ($P < 0.05$) mean square for male, female, or the male × female interaction in the F_2, F_3, and F_4 generations of the Design II was evidence for significant genetic variation for all of the fiber properties (Table 1). Genetic variation composed of additive or additive × additive types of epistasis would be necessary to make further improvements in fiber properties. With the exception of E_1, one or both main effect mean squares was less than the male × female mean square, suggesting the presence of dominance or epistatic genetic variance. Because three generations of the Design II progeny differing in level of inbreeding were grown in the experiment, we could resolve mating design variances into separate estimates of σ^2_a, σ^2_d, and σ^2_{aa} (Stuber, 1970). For all of the fiber traits, the magnitude of σ^2_d was greater than fixable genetic variance ($\sigma^2_a + \sigma^2_{aa}$), although for each fiber trait, some σ^2_a and/or σ^2_{aa} was detected (Table 2). This was true in both the F_3-F_2 and F_4-F_3 (data not shown) resolutions of mating variances into estimates of σ^2_a, σ^2_d, and σ^2_{aa} and whether or not the F_2 was defined as the S_0 or S_1 generation. Standard errors computed from linear functions of several mean squares tend to be large, and thus with the exception of E_1, estimates of σ^2_a and σ^2_{aa} were smaller than their standard errors (Table 2). The fact that additive genetic variance was less than dominance variance for key fiber traits, such as SL and T_1, conflicts with reports that they are mainly under the control of additive genetic variance (Miller and Marani, 1963; Ramey and Miller, 1966; Lee et al., 1967; Verhalen and Murray, 1967; Al-Rawi and Kohel, 1969; Meredith and Bridge, 1972; Quisenberry, 1975). However, it is possible that fixable genetic variance has been reduced in populations derived from germplasm that is the result of a long-term selection program.

Table 1. Mean squares for cotton fiber properties measured on the F_2, F_3, and F_4 generations of a Design II at Florence, SC, in 1988, 1989, and 1990, respectively.

Source	df	Fiber properties†					
		T_1	2.5%SL	50%SL	UR	E_1	MIC
		F_2 generation mean square					
Male	3	4.3	0.038	0.0019	0.0030	14.05	1.47
Female	3	14.7	0.008	0.0089	0.0133*	11.07	4.34
Male × female	9	23.9**	0.042**	0.0049**	0.0026**	8.56**	1.65**
Error	45	6.5	0.005	0.0015	0.0003	2.04	0.36
Within plot	568	3.0	0.004	0.0008	0.0002	0.73	0.20
		F_3 generation mean square					
Male	3	1.09	0.0011	0.00003	0.00019	0.21	0.063
Female	3	0.54	0.0020	0.00046*	0.00009	0.25	0.016
Male × female	9	0.42*	0.0010**	0.00011*	0.00012**	0.09	0.054**
Error	45	0.16	0.0001	0.00005	0.00002	0.05	0.006
		F_4 generation mean square					
Male	3	0.34	0.0002	0.00001	0.00003	0.07	0.022
Female	3	0.34	0.0009	0.00022**	0.00001	0.17**	0.019
Male × female	9	0.36	0.0004**	0.00008	0.00004	0.02	0.020**
Error	30	0.23	0.0001	0.00005	0.00002	0.04	0.008

*, ** Significant at $P < 0.05$ and 0.01, respectively.
† T_1, fiber strength; SL, span length; UR, fiber length uniformity ratio; E_1, fiber elongation; and MIC, micronaire.

In resolving mating design variances into estimates of genetic variance, we limited the genetic model to σ_a^2, σ_d^2, and σ_{aa}^2, and consequently, our estimates of genetic variance could be confounded with higher order dominance or additive epistasis. However, we estimate this bias to be relatively unimportant in the estimation of the relative ratio of fixable to nonfixable genetic variance for the following reason. Our estimate of σ_a^2 is confounded only with additive types of epistasis; σ_{aa}^2 is confounded with higher order additive epistasis and only a small amount of epistasis involving dominance, and σ_d^2 is confounded with only nonfixable types of epistasis involving dominance and the interaction of additive and dominance (data not shown). The usual assumption employed in two-factor mating designs to resolve mating design variance components into estimates of genetic variance is that epistasis is negligible. Thus, the male × female variance estimates only dominance variance. However, for traits in which additive types of epistasis are important, the assumption of no epistasis would underestimate the relative ratio of fixable to nonfixable genetic variance. In this study, σ_{aa}^2 contributed to the expression of UR, MIC, and 2.5% SL. An additional bias in the estimates of genetic variance could come from interactions of genotypes, years, and locations because generations were evaluated in a single environment. In contrast to quantitative traits such as yield, variance due to genotype × environment interaction has been found to be small relative to genetic variance for most of the fiber properties, with the occasional exception of MIC (Al-Jibouri et al., 1958; Miller et al., 1958, 1962; Lee et al., 1967; Abou-El-Fittouh et al., 1969; Bridge et al., 1969; Murray and Verhalen, 1969; Meredith et al., 1970; Meredith and Bridge, 1972).

