

ASA, CSSA, and SSSA Virtual Issue Call for Papers: Advancing Resilient Agricultural Systems: Adapting to and Mitigating Climate Change

Content will focus on resilience to climate change in agricultural systems, exploring the latest research investigating strategies to adapt to and mitigate climate change. Innovation and imagination backed by good science, as well as diverse voices and perspectives are encouraged. Where are we now and how can we address those challenges? Abstracts must reflect original research, reviews and analyses, datasets, or issues and perspectives related to objectives in the topics below. Authors are expected to review papers in their subject area that are submitted to this virtual issue.

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Deadlines

Abstract/Proposal Deadline: Ongoing
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Submit your proposal to
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ORIGINAL RESEARCH ARTICLE

Crop Breeding & Genetics

Examining the relationship between agronomic performance and fiber quality in ten cotton breeding populations

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Abstract

Future cotton production systems need improved fiber quality to meet global market demands and provide the textile industry with high-quality fiber. To achieve this, cotton (*Gossypium hirsutum* L.) breeding programs must develop cultivars that overcome the negative relationship between agronomic performance and fiber quality. Since 1935, the USDA-ARS Pee Dee germplasm enhancement program has prioritized improving fiber quality while also maintaining or enhancing agronomic performance. Along with a number of other breeding programs, the Pee Dee program documented that the negative relationship between agronomic performance and fiber quality is most often caused by genetic linkage. Several of these breeding programs have demonstrated that the negative genetic linkage can be overcome. In this study, we test the hypothesis that three Pee Dee germplasm lines previously identified as rare recombinants can generate populations with a decreased negative relationship between agronomic performance and fiber quality. The results suggest that two of the three Pee Dee germplasm lines generate populations with a decreased negative relationship and presumably transmit beneficial allelic combinations for lint percent and fiber quality traits in coupling phase linkage with one another or fixed in offspring.

1 | INTRODUCTION

A long-standing objective for upland cotton (*Gossypium hirsutum* L.) breeding programs has been the simultaneous improvement of agronomic performance and fiber quality. This has continued to be a major breeding objective to meet global market demands while also providing the textile industry with higher quality fiber to improve yarn manufacturing efficiency. Unfortunately, the simultaneous improvement of agronomic performance and fiber quality has been slow and difficult, because a negative relationship very often exists between yield and fiber quality (Campbell & Myers, 2015).

Studies have documented this negative relationship in a variety of breeding programs, and although pleiotropy has not been completely ruled out in all cases, the most frequent explanation suggests that genetic linkage is responsible for the negative relationship (Campbell et al., 2011; Clement, Constable, Stiller, & Liu, 2012; Culp, Harrell, & Kerr, 1979; Meredith & Bridge, 1971).

Rather than solely evaluating lint yield when assessing the relationship, a number of studies have evaluated the associations between fiber quality parameters and lint yield component traits. Smith and Coyle (1997) advocated for a more in-depth analysis of the yield–fiber quality relationship by focusing on associations of within-boll yield components such as boll weight, lint percentage, seeds per boll, seed surface area per seed, seed cotton per seed, lint cotton per

Abbreviations: HVI, High Volume Instrument; PDREC, Pee Dee Research and Education Center

seed, fibers per seed, and fibers per seed surface area. Studies using various yield component traits minimize the confounding effects of the components of yield that are often unaccounted for in studies examining the relationships between lint yield and fiber quality. In general, the number of bolls per m² and lint percentage are considered to be the yield component traits most associated with lint yield (Worley, Culp, & Harrell, 1974; Meredith, 1984), and a number of studies have documented that improvement in both yield components resulted in increased lint yield over time (Campbell et al., 2011; Campbell, Boykin, Meredith, & Abdo, 2014; Lui, Constable, Reid, Stiller, & Cullis, 2013). However, it is widely documented that a strong, negative relationship generally exists between lint percentage and fiber quality parameters such as fiber strength and length (Campbell et al., 2012; Miller & Rawlings, 1967; Zeng, Meredith, Boykin, & Taliercio, 2007; Zeng & Meredith, 2009).

Campbell et al. (2012), Culp et al. (1979), Meredith and Bridge (1971), and Clement et al. (2012) documented that the negative relationship between agronomic performance and fiber quality can be overcome through intensive recombination-based plant breeding methods that generate rare recombinant progeny with high yield and high fiber quality. Meredith and Bridge (1971) and Culp et al. (1979) recommended using repeated backcrossing and/or repeated intermating as methods to break up negative linkages. Clement et al. (2012), Clement, Constable, Stiller, and Liu (2015); and Koebernick, Liu, Constable, and Stiller, 2019 outlined several key considerations for breeding programs that focus on overcoming the negative relationship between agronomic performance and fiber quality. These included parental line selection, having an adequate population size to identify rare recombinants, and early generation selection strategies. The parental line strategy noted the importance of using parents with high per se values and good combining ability for lint yield and fiber quality (Koebernick et al., 2019). Similar to the recommendations of Clement et al. (2012), Culp et al. (1979) promoted recurrent selection with large population sizes as a way to identify rare recombinants. Early generation strategies evaluate large population sizes and implement the selection of single plants on the basis of lint percentage (high heritability compared with lint yield) and a fiber quality index, followed by replicated testing with emphasis on lint yield and fiber quality potential (Clement et al., 2015). This strategy promotes increased efficiency by allocating more resources in early generations to improve the mean of breeding material evaluated in costly, replicated multienvironment trials.

