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Assessing the breeding potential of day-neutral converted racestock germplasm in the Pee Dee cotton germplasm enhancement program

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Abstract The primitive, upland cotton landrace collection represents one of the untapped genetic resources in cotton breeding programs. Efforts to utilize these resources have been slow, but the development of day-neutral converted germplasm lines offers tremendous potential for broadening the genetic base in upland cotton. Using topcross hybrids involving elite germplasm from the unique Pee Dee germplasm enhancement program, we evaluated the breeding potential of a select number of day-neutral converted racestocks. The mean performance of parental lines and F_2 topcross hybrids along with genetic effect estimates indicate that day-neutral converted germplasm lines decreased agronomic performance while increasing fiber quality performance. Results suggest that crosses between day-neutral converted racestocks and elite Pee Dee germplasm lines result in new allelic combinations associated with improved fiber quality performance that interact in a non-additive way. However, it appears that converted racestocks transmit negatively correlated alleles for agronomic performance and fiber quality. These negatively correlated allelic combinations present a major challenge for cotton breeding programs. Future efforts that incorporate DNA based selection methods to identify and fix introgressed segments from converted racestocks and their offspring should enhance the use of the genetic variation present in the primitive racestock germplasm accessions.

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Abbreviations

HVI®	High volume instrument
AD	Additive-dominance
LSD	Least significant difference

Introduction

Continued genetic improvement of upland cotton (*Gossypium hirsutum* L.) is dependent upon the exploitation and efficient use of available genetic resources. The extensive genetic resources from 50 cotton species have been documented and many are available (Campbell et al. 2010). Based on the relative genetic accessibility and utility of species to crop improvement efforts, Stewart (1995) classified these genetic resources into primary, secondary, and tertiary gene pools. The primary gene pool for upland cotton consists of five tetraploid species (combined A and D genomes), the secondary gene pool consists of 20 diploid species (A, B, or D), and the tertiary gene pool consists of 25 diploid species (C, E, or K). Although artificial hybridization between species within the primary gene pool is possible and results in fertile offspring, there are numerous reports of aberrant segregation and instability following successive generations of inbreeding (Saha et al. 2012). As a result, upland cotton cultivar development programs often exclusively use upland cotton parents as a primary source of parental lines. Parental lines often include elite, upland cotton breeding lines, germplasm lines, and cultivars (Bowman and Gutierrez 2003). An unintended consequence of organized breeding efforts has resulted in a concentration of the genetic base used in cultivar development (Paterson et al. 2004).

One of the untapped genetic resources available to upland cotton breeders resides in the primitive, landrace collections accumulated over years of plant collections (Campbell et al. 2010). In the cotton collection of the United States alone, there are ~2,500 landrace accessions available. Lewis and Richmond (1957) reported on the photoperiodic nature of many of the *G. hirsutum* primitive landrace accessions and the difficulty of using them in cotton improvement programs. McCarty et al. (1979) initiated a backcross-based conversion program to transfer day-neutral genes from adapted genotypes into primitive landrace genetic backgrounds. To date, more than 100 backcross-derived day-neutral conversion lines have been released (McCarty and Jenkins 1993, 2002, 2005a, b). In conjunction with the release of these materials, McCarty et al. (1996, 1998a, b, 2006) conducted a number of studies providing per se agronomic and fiber quality performance data. Additional studies were conducted to provide evidence of their utility in genetic enhancement and cultivar development programs (McCarty et al. 2004a, b, 2007, 2008).

In this report, we examined the mean performance and genetic effects of breeding populations derived from crosses involving four day-neutral converted racestocks and four elite Pee Dee germplasm lines. Previous studies demonstrated the genetic properties and breeding potential of the high fiber quality Pee Dee germplasm (Campbell et al. 2009, 2011, 2012, 2013). However, no studies have evaluated the breeding potential of day-neutral converted racestocks when crossed to elite Pee Dee germplasm. 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 Pee Dee germplasm and day-neutral converted racestocks.