In addition to estimates of genetic variance, a breeder requires estimates of heritability to choose an effective population advance scheme. A common population advance in self-pollinated crops is a pedigree system beginning with F_2 plant selection followed by F_3 progeny row evaluation. Little progress from F_2 plant selection to improve fiber properties in these elite Pee Dee populations would be expected because narrow-sense heritabilities were low (Table 3). Among the 10% of F_3 progeny rows with highest T_1 (62 lines), only 15 were progeny of F_2 plants with highest T_1. We obtained similar results for the other fiber traits (data not shown). We did find significant estimates of F_2 plant and F_3 progeny row heritability from parent–offspring regression and standard unit methods for all of the fiber properties. However, the parent–offspring and standard unit heritabilities may reflect nonadditive variance because the covariance between parent–offspring under self-pollination can include dominance variance and dominance types of epistatic genetic variance.

A breeder must choose a population advance scheme that will yield progress from selection yet operate within

Table 2. Estimates of additive (σ_a^2), dominance (σ_d^2), and additive × additive epistasis (σ_{aa}^2), and their standard errors, for fiber properties resolved from the F_2 and F_3 generations of a Design II, grown at Florence, SC, in 1988 and 1989, respectively.

Trait†	σ_a^2	σ_d^2	σ_{aa}^2
T_1	0.04934 ± 0.05441	1.969850 ± 1.39266	–
2.5%SL	0.00005 ± 0.00126	0.003680 ± 0.002807	0.000015 ± 0.000458
50%SL	0.00002 ± 0.00005	0.000382 ± 0.000246	–
UR	–	0.000155 ± 0.000158	0.000036 ± 0.000035
E_1	0.01740 ± 0.01326	0.814528 ± 0.492932	–
MIC	–	0.107452 ± 0.099036	0.010533 ± 0.019332

† T_1, fiber strength; SL, span length; UR, fiber length uniformity ratio; E_1, fiber elongation; and MIC, micronaire.

Table 3. Heritability estimates for fiber properties resolved from the F_2 and F_3 generations of elite Pee Dee cotton populations grown at Florence, SC, in 1988 and 1989, respectively.

Selection unit	Method‡	Trait†					
		T_1	2.5%SL	50%SL	UR	E_1	MIC
F_2 plant	variance	0	0	0.05	0.01	0.07	0.13
	F_3-F_2 β	0.17**	0.26**	0.10	0.30**	0.25**	0.27**
	Std. unit	0.27**	0.48**	0.14**	0.38**	0.36**	0.49**
F_2 bulk	variance	0	0	0.28	0.51	0.19	0.45
	F_3-F_2 β	0.37**	0.48**	0.03	0.29	0.29*	0.39**
	Std. unit	0.64**	0.77**	0.07	0.61**	0.77**	0.82**
F_3 row	variance	0	0.01	0.06	0.19	0.03	0.17
	F_4-F_3 β	0.17**	0.41**	0.08	0.14*	0.14**	0.40**
	Std. unit	0.15**	0.54**	0.10	0.17*	0.21**	0.53**

*, ** Significant at $P < 0.05$ and 0.01, respectively.
† T_1, fiber strength; SL, span length; UR, fiber length uniformity ratio; E_1, fiber elongation; and MIC, micronaire.
‡ variance, variance component; F_3-F_2 β, regression; Std. unit, standard unit.

the confines of available resources. Single-plant selection in cotton in a pedigree system is labor intensive, and there is also a limit to the number of fiber samples that can be tested. Selecting F_2 bulks to advance to F_3 based on replicated yield and fiber testing is an attractive scheme in that many crosses can be evaluated. Also, labor and fiber-testing costs of single-plant selection can be reduced by one generation and concentrated on fewer populations. An additional consideration in conducting a cycle of bulk selection is that when dominance genetic variance predominates, it would be reduced by a generation of selfing prior to the initiation of single-plant selection. Most cotton breeding programs have access to a relatively cost-efficient winter nursery from which sufficient F_2 seed can be generated to allow F_2 populations to be evaluated in replicated tests. In this study, heritability estimates for selection of F_2 bulks for 50% SL, UR, E_1, and MIC were considerably higher than those for single F_2 plants suggesting that bulk selection would be profitable (Table 3). We recognize, however, that the extent to which the F_2 mean will be indicative of succeeding generation performance would be reduced if little fixable genetic variance is involved in the expression of fiber traits and genotype × environment interactions are large.