The Pee Dee cotton germplasm enhancement program adopted the repeated intermating strategy described by Culp et al. (1979) over more than 70 years of intensive plant breeding. Culp et al. (1979) demonstrated that the negative linkage between yield and fiber quality could be overcome; later, Campbell et al. (2012) determined that the negative rela-

Core Ideas

- Two of 3 Pee Dee genotypes transmit beneficial alleles for lint % and fiber quality
- The negative relationship between lint percentage and fiber quality often persists
- Large populations are needed to identify high lint % and fiber quality offspring

tionship lessened within the Pee Dee germplasm enhancement program over eight breeding cycles. Moreover, Campbell et al. (2012) identified a number of Pee Dee germplasm lines as rare, recombinant genotypes that can overcome the negative relationship between lint percentage and fiber quality.

In this study, we test the hypothesis that Pee Dee germplasm lines previously identified as rare recombinants can generate populations with a decreased negative relationship between agronomic performance and fiber quality. This hypothesis assumes that the rare recombinant Pee Dee genotypes contain beneficial combinations of alleles for agronomic performance and fiber quality that can be inherited together in offspring. Hence, in this study, our objective was to evaluate the agronomic performance and fiber quality of a number of different breeding populations derived with and among several Pee Dee germplasm lines in successive early generations.

2 | MATERIALS AND METHODS

2.1 | Population development

Three Pee Dee germplasm lines, previously identified as rare, high lint percentage, and fiber quality recombinants, were used as parents in this study (Campbell et al., 2012). These included 'PD 2164' (PI 529617), 'PD 7723' (PI 533652), and 'PD 94042' (PI 603219). PD 2164 (Culp & Harrell, 1980), PD 7723 (Culp, Green, & Kittrell, 1990), and PD 94042 (May, 1999) were released from the USDA-ARS Pee Dee cotton breeding program as high-yield and high-quality germplasm lines. Two additional genotypes were included in this study to serve as a high-yield–high-quality check and a high-yield–low-quality check: 'UA48' (PI 660508) as the high yield–high quality check and 'SG 747' (PI 656375) as the high yield–low quality check. UA48 is a cultivar released by the University of Arkansas and displays a rare combination of high yield potential and exceptional fiber quality (Bourland & Jones, 2012). SG 747 (PVP 9800118) is a cultivar released by Sure-Grow Seed (Centre, AL) and was included as a high-yield–low fiber quality check.

TABLE 1 A description of the 10 populations evaluated in this study

Population	Pedigree	Type	F ₂ population size	F _{2:3} population size
1	PD 2164 × PD 7723	Pee Dee × Pee Dee	268	120
2	PD 2164 × PD 94042	Pee Dee × Pee Dee	235	120
3	PD 7723 × PD 94042	Pee Dee × Pee Dee	189	120
4	PD 2164 × UA 48	Pee Dee × Good	237	120
5	PD 7723 × UA 48	Pee Dee × Good	266	120
6	PD 94042 × UA 48	Pee Dee × Good	257	120
7	PD 7723 × SG 747	Pee Dee × Poor	244	120
8	PD 94042 × SG 747	Pee Dee × Poor	243	120
9	PD 2164 × SG 747	Pee Dee × Poor	252	120
10	UA 48 × SG 747	Good × Poor	251	120

In 2014, the three Pee Dee genotypes (PD 2164, PD 7723, and PD 94042) were intermated and each was crossed to UA48 and SG 747 to develop nine populations. UA48 and SG 747 were crossed to develop a reference high-yield–high-quality × high-yield–low-quality population. In addition to the UA48 × SG 747 reference population, this scheme developed three types of populations: (a) Pee Dee × Pee Dee, (b) Pee Dee × Good Quality, and (c) Pee Dee × Poor Quality (Table 1). The 10 crosses were made in a field at the Clemson University Pee Dee Research and Education Center (Clemson PDREC) in Florence, SC. The F₁ seed was harvested and space planted at the Clemson PDREC during 2015. Individual F₁ plants were self-pollinated to produce F₂ seed.

2.2 | Field evaluations

In 2016, four-row plots of F₂ seed for each of the 10 populations were planted on 25 May 2016 at the Clemson PDREC with a cone planter. Rows were 30.5 m long with 96-cm row spacing. After emergence, the four-row plots were thinned to a density of one plant 30.5 cm⁻¹ for a total of 400 plants. Fertilization, weed control, insect control, and defoliation measures were managed following established local practices. Supplemental irrigation was applied with a surface drip irrigation system at a rate of 25.4 mm h⁻¹. Water was applied as needed beginning the week of first flower throughout the entire flowering period.

Plots were defoliated when the bolls were 80% open on 26 Sept. 2016. Because of the forecast of Hurricane Matthew, on 3–4 October, individual F₂ plants were excised from the field and stored in a warehouse. Individual plants were bulk harvested by hand within 3 weeks after removal from the field. All samples 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. A portion of the lint sample was sent to the Cotton Incorporated Fiber Testing Laboratory

(Cary, NC) for determination of the High Volume Instrument (HVI) fiber properties (Uster Technologies, Knoxville, TN). The fiber properties measured included upper half mean fiber length, micronaire, fiber strength, and uniformity. Two fiber quality indices were calculated based on a weighted average of HVI fiber properties following the procedure described by Bourland, Hogan, Jones, and Barnes (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%).

After delinting individual F₂ plant seed for each population, 120 F₂ plants with sufficient seed supplies were advanced for F_{2:3} field evaluations. For each of the 10 populations, the 120 F_{2:3} lines were evaluated in a two-replicate randomized complete block field design. Because of the large volume of total plots (2,400), five of the populations were evaluated at the Clemson PDREC in 2017 and the remaining five in 2018. Hence, Populations 1 to 5 were evaluated in 2017 and 6 to 10 in 2018. In all trials, plots consisted of two rows 6.1 m long with 96-cm row spacing. Trial management followed the established local production practices for rainfed cotton production in both years. In 2017 and 2018, trials were planted on 15 and 14 May, respectively.