Materials and methods

Development of topcross hybrids

A total of 22 topcross hybrids were developed using four day-neutral converted racestock germplasm lines (converted racestocks) and four Pee Dee breeding lines. The converted racestocks consisted of M-0044-149 (PI 636702), M1388-2 (PI 639150), M237-1 (PI 639159), and M237-3 (PI 639161) (McCarty and Jenkins 2005a, b). The Pee Dee breeding lines included obsolete germplasm lines (PD 2164, PI 529617 and Sealand 542, PI 528730) (Culp and Harrell 1980) and modern breeding lines (PD 97072 and PD 99041). PD 97072 (PI 612480) resulted from a cross between PD 5582 (PI 543863, Green et al. 1991) and a breeding line developed in Mississippi (MD14-B). PD 99041 resulted from a cross between PD 93043 (PI 591424, May and Howle 1997) and an experimental breeding line B200908-8. All parents used to develop topcross hybrids were selected based upon previous per se agronomic and fiber quality performance data. In 2005, these four Pee Dee breeding lines were each topcrossed as males onto the converted racestocks. In addition, each Pee Dee breeding line was crossed to one another to develop six Pee Dee × Pee Dee modified topcross (half-diallel) hybrids. Collectively, the F_1 and parental line seeds of topcross and modified topcross hybrids (22) were sent to a winter nursery in Tecoman, Mexico and manually self-pollinated to produce copious amounts of F_2 and parental line seed.

Field design and procedures

The 22 F_2 hybrids, 8 parental lines, and two commercial checks were evaluated in three environments in 2006 and two environments in 2007. In 2006, two independent trials were conducted at the Clemson University Pee Dee Research and Education Center near Florence, SC. The first trial was evaluated on a Goldsboro loamy sand soil (Fine-loamy, siliceous, subactive, thermic Aquic Paleudults) and planted on May 18, 2006. The second trial was evaluated on a Norfolk loamy sand soil (Fine-loamy, kaolinitic, thermic Typic Kandiudults) and planted on May 25, 2006. In 2007, a single trial was conducted at the Clemson University Pee Dee Research and Education Center on a Norfolk loamy sand soil (Fine-loamy, kaolinitic, thermic Typic Kandiudults) and planted on May 15, 2007. In 2006 and 2007, trials were conducted on a Barnwell loamy sand soil (Fine-loamy, kaolinitic, thermic Typic Kanhapludults) at the Clemson University Edisto Research and Education Center in Blackville, SC. Trials were planted on May 16, 2006 and May 22, 2007, respectively. The experimental design in each trial was a randomized complete block with three and four-replicates used in 2006 and 2007, respectively. In all trials, plots consisted of two rows 10.6 m × 96 cm row spacing. Plots were managed using Clemson University recommendations for soil fertility, insect management, and defoliation. Weeds were controlled using a combination of pre- and post-plant herbicides and handweeding. 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 yield components and fiber quality properties. Boll weight was determined by dividing the 25-boll sample by 25. All samples from each location were ginned on a common 10-saw laboratory gin, and lint percent 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 percent by seed cotton yield. Seed index was measured as the mass of 100 fuzzy seeds. Bolls m^{-2} was calculated by dividing seed cotton yield by boll weight. In addition, 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 upper half mean fiber length, fiber strength, and micronaire.

Data analysis

Analysis of phenotypic data

All agronomic and fiber quality data were analyzed using a mixed model and the PROC GLM module of SAS ver. 9.2 (SAS 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 analysis of variance could be conducted for each trait. After confirming homogenous error variance for each trait, the data were analyzed using two analysis of variance procedures. Block and environment (each year-location) were considered random effects. Genotypes were considered fixed effects. Fisher's protected least significant difference (LSD) was calculated and used to make planned comparisons among least square means.

Genetic analysis

The data were analyzed by an additive-dominance (AD) genetic model with genotype × environment interaction following the procedures described by Jenkins et al. (2006). Due to some coefficients for genetic effects being fractions rather than 0 and 1, 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 environment (V_E), block (or replicate) within environment (V_B), additive (V_A), dominance (V_D), additive by environment (V_{AE}), dominance by environment (V_{DE}), and residual (V_e); 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 (Wu et al. 2008, 2012; Zhu 1993). An

Table 1 Mean agronomic and fiber quality performance for four converted racestock lines, four Pee Dee breeding lines, and two commercial checks combined over five environments