Fiber strength is a key trait to cotton geneticists seeking to improve YS. Yarn strength is expensive to measure, currently $28.50 per sample, and is thus not measured on early generation breeding material because of the number of genotypes that must be screened. Rather, indirect selection for YS occurs through selection for high T_1. Although we found single-plant selection to improve T_1 to be ineffective, F_2 bulk selection may be an alternative. Crosses 9 and 15 were ranked 1 and 2, respectively, for T_1 in both the F_2 and F_3 (Table 4). These two crosses also contained 17 of the 62 F_3 lines with highest T_1. Crosses with low F_2 and F_3 means for

Table 4. Cross mean and rank for fiber strength (T_1) of 16 F_2 and F_3 elite Pee Dee cotton crosses evaluated in 1988 and 1989, respectively, and number of F_4 lines with highest yarn strength (YS) that were progeny of F_3 lines selected (Sel) and unselected (Unsel) for highest T_1 evaluated in 1990 at Florence, SC.

Cross	F2		F3		Top 10% F3 highest T_1	Top 10% F4 highest YS†	
	Mean	Rank	Mean	Rank		Sel	Unsel
	kN m kg^{-1}		kN m kg^{-1}		No.‡	No.	
9	223.5	1	207.3	1	9	6	5
15	223.4	2	206.5	2	8	3	3
6	222.9	3	200.9	10	2	0	3
4	221.1	4	199.2	12t§	3	1	1
8	220.5	5	202.8	5	2	2	0
3	218.3	6	199.6	11	2	2	2
5	218.2	7	201.9	6	4	0	0
1	216.9	8	205.4	3	6	1	2
14	214.7	9	201.8	7	3	2	2
16	212.6	10	201.6	8	1	1	6
10	211.9	11	198.9	13	4	3	4
13	209.5	12t	205.1	4	4	4	3
7	209.5	12t	195.7	14	2	0	0
2	208.9	13	201.3	9	5	0	1
12	206.6	14	199.2	12t§	5	1	2
11	200.9	15	192.9	15	2	0	2
LSD0.05	11.4		5.7			Total 26	36

† Number of F_4 lines in highest 10% for YS that are progeny of F_3 lines selected and unselected for T_1, respectively.
‡ Number of F_3 lines in each cross in the 10% of F3 lines with highest T_1.
§ t, tied for Rank 12.

T_1 (Crosses 2 and 12) contained 10 of the F_3 lines with highest T_1. We acknowledge that bulk selection would entail loss of low-frequency desirable segregates in crosses with a low mean.

One disadvantage of bulk selection is that the decision to keep or discard a population is based on a test conducted at one location and one year. Consequently, changes in rank could reduce progress from selection. Although previous studies indicate little genotype × environment interaction for most fiber properties (Miller et al., 1962; Lee et al., 1967; Meredith and Bridge, 1972), we observed changes in rank for T_1 cross means between the F_2 and F_3 generations (Table 4). For example, Crosses 6 and 4 were ranked 3 and 4, respectively, in the F_2 but 10 and 12, respectively, in the F_3. We suggest a low selection intensity to address population rank changes. For example, selection of the top 50% of the F_2 bulks would have identified three F_3 populations with highest T_1 and still discarded the populations with lowest T_1. We similarly found that a 50% selection intensity identified at least the top four populations for highest 2.5% SL, 50% SL, UR, and E_1 and discarded most of the poor populations (data not shown).

Selection for yield and fiber properties, primarily high T_1, in early generations of past cycles of intermating and selection in the Pee Dee breeding program resulted in germplasm with superior YS (Culp and Harrell, 1973; Culp et al., 1985; Culp and Green, 1988). In current populations, however, T_1 and YS are not consistently correlated. The correlation between T_1 and YS among the unselected F_4 progeny was only 0.25 ($P < 0.01$; $N = 283$). A wide range in T_1 and YS was observed among the unselected F_4 progeny (data not shown) and thus was likely not related to the low correlation between T_1 and YS. Additional evidence that indirect selection for YS through selection for T_1 is not always effective is that the F_4 line with highest YS was not the offspring of an F_3 row selected for high T_1. Similarly, 36 of the 62 F_4 with highest YS were not offspring of F_3 rows with highest T_1 (Table 4). To obtain genotypes with improved YS, it may be necessary to simultaneously consider several fiber properties. Alternatively, progress in improving YS may necessitate measurement of components of YS not obtained from measurement of T_1, 2.5% SL, 50% SL, UR, E_1, or MIC.

In summary, genetic variation for fiber traits remains in Pee Dee cotton populations despite more than 40 yr of intense selection. Single-plant selection for fiber traits in the F_2 may be hindered by nonadditive genetic variance as well as plant-to-plant environmental variance. Selection of F_2 bulk populations appears to be a viable alternative to initiation of a pedigree generation advance beginning with F_2 plant selection in the improvement of fiber traits. Long-term progress, however, will almost certainly require that new sources of variation for fiber length and strength be introgressed into the Pee Dee germplasm. Lastly, selection for high T_1 does not guarantee progeny with higher YS. Additional fiber characteristics that are reflective of YS may need to be considered in selection for higher YS. Studies that address this problem are currently underway.

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