After defoliation, a 25-boll sample was hand-harvested (16 Oct. 2017 and 15 Oct. 2018) from each plot to determine yield components and fiber quality properties. Boll weight was determined by dividing the 25-boll sample by 25. All samples from both years 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. The seed index was measured by recording the mass of 100 fuzzy seeds. A portion of the lint sample was sent to the Cotton Incorporated Fiber Testing Laboratory (Cary, NC) for determination of HVI fiber properties. The fiber properties measured included upper half mean fiber length, micronaire, fiber strength, and uniformity. Two quality indices, as described above, were calculated from

HVI fiber properties. Additional yield components, including lint index, fibers per seed, seeds per boll, and fiber density, were calculated according to Clement, Constable, and Walford (2014).

2.3 | Data analysis

For each of the 10 F_2 and $F_{2:3}$ populations, phenotypic data were analyzed via the PROC UNIVARIATE and PROC CORR modules of SAS version 9.2 (SAS, 2008). PROC UNIVARIATE was used to test for normality and estimate the mean and standard deviation for each population. In addition, 95% confidence intervals were estimated for each trait in each population. This allowed for comparisons among the F_2 populations. Differences were declared when the confidence intervals for two F_2 populations were void of any overlap. Since half of the $F_{2:3}$ populations were evaluated in 2016 and the other half in 2017, phenotypic data among the 10 $F_{2:3}$ populations were not compared. Following confirmation of normality, PROC CORR was used to generate Pearson correlation coefficients among yield component and fiber quality traits for both the F_2 and $F_{2:3}$ generations.

For the $F_{2:3}$ phenotypic data, PROC GLM with the RANDOM statement was used to test for significant differences among the 120 entries in each of the 10 trials. Block was considered as a random effect, and genotypes were considered to be fixed effects. In an effort to compare the F_2 and $F_{2:3}$ generations and estimate a response to selection, F_2 parent– $F_{2:3}$ offspring regression heritabilities were estimated for each trait within each population via the approach described by Holland, Nyquist, and Cervantes-Martinez (2003).

On a pairwise basis for lint percentage and fiber quality traits, the mean and standard deviation in each population were used to classify F_2 individuals and $F_{2:3}$ offspring into four trait categories. For example, considering Trait 1 and Trait 2, individuals or offspring were classified as: (a) Category 1: one SD above the mean for both traits (+/+); (b) Category 2: one SD above the mean for Trait 1 and one SD below the mean for Trait 2 (+/-); (c) Category 3: one SD below the mean for Trait 1 and one SD above the mean for Trait 2 (-/+); and (d) Category 4: one SD below the mean for both traits (-/-). Individuals or offspring in Categories 1 (+/+) and 4 (-/-) represented putative recombination products overcoming the negative relationship between lint percentage and fiber quality.

3 | RESULTS

Figure 1 shows the mean and 95% confidence interval for lint percentage, upper half mean, micronaire, uniformity, fiber strength, Quality Score 1, and Quality Score 2 in the F_2 and

$F_{2:3}$ generations. Among the Pee Dee × Pee Dee populations (1–3) in the F_2 generation; Population 2 produced the highest lint percentage, micronaire, and fiber strength. Population 1 produced the highest upper half mean, whereas Population 3 produced the lowest upper half mean and fiber strength. Among the Pee Dee × Good Quality populations (4–6) in the F_2 generation, Population 4 produced the highest lint percentage, whereas Population 6 produced the lowest. Population 6 also produced the highest upper half mean, micronaire, uniformity, and fiber strength. Among the Pee Dee × Poor Quality populations (7–9) in the F_2 generation, Populations 7 and 8 produced the highest lint percentage, upper half mean, micronaire, uniformity, and fiber strength. The UA48 × SG 747 reference population (10) produced a lint percentage lower than Populations 2, 4, 7, and 8 but higher than Populations 1, 3, 5, 6, and 9; an upper half mean and fiber strength less than Population 6 but higher than the remaining populations; a micronaire similar to Populations 2, 3, 6, and 8 but higher than Populations 1, 4, 5, and 7; and a uniformity lower than Populations 6 and 8 but higher than the remaining populations.

Table 2 shows the results of the ANOVA for the 10 $F_{2:3}$ populations. Overall, with the exception of Population 5 and seeds per boll, we identified significant differences for most population–trait combinations. All populations showed significant differences for lint percentage, upper half mean, and micronaire. Nine populations showed significant differences for boll weight, seed index, lint index, fibers per seed, fiber density, fiber strength, Quality Score 1, and Quality Score 2. Eight populations showed a significant difference for uniformity.

In an effort to compare F_2 and $F_{2:3}$ generations and estimate a response to selection, F_2 parent– $F_{2:3}$ offspring regression heritabilities were estimated for each trait within each population (Table 3). With the exception of uniformity, heritabilities were moderate across traits and populations. Population 8 had the lowest heritability across the six traits, as two of the six parent–offspring regressions were not significant. These results suggested that the $F_{2:3}$ population data were generally consistent with individual F_2 plant data. The mean heritability across populations for traits ranged from 0.27 for Quality Score 2 to 0.43 for upper half mean.