Parental line	Lint percent (%)	Lint yield (kg ha^{-1})	Seed index (g)	Boll weight (g)	Boll m^{-2} no.	Fiber strength (kN m kg^{-1})	Fiber length (mm)	Micronaire (units)
M-0044-149	30.58	532	11.29	5.45	32.0	287.6	26.77	4.8
M1388-2	31.86	584	10.38	4.95	37.0	310.8	27.85	4.6
M237-1	30.27	599	10.59	5.17	38.0	315.2	27.39	4.9
M237-3	32.14	635	11.04	5.42	36.6	306.7	29.03	4.5
PD 2164	37.05	674	11.85	6.24	29.5	287.2	28.18	4.5
PD 97072	37.67	1,008	10.50	5.42	48.0	290.7	27.77	4.8
PD 99041	36.60	1,072	11.01	5.58	51.2	283.5	28.85	4.9
Sealand 542	33.53	617	12.07	5.94	30.5	290.5	29.69	4.1
DP 491	42.57	916	9.45	5.85	36.8	288.2	29.42	4.7
FM 966	41.06	1,250	11.00	6.08	47.7	307.6	28.39	4.7
LSD (0.05)	0.66	73	0.26	0.16	3.7	6.4	0.43	0.1

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). Similar to Campbell et al. (2013), lower and upper limits of 95 % confidence interval for parameters of interest were calculated to make multiple comparisons among parameters of interest (i.e. additive effects) accordingly.

The predicted genetic effects were deviations from the respective population grand mean. A t test was utilized to detect the significance of genetic effects from zero. These effects are measures of the additive or homozygous dominance effects for each of the eight topcross parents. The 95 % confidence intervals for additive and homozygous dominance effects were compared between the converted racestocks and Pee Dee breeding lines. Heterozygous dominance effects were estimated for each F_2 hybrid combination. All of these genetic analyses were conducted using the GenMod package in R (Wu et al. 2012).

Results

Mean comparisons among parents and F_2 hybrids

Table 1 provides mean trait values for each parent combined across five environments. Compared with the Pee Dee breeding lines, the converted racestocks produced low lint percent. M-0044-149 produced the lowest lint yield among all parents. M237-3 produced a lint yield similar to the second lowest yielding Pee Dee breeding line PD 2164. PD 97072 and PD 99041 produced the highest yield among parents. On average, compared with the Pee Dee breeding lines, the converted racestocks produced lower seed index, smaller bolls, and fewer bolls m^{-2}.

The converted racestocks produced fiber strength, fiber length, and micronaire values similar to the Pee Dee breeding lines. M237-1, M1388-2, and M237-2 produced the strongest fibers among parental lines. M-0044-0149 produced the lowest strength among converted racestocks but was not different than any of the Pee Dee breeding lines. Sealand 542 produced the longest fibers among parental lines. M237-1 produced the longest fibers of any of the four converted racestocks. M-0044-149 produced the lowest fiber length among all parental lines. For micronaire, Sealand 542 produced the lowest (desired) value among all parental lines. M1388-2 and M237-3 produced values lower than two of the Pee Dee breeding lines but not different than PD 2164.

Tables 2, 3, 4, 5, 6, 7, 8, and 9 provide mean trait values for all F_2 hybrids combined across environments. Among the converted racestocks, crosses involving M237-3 produced hybrids with the highest lint percent. Compared to hybrids among Pee Dee breeding lines only, the converted racestock hybrids consistently produced lower lint percent. Among the converted racestock × Pee Dee breeding line crosses, M237-1 × PD 97072 produced the highest lint percent (Table 2). Crosses involving the converted racestocks had similar lint yields. Mean racestock hybrid lint yields were lower than hybrids involving

Table 2 Lint percent (%) of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	33.84	34.17	33.03	34.42	33.87
M1388-2	32.10	31.97	34.93	30.97	32.49
M237-1	33.96	36.95	32.95	30.17	33.51
M237-3	35.12	35.18	33.81	32.86	34.24
PD 2164	–	36.01	37.72	35.51	36.41
PD 97072	36.01	–	36.41	33.33	35.25
PD 99041	37.72	36.41	–	36.13	36.75
Sealand 542	35.51	33.33	36.13	–	34.99
Male parent mean	34.89	34.86	35.00	33.34	

The least significant difference between means at the two-tailed 95 % probability level is 0.66 %

PD 99041 and Sealand 542 but similar to hybrids involving PD 2164 and PD 97072. Among the converted racestock × Pee Dee breeding line crosses, M237-3 × PD 97072 produced the highest lint yield (Table 3). Compared to hybrids among Pee Dee breeding lines only, the converted racestock hybrids produced seed index and boll weights similar to PD 97072 and PD 99041 but lower than PD 2164 and Sealand 542 (Tables 4, 5). Crosses involving M1388-2 produced the lowest boll weight. For bolls m^{-2}, hybrids involving converted racestocks were similar to one another and both PD 2164 and PD 97072 hybrids but lower than PD 99041 and Sealand 542 hybrids (Table 6).