To study the relationships among yield component traits in these 10 populations, we examined the correlation of yield component traits with two primary yield components: lint percentage and seed index. Table 4 shows a summary of the correlations among lint percentage, boll weight, seed index, seeds per boll, lint index, fibers per seed, and fiber density. Overall, there were several notable trends in these relationships. Lint percentage was negatively correlated with seed index, seeds per boll, lint index, and fibers per seed. Boll weight was positively correlated with seed index, seeds per boll, lint index, and fibers per seed. Seed index was positively correlated with

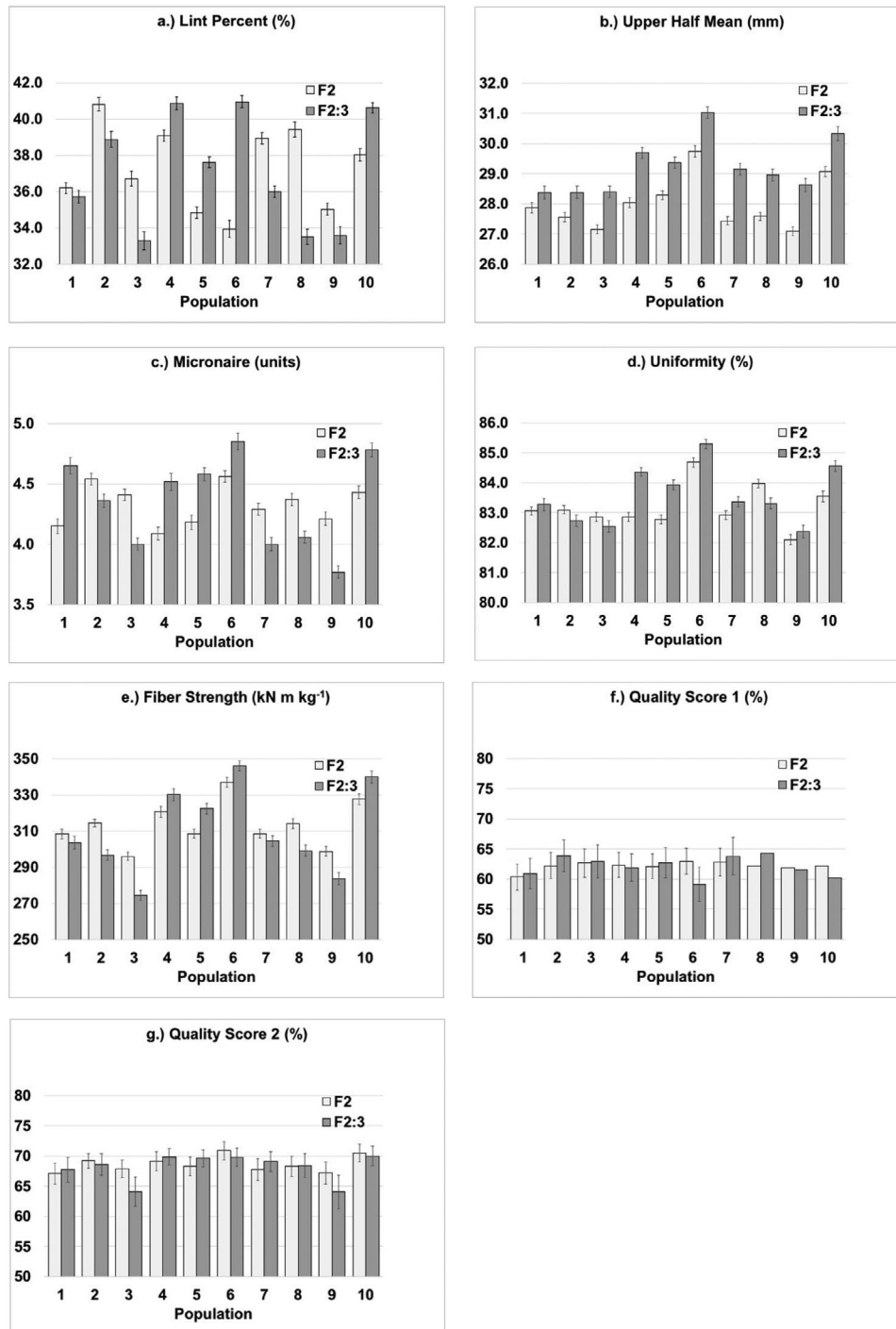


FIGURE 1 Mean values and 95% confidence intervals of F₂ and F_{2:3} generations of 10 populations for (a) lint percentage, (b) upper half mean, (c) micronaire, (d) uniformity, (e) fiber strength, (f) Quality Score 1, and (g) Quality Score 2

the lint index and fibers per seed but negatively correlated with fiber density. Lint index, fibers per seed, and fiber density were positively correlated.

Based on these relationships, the two primary yield components interacting with one another in a negative way were lint percentage and seed index. Increased lint percentage was associated with lower seed size, seed number, lint index, number of fibers per seed, and fiber density. Likewise, larger seed

size was associated with larger bolls, higher lint index, and a greater number of fibers per seed but negatively correlated with lint percentage and fiber density. Lint percentage and seed index were both negatively correlated with fiber density.

Table 5 provides a summary of the relationships of lint percentage and seed index with fiber quality traits. Overall, 4 of the 10 populations (1, 5, 6, and 10) consistently showed negative relationships with lint percentage for upper half mean,

TABLE 2 Tests of significance (*p*-values) within 10 F_{2,3} populations for lint percentage, upper half mean, micronaire, uniformity, fiber strength, Quality Score 1, and Quality Score 2

Population	Lint percentage	Boll weight	Seed index	Seeds per boll	Lint index	Fibers per seed	Fiber density	Upper half mean	Micronaire	Uniformity	Fiber strength	Quality Score 1	Quality Score 2
1	<.0001	<.0001	<.0001	.0509	<.0001	<.0001	<.0001	<.0001	<.0001	.0008	<.0001	<.0001	<.0001
2	.0051	.0037	.0086	.0641	<.0001	<.0001	<.0001	<.0001	<.0001	.0373	.0002	<.0001	.0078
3	.0020	.0159	<.0001	.0008	<.0001	<.0001	<.0001	.0096	.0060	.0387	.6087	.0904	.5210
4	<.0001	.0014	.0081	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	.0018	.0021	<.0001	.0018
5	.0083	.0825	.7808	.5198	.4163	.8323	.7839	.0049	.0382	.2188	.0176	.0342	.1606
6	<.0001	<.0001	<.0001	<.0001	.0017	<.0001	<.0001	<.0001	.0113	.0110	<.0001	<.0001	.0004
7	.0044	.0071	<.0001	.3873	.0002	<.0001	.0001	<.0001	<.0001	.2683	<.0001	.0053	.0788
8	.0472	.1012	<.0001	.9217	<.0001	<.0001	<.0001	<.0001	<.0001	.0332	<.0001	<.0001	.0033
9	<.0001	.0316	.0013	.0067	<.0001	<.0001	<.0001	<.0001	<.0001	.0010	<.0001	<.0001	.0004
10	<.0001	<.0001	<.0001	.0074	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

TABLE 3 Parent-offspring heritability estimates for lint percentage, upper half mean, micronaire, uniformity, fiber strength, Quality Score 1, and Quality Score 2 for 10 F₂ and F_{2,3} populations

Population	Lint percentage	Upper half mean	Micronaire	Uniformity	Fiber strength	Quality Score 1	Quality Score 2
1	0.43 ± 0.06	0.51 ± 0.05	0.54 ± 0.07	0.21 ± 0.05	0.52 ± 0.06	0.34 ± 0.05	0.25 ± 0.06
2	0.30 ± 0.07	0.62 ± 0.06	0.54 ± 0.07	0.26 ± 0.06	0.42 ± 0.06	0.66 ± 0.06	0.41 ± 0.06
3	0.44 ± 0.06	0.42 ± 0.06	0.45 ± 0.08	NS	0.31 ± 0.07	0.32 ± 0.07	0.12 ± 0.05
4	0.42 ± 0.08	0.56 ± 0.07	0.31 ± 0.07	0.47 ± 0.10	0.33 ± 0.08	0.50 ± 0.07	0.52 ± 0.09
5	0.19 ± 0.08	0.25 ± 0.07	NS ^a	NS	0.16 ± 0.06	0.27 ± 0.07	0.15 ± 0.08
6	-0.11 ± 0.12	0.54 ± 0.07	0.14 ± 0.05	NS	0.48 ± 0.08	0.39 ± 0.06	0.28 ± 0.07
7	0.28 ± 0.07	0.18 ± 0.06	0.30 ± 0.08	NS	0.19 ± 0.07	0.17 ± 0.07	NS
8	0.10 ± 0.06	0.21 ± 0.07	NS	NS	NS	NS	NS
9	0.31 ± 0.05	0.47 ± 0.05	0.51 ± 0.09	0.36 ± 0.07	0.43 ± 0.06	0.41 ± 0.06	0.28 ± 0.05
10	0.79 ± 0.09	0.53 ± 0.05	0.45 ± 0.07	0.15 ± 0.09	0.48 ± 0.08	0.40 ± 0.06	0.18 ± 0.08

^a NS, not significant.

TABLE 4 Pearson phenotypic correlations among lint percentage, boll weight, seed index, seeds per boll, lint index, fibers per seed, and fiber density for 10 F_{2:3} populations

	Population									
	1	2	3	4	5	6	7	8	9	10
					Lint percentage					
Boll weight	-0.08	-0.21**	0.21**	0.17**	0.17**	0.13*	0.06	0.03	0.01	-0.00
Seed index	-0.43**	-0.25**	-0.24**	-0.20**	-0.12	-0.07	-0.17**	0.00	-0.18**	-0.38**
Seeds per boll	0.02	-0.34**	0.06	0.07	0.01	-0.02	-0.07	-0.07	-0.18**	0.04
Lint Index	0.48**	0.71**	0.67**	0.64**	-0.04	0.74**	0.63**	0.63**	0.82**	0.48**
Fibers per seed	0.25**	0.61**	0.56**	0.52**	-0.04	0.49**	0.46**	0.55**	0.71**	0.49**
Fiber density	0.57**	0.75**	0.66**	0.61**	0.03	0.48**	0.62**	0.64**	0.76**	0.72**
					Boll weight					
Seed index	0.54**	0.33**	0.23**	0.48**	0.30**	0.38**	0.45**	0.54**	0.37**	0.61**
Seeds per boll	0.73**	0.72**	0.65**	0.75**	-0.03	0.89**	0.77**	0.71**	0.87**	0.77**
Lint index	0.45**	0.04	0.19**	0.53**	0.21**	0.35**	0.41**	0.51**	0.20**	0.57**
Fibers per seed	0.38**	-0.02	0.17**	0.20**	0.17**	-0.16**	0.24**	0.36**	0.10	0.28**
Fiber density	0.06	-0.18**	0.08	-0.04	0.05	-0.34**	-0.01	0.08	-0.03	-0.11
					Seed index					
Seeds per boll	-0.12	-0.31**	-0.16**	-0.14*	-0.76**	-0.01	-0.17**	-0.10	-0.04	0.03
Lint index	0.56**	0.47**	0.27**	0.61**	0.81**	0.58**	0.64**	0.70**	0.37**	0.62**
Fibers per seed	0.44**	0.31**	0.20**	0.23**	0.70**	0.14*	0.45**	0.51**	0.13*	0.30**
Fiber density	-0.18**	-0.16*	-0.20**	-0.27**	0.40**	-0.36**	-0.07	-0.02	-0.22**	-0.33**
					Seeds per boll					
Lint index	-0.12	-0.55**	-0.05	-0.05	-0.62**	-0.05	-0.18**	-0.11	-0.21**	0.05
Fibers per seed	-0.02	-0.44**	-0.07	-0.13*	-0.62**	-0.36**	-0.20**	-0.13*	-0.17**	-0.07
Fiber density	0.05	-0.31**	0.00	-0.06	-0.47**	-0.34**	-0.14*	-0.09	-0.15*	-0.09
					Lint index					
Fibers per seed	0.66**	0.77**	0.77**	0.62**	0.85**	0.52**	0.73**	0.80**	0.78**	0.72**
Fiber density	0.36**	0.57**	0.66**	0.30**	0.67**	0.19**	0.44**	0.50**	0.64**	0.32**
					Fibers per seed					
Fiber density	0.80**	0.89**	0.92**	0.87**	0.92**	0.87**	0.85**	0.84**	0.94**	0.80**