For fiber strength, M1388-2, M237-1, and M237-3 produced hybrids with the highest fiber strength. On average, M237-1 produced hybrids with higher fiber strength than hybrids involving three of the four Pee Dee breeding lines (Table 7). Specific converted racestock × Pee Dee breeding line crosses with particularly high fiber strengths included; (1) M1388-2 × PD 2164 (306.5 kN m kg^{-1}), M1388-2 × PD 97072 (308.1 kN m kg^{-1}), M237-1 × PD 2164 (308.6 kN m kg^{-1}), M237-1 × Sealand 542 (311.4 kN m kg^{-1}), M237-3 × PD 2164 (308.6 kN m kg^{-1}), and M237-3 × PD 99041 (308.5 kN m kg^{-1}). For fiber length, hybrids involving M1388-2, M237-1, and M237-3 produced similar fiber lengths. On average, these converted racestock hybrids produced lengths similar to hybrids involving PD 97072 and PD 99041 but lower than PD 2164 and Sealand 542. Among all topcross hybrids, M237-3 × Sealand 542 produced the highest fiber length (Table 8). For micronaire, the converted racestock hybrids each produced micronaire below the discount level of 5.0 (Hake et al. 1990). Among converted racestock hybrids, those involving M1388-2 produced the lowest micronaire. Interestingly, all converted racestock hybrids involving PD 99041 produced high micronaire (Table 9). Collectively, these results

Table 3 Lint yield (kg ha^{-1}) of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	640	765	686	695	697
M1388-2	540	735	786	576	659
M237-1	661	844	603	691	700
M237-3	718	920	808	506	738
PD 2164	–	720	845	691	752
PD 97072	720	–	769	785	758
PD 99041	845	769	–	976	863
Sealand 542	691	785	976	–	817
Male parent mean	688	791	782	703	

The least significant difference between means at the two-tailed 95 % probability level is 73 kg ha^{-1}

Table 4 Seed index (g) of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	11.53	11.37	11.41	11.21	11.38
M1388-2	11.90	11.33	10.93	11.01	11.29
M237-1	11.74	11.28	10.91	11.03	11.24
M237-3	12.12	10.47	10.91	11.33	11.21
PD 2164	–	11.50	11.48	11.80	11.59
PD 97072	11.50	–	11.01	11.65	11.39
PD 99041	11.48	11.01	–	11.16	11.22
Sealand 542	11.80	11.65	11.16	–	11.54
Male parent mean	11.72	11.23	11.12	11.31	

The least significant difference between means at the two-tailed 95 % probability level is 0.26 g

Table 5 Boll weight (g) of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	5.68	5.68	5.47	5.49	5.58
M1388-2	5.50	5.27	5.36	5.14	5.32
M237-1	5.81	5.75	5.78	5.13	5.62
M237-3	6.06	5.47	5.57	5.54	5.66
PD 2164	–	5.79	5.87	5.78	5.81
PD 97072	5.79	–	5.60	5.68	5.69
PD 99041	5.87	5.60	–	5.59	5.69
Sealand 542	5.78	5.68	5.59	–	5.68
Male parent mean	5.78	5.61	5.61	5.48	

The least significant difference between means at the two-tailed 95 % probability level is 0.16 g

Table 6 Bolls m^{-2} of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	33.6	39.8	37.7	37.0	37.0
M1388-2	30.1	43.4	41.9	36.2	37.9
M237-1	33.6	39.7	32.3	44.9	37.6
M237-3	34.2	47.7	43.4	28.4	38.4
PD 2164	–	34.7	38.2	33.6	35.5
PD 97072	34.7	–	37.7	41.5	38.0
PD 99041	38.2	37.7	–	48.6	41.5
Sealand 542	33.6	41.5	48.6	–	41.2
Male parent mean	34.0	40.6	40.0	38.6	

The least significant difference between means at the two-tailed 95 % probability level is 3.7 bolls

indicated that both additive and dominance effects played important roles on these agronomic and fiber quality traits.