* Significant at the .05 probability level. ** Significant at the .01 probability level. *** Significant at the .001 probability level.

TABLE 5 Pearson phenotypic correlations for lint percentage, seed index, seeds per boll, lint index, fibers per seed, and fiber density with upper half mean, micronaire, uniformity, fiber strength, Quality Score 1, and Quality Score 2 for 10 $F_{2,3}$ populations

	Population									
	1	2	3	4	5	6	7	8	9	10
	Lint percentage									
Upper half mean	-0.18**	0.01	0.01	-0.10	-0.23**	-0.34**	-0.16**	0.14*	-0.03	-0.13*
Micronaire	0.32**	0.19**	0.37**	0.20**	0.29**	0.52**	0.28**	0.09	0.13*	0.11
Uniformity	-0.10	0.08	0.12	-0.24**	-0.20**	-0.07	0.10	0.18**	0.02	-0.25**
Fiber strength	-0.21**	-0.06	0.13*	0.00	-0.20**	-0.06	-0.05	-0.06	0.01	-0.27**
Quality Score 1	-0.23**	0.05	0.1	-0.12	-0.28**	-0.32**	-0.05	0.18**	0.02	-0.15*
Quality Score 2	-0.22**	0.06	0.17**	-0.18**	-0.27**	-0.19**	0.06	0.14*	0.01	-0.26**
	Seed index									
Upper half mean	0.25**	0.25**	0.39**	0.07	0.15*	0.24**	0.31**	0.30**	0.47**	-0.1
Micronaire	-0.1	0.11	-0.14*	0.36**	0.17**	0.38**	0.08	0.20**	0.07	0.38**
Uniformity	0.32**	0.11	0.26**	0.24**	0.18**	0.27**	0.18**	0.37**	0.20**	0.14*
Fiber strength	0.44**	0.22**	0.21**	0.07	0.16**	0.23**	0.43**	0.45**	0.21**	0.27**
Quality Score 1	0.29**	0.20**	0.37**	0.02	0.13*	0.26**	0.35**	0.33**	0.47**	-0.06
Quality Score 2	0.39**	0.15*	0.31**	0.13*	0.18**	0.32**	0.26**	0.38**	0.27**	0.11

* Significant at the .05 probability level. ** Significant at the .01 probability level. *** Significant at the .001 probability level.

fiber strength, and both quality score indices. Among the Pee Dee \times Pee Dee populations (1–3), Population 1 showed a negative relationship with upper half mean, fiber strength, and both fiber quality indices, whereas Populations 2 and 3 did not show a negative relationship between lint percentage and any of the fiber quality traits. Among the Pee Dee \times Good Quality populations (4–6), each displayed a negative relationship between lint percentage and one or more of the fiber quality traits. Among the Pee Dee \times Poor Quality populations (7–9), Populations 8 and 9 displayed no relationship with lint percentage, whereas Population 7 displayed a negative relationship only between upper half mean and lint percentage. As expected, the UA48 \times SG 747 reference population (10) displayed a negative relationship for upper half mean, uniformity, fiber strength, and both fiber quality scores. Collectively, these results show that Populations 2, 3, 8, and 9 did not maintain a negative relationship between lint percentage and fiber quality.

In contrast to lint percentage, upper half mean, uniformity, fiber strength, and both quality scores showed a positive relationship with seed index for most of the populations. None of the 10 populations showed a negative relationship with seed index for these fiber quality traits. For micronaire, five populations showed a positive relationship with seed index, although one population showed a negative relationship.

Table 6 provides a summary of the relationships of fiber quality traits with seeds per boll, lint index, fibers per seed, and fiber density. Overall, differences in these relationships were not evident among the Pee Dee \times Pee Dee, Pee Dee \times Good Quality, and the Pee Dee \times Poor Quality populations. There was very little evidence of a relationship between seed per boll and fiber quality. For fibers per seed, there was a negative relationship with micronaire across populations, whereas Populations 2, 6, 9, and 10 showed a negative relationship with most of the other fiber quality traits. For fiber density, most of the fiber quality traits were negatively associated, with the exception of Populations 4 and 5, which showed very little relationship between fiber density and fiber quality.