Variance components

Variance components were estimated and expressed as proportions of the phenotypic variance and can be used to estimate measures of heritability (Table 10). Variance components for environment, dominance,

Table 7 Fiber strength (kN m kg^{-1}) of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	288.5	290.3	299.7	280.0	289.6
M1388-2	306.5	308.1	294.5	298.4	301.9
M237-1	308.6	295.9	301.8	311.4	304.4
M237-3	308.6	297.7	308.5	295.2	302.5
PD 2164	–	289.1	291.8	293.8	291.6
PD 97072	289.1	–	294.1	306.7	296.6
PD 99041	291.8	294.1	–	293.8	293.2
Sealand 542	293.8	306.7	293.8	–	298.1
Male parent mean	298.1	297.4	297.7	297.0	

The least significant difference between means at the two-tailed 95 % probability level is 6.4 kN m kg^{-1}

Table 8 Fiber length (mm) of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	27.64	27.71	27.84	27.04	27.56
M1388-2	29.55	28.37	27.64	28.16	28.43
M237-1	28.97	29.27	26.89	29.04	28.54
M237-3	29.35	26.72	27.13	30.30	28.38
PD 2164	–	28.94	28.86	29.69	29.16
PD 97072	28.94	–	28.15	29.58	28.89
PD 99041	28.86	28.15	–	28.41	28.47
Sealand 542	29.69	29.58	28.41	–	29.23
Male parent mean	29.00	28.39	27.85	28.89	

The least significant difference between means at the two-tailed 95 % probability level is 0.43 mm

and residuals were significant ($p < 0.01$) for all phenotypic traits. Additive effects were significant for lint percent, lint yield, seed index, boll weight, and micronaire. Additive × environment interactions were not significant for any phenotypic traits. However, dominance × environment interactions were significant for lint yield, seed index, boll weight, bolls m^{-2}, fiber strength, and micronaire. Additive effects accounted for between 9.6 % (seed index) and 40.8 %

Table 9 Micronaire (units) of F_2 hybrids derived from crosses of four converted racestock lines and four Pee Dee breeding lines

Female parent	Male parents				Female parent mean
	PD 2164	PD 97072	PD 99041	Sealand 542	
M-0044-149	4.7	4.6	5.0	4.7	4.8
M1388-2	4.3	4.6	5.0	4.2	4.5
M237-1	4.7	4.7	5.3	4.5	4.8
M237-3	4.7	4.9	5.2	4.1	4.7
PD 2164	–	4.4	4.5	4.1	4.3
PD 97072	4.4	–	4.7	4.2	4.4
PD 99041	4.5	4.7	–	4.6	4.6
Sealand 542	4.1	4.2	4.6	–	4.3
Male parent mean	4.5	4.6	4.9	4.3	

The least significant difference between means at the two-tailed 95 % probability level is 0.1 units

(lint percent) of the total variance. Dominance effects accounted for between 10.7 % (bolls m^{-2}) and 44.7 % (fiber length) of the total variance. Dominance × environment interactions accounted for between 4.2 % (fiber strength) and 68.9 % (bolls m^{-2}) of the total variance. Environment accounted for between 2.5 % (micronaire) and 69.0 % (fiber strength) of the total variance. Residuals accounted for between 8.2 % (lint percent) to 25.2 % (micronaire) of the total variance. The lack of significant additive × environment interactions was consistent with other recent cotton combining ability studies (Jenkins et al. 2009; Zeng and Wu 2012). Not surprisingly, the proportion of the total variance attributed to each variance component differed from previously conducted studies (Jenkins et al. 2009; Zeng and Wu 2012). As noted in Zeng et al. (2011), variance component proportions often differ depending upon the genotypes being evaluated.

Predicted genetic effects

To assess the breeding potential of the four converted racestocks 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: (1) additive effects represent general combining ability, (2) homozygous dominance effects represent inbreeding depression, and (3) 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 four converted racestocks and the four Pee Dee lines.