Since our results showed that the primary yield component negatively associated with fiber quality was lint percentage, the mean and standard deviation in each population was used to classify F_2 individuals and $F_{2:3}$ offspring into four pairwise trait categories to represent putative recombination products overcoming the negative relationship between lint percentage and fiber quality (+/+ and -/- categories). Table 7 and Table 8 show the results of this classification for F_2 individuals and $F_{2:3}$ offspring, respectively. Since Populations 2, 3, 8, and 9 did not display a negative relationship between lint percentage and fiber quality traits (Table 5), we expected that more F_2 individuals and $F_{2:3}$ offspring would appear in the high lint percentage and high fiber quality category (+/+). However, according to data from both generations, the number of individuals in this category did not appear to be different from the

other populations (Table 7 and Table 8). It was interesting that no high lint percentage–high fiber quality $F_{2:3}$ offspring were identified in Population 5 for upper half mean, fiber strength, or either quality score. Only one $F_{2:3}$ offspring was detected in both Population 6 and 7 in the high lint percentage and high fiber strength category. This finding illustrates the difficulty in identifying a rare high lint percentage and high fiber quality recombinant for these populations. We detected a single high lint percentage and high fiber quality recombinant in the UA48 \times SG 747 reference population, although more offspring fell into the undesirable high lint percentage and low fiber quality category (+/-).

4 | DISCUSSION

Historically, the negative relationship between lint yield or yield component traits and fiber quality has hindered efforts to develop high-yield and high-quality cultivars. A number of cotton breeding programs, including the USDA-ARS Pee Dee program, have made overcoming the negative relationship between yield and fiber quality a major breeding objective. In this study, we evaluated three types of early-generation breeding populations derived from three high-yield and high-quality Pee Dee germplasm lines, a high-yield and high-quality commercial cultivar developed by the University of Arkansas, and a high-yield and low-quality commercial cultivar (SG 747) to determine the status of the relationship between yield component traits and fiber quality. Each of the three Pee Dee germplasm lines was selected because prior data suggested they each overcame the negative yield–fiber quality relationship.

Among the yield component traits assessed in this study, a correlation analysis indicated that the two predominant yield components interacting with fiber quality were lint percentage and seed index; these two yield components displayed a strong negative relationship with one another. Generally, significant correlations between lint percentage and fiber quality were negative, whereas the significant correlations between seed index and fiber quality were positive. The direction of these relationships is in agreement with previous reports (Campbell et al., 2012; Culp et al., 1979; Meredith & Bridge, 1971; Clement et al., 2012).

Four of the ten populations (1, 5, 6, and 10) displayed negative relationships between lint percentage and fiber quality (Table 5). This included one population in the Pee Dee \times Pee Dee populations, two within the Pee Dee \times Good Quality populations, and the UA48 \times SG 747 reference population. Four of the ten populations (2, 3, 8, and 9) displayed no relationship between lint percentage and fiber quality. These populations included two of the three Pee Dee \times Pee Dee populations and two of the three Pee Dee \times Poor Quality populations. Two of the ten populations (4 and 7) displayed a negative relationship

TABLE 6 Pearson phenotypic correlations for seeds per boll, lint index, fibers per seed, and fiber density with upper half mean, micronaire, uniformity, fiber strength, Quality Score 1, and Quality Score 2 for 10 F_{2,3} populations

	Population									
	1	2	3	4	5	6	7	8	9	10
	Seed per boll									
Upper half mean	-0.04	-0.03	0.10	0.05	-0.15*	-0.07	0.01	-0.06	0.08	-0.12
Micronaire	-0.09	-0.19**	-0.05	0.04	-0.05	0.28**	0.00	0.05	-0.13*	0.21**
Uniformity	-0.10	-0.04	0.07	0.15*	-0.07	0.08	0.06	0.00	0.05	-0.08
Fiber strength	-0.13*	-0.03	0.12	0.15*	-0.12	0.03	-0.04	0.02	0.12	0.01
Quality Score 1	-0.03	-0.02	0.12	0.08	-0.11	-0.04	0.03	-0.07	0.07	-0.13*
Quality Score 2	-0.13*	-0.05	0.12	0.15*	-0.09	0.04	0.04	-0.06	0.08	-0.10
	Lint index									
Upper half mean	0.06	0.19**	0.28**	-0.03	0.16**	-0.13*	0.11	0.32**	0.22**	-0.22**
Micronaire	0.22**	0.27**	0.15*	0.43**	0.14*	0.67**	0.28**	0.25**	0.16*	0.45**
Uniformity	0.21**	0.15*	0.23**	-0.02	0.17**	0.11	0.22**	0.35**	0.13*	-0.09
Fiber strength	0.24**	0.12	0.21**	0.05	0.12	0.10	0.31**	0.25**	0.11	0.02
Quality Score 1	0.05	0.19**	0.31**	-0.09	0.13*	-0.11	0.23**	0.36**	0.26**	-0.20**
Quality Score 2	0.17**	0.16**	0.30**	-0.06	0.17**	0.04	0.26**	0.35**	0.16*	-0.14*
	Fibers per seed									
Upper half mean	-0.08	0.02	0.09	0.03	0.12	-0.35**	0.00	0.09	-0.07	-0.26**
Micronaire	-0.44**	-0.24**	-0.24**	-0.35**	0.06	-0.15*	-0.33**	-0.28**	-0.33**	-0.07
Uniformity	-0.11	-0.15*	-0.08	-0.13*	0.11	-0.30**	-0.05	0.01	-0.17**	-0.30**
Fiber strength	-0.01	-0.19**	0.03	0.13*	0.10	-0.13*	0.13*	0.06	-0.17**	-0.11
Quality Score 1	0.02	-0.01	0.01	0.04	0.10	-0.35**	-0.05	0.03	-0.18**	-0.22**
Quality Score 2	-0.01	-0.16**	-0.01	-0.01	0.12	-0.34**	-0.04	-0.01	-0.22**	-0.27**
	Fiber density									
Upper half mean	-0.25**	-0.11	-0.07	-0.01	0.07	-0.44**	-0.17**	-0.08	-0.22**	-0.19**
Micronaire	-0.41**	-0.30**	-0.18**	-0.52**	-0.02	-0.35**	-0.42**	-0.44**	-0.35**	-0.31**
Uniformity	-0.33**	-0.21**	-0.19**	-0.25**	0.03	-0.41**	-0.17**	-0.22**	-0.23**	-0.39**
Fiber strength	-0.30**	-0.31**	-0.05	0.09	0.05	-0.24**	-0.10	-0.22**	-0.24**	-0.28**
Quality Score 1	-0.17**	-0.12	-0.14*	0.02	0.07	-0.46**	-0.26**	-0.18**	-0.34**	-0.19**
Quality Score 2	-0.27**	-0.24**	-0.13*	-0.08	0.06	-0.48**	-0.19**	-0.26**	-0.32**	-0.34**

* Significant at the .05 probability level. ** Significant at the .01 probability level. *** Significant at the .001 probability level.

TABLE 7 Pairwise classification of individuals greater or less than one standard deviation for lint percentage, upper half mean, and fiber strength within 10 F₂ populations

Population	Lint percentage/Upper half mean				Lint percentage/Fiber strength			
	+/+	+/-	-/+	-/-	+/+	+/-	-/+	-/-
	number of individuals							
1	2	10	11	7	5	5	12	6
2	3	6	5	7	6	3	3	6
3	4	8	4	10	6	5	2	8
4	2	6	6	8	3	6	5	9
5	6	4	6	8	7	6	5	3
6	3	4	3	4	4	7	2	0
7	2	5	10	4	1	9	8	2
8	4	4	3	8	3	6	5	3
9	4	2	5	5	6	7	5	3
10	6	3	4	9	6	10	3	7

TABLE 8 Pairwise classification of progeny rows with greater or less than one standard deviation for lint percentage, upper half mean, and fiber strength within 10 F_{2:3} populations

Population	Lint percentage/upper half mean				Lint percentage/fiber strength			
	+/+	+/-	-/+	-/-	+/+	+/-	-/+	-/-
	number of individuals							
1	2	3	2	1	1	4	4	1
2	1	2	1	0	1	4	2	1
3	1	1	1	1	2	1	1	0
4	1	1	6	0	1	1	3	1
5	0	1	3	0	0	2	0	0
6	0	2	3	2	1	1	3	3
7	0	1	4	0	1	0	2	0
8	1	1	0	0	2	0	1	2
9	2	1	2	4	0	2	1	1
10	1	6	2	3	1	5	0	0

between lint percentage and one or two of the fiber quality traits, although other fiber quality traits showed no relationship with lint percentage. Both populations involved one of the Pee Dee germplasm lines in their pedigree.

These results support the notion that PD 2164 and PD 94042 are rare recombination products that overcome the negative relationship between yield and fiber quality while also having the ability to transmit the phenotypes to their offspring. However, PD 7723 does not follow this trend. It is interesting that both PD 2164 and PD 94042, when crossed to the high lint percentage–low fiber quality check SG 747, generated a population void of a negative relationship between lint percentage and fiber quality. One possible hypothesis to explain these findings suggests that more beneficial allelic combinations for lint percentage and these fiber quality traits are in coupling phase linkage with one another or fixed in offspring derived from PD 2164 and PD 94042. According to this

hypothesis, data involving the UA48 and PD 7723 populations indicate that lint percentage and fiber quality trait allelic combinations in offspring are in repulsion phase linkage, in which the strong negative relationship persists. Although UA48 is a high-yield high-quality cultivar, this finding is consistent with UA48's moderate to low lint percentage, (F. Bourland, personal communication, 8 Jan. 2020). In a previous study evaluating the relationship between yield components and fiber quality, Smith and Coyle (1997) suggested that repulsion phase linkage was the most probable explanation for the negative relationship. Similarly, Constable and Bange (2007) and Clement et al. (2012) concluded that the negative relationship between yield and fiber quality was the result of linkage that could be overcome through repeated recombination opportunities in the resulting offspring.

In conclusion, the data from this study support the key considerations for breeding programs focused on overcom-

ing the negative relationship between agronomic performance and fiber quality proposed by Clement et al. (2012, 2015) and Koebernick et al. (2019). The ability of PD 2164 and PD 94042 to transmit beneficial allele combinations for lint percentage and fiber quality highlight the importance of parental line selection. It should be noted that our F_2 parent and $F_{2:3}$ offspring population distributions indicate that the occurrence of selecting recombinant individuals with both high lint percentage and high fiber quality is extremely low. In the F_2 analysis, the number of high lint percentage and upper half mean individuals ranged from 0.75 to 2.39%, and individuals with a high lint percentage and fiber strength ranged from 0.41 to 3.17%. In the $F_{2:3}$ analysis, the number of offspring with both high lint percentage and upper half mean and offspring with high lint percentage and fiber strength both ranged from 0 to 1.67%. These findings emphasize the importance of evaluating large population sizes to identify these rare recombinants. Fortunately, the moderate parent–offspring heritabilities for the F_2 parent and $F_{2:3}$ offspring populations suggest that early-generation selection for rare recombinants, as suggested by Clement et al. (2015), provides a beneficial way to better focus costly, replicated multi-environment field trials for greater breeding efficiency.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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