Additive effects and their standard errors were predicted on a per trait basis and are provided in Table 11. For lint percent, with one exception, converted racestocks had negative additive effects that were lower than each of the four Pee Dee breeding lines. The lone exception was M237-3, which had an additive effect similar to Sealand 542. Similarly, the four converted racestocks displayed negative additive effects for lint yield. Lint yield additive effects for converted racestocks were each lower than PD 97072 and PD 99041. For seed index, two converted racestocks (M-0044-149, positive, and M237-3, negative) had significant additive effects. With the exception of M-0044-149, compared to Sealand 542, converted racestocks had additive effects less than or equal to the Pee Dee breeding lines. For boll weight and bolls m^{-2}, converted racestocks had additive effects less than or equal to zero. Converted racestock additive effects for both traits were less than those for the Pee Dee breeding lines except for Sealand 542 (boll weight). Additive effects for fiber strength and length were not significant and no differences were detected between converted racestocks and Pee Dee breeding lines. For micronaire, additive effects for converted racestocks were generally higher than those for the Pee Dee breeding lines except for PD 99041.

Homozygous dominance effects were predicted and their standard errors estimated on a per trait basis. These effects represented inbreeding depression effects and are listed in Table 12. For lint percent, M-0044-149, M237-1, and M237-3 had lower inbreeding depression effects compared to PD 2164, PD 97072, and Sealand 542. For lint yield, each converted racestock had lower inbreeding depression effects than PD 99041. M-0044-149 had a lower inbreeding depression effect compared to PD 97072 while M-1388-2 had a higher inbreeding depression effect compared to Sealand 542. For seed index and boll weight, converted racestocks had inbreeding depression effects equal to or less than zero. For both traits, in most cases converted racestocks had inbreeding depression effects equal to or less than the Pee Dee breeding lines. For bolls m^{-2}, two converted racestocks had negligible inbreeding depression effects. M-0044-149 had decreased inbreeding depression

Table 10 Variance components and standard errors expressed as proportions of the phenotypic variances for agronomic and fiber quality traits

	Lint percent	Lint yield	Seed index	Boll weight	Bolls (m^{-2})	Fiber strength	Fiber length	Micronaire
V_E/V_P	0.069 ± 0.003**	0.046 ± 0.005**	0.472 ± 0.010**	0.270 ± 0.011**	0.044 ± 0.006**	0.690 ± 0.005**	0.404 ± 0.007**	0.025 ± 0.005**
V_B/V_P	0.000 ± 0.000	0.010 ± 0.002**	0.014 ± 0.002**	0.019 ± 0.004**	0.005 ± 0.002	0.009 ± 0.003*	0.015 ± 0.002**	0.035 ± 0.004**
V_A/V_P	0.408 ± 0.008**	0.126 ± 0.010**	0.096 ± 0.008**	0.124 ± 0.014**	0.002 ± 0.003	0.008 ± 0.004	0.000 ± 0.001	0.155 ± 0.017**
V_D/V_P	0.409 ± 0.010**	0.116 ± 0.016**	0.198 ± 0.012**	0.233 ± 0.015**	0.107 ± 0.024**	0.128 ± 0.011**	0.447 ± 0.015**	0.358 ± 0.022**
V_{AE}/V_P	0.002 ± 0.002	0.000 ± 0.000	0.001 ± 0.002	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
V_{DE}/V_P	0.029 ± 0.010	0.562 ± 0.021**	0.087 ± 0.021**	0.019 ± 0.021**	0.689 ± 0.002**	0.042 ± 0.007**	0.031 ± 0.012	0.175 ± 0.042**
V_e/V_P	0.082 ± 0.004**	0.141 ± 0.009**	0.133 ± 0.004**	0.245 ± 0.011**	0.153 ± 0.010**	0.123 ± 0.006**	0.102 ± 0.007**	0.252 ± 0.023**

V_E environment variance, V_B block (environment) variance, V_A additive variance, V_D dominance variance, V_{AE} additive by environment variance, V_{DE} dominance by environment variance, V_e error variance, V_P phenotypic variance

* Significantly different at the 0.05 level of probability

** Significantly different at the 0.01 level of probability

effects while M237-1 had increased effects. In comparison with Pee Dee breeding lines, the converted racestocks had inbreeding depression effects similar to or lower than PD 97072 and PD 99041 and equal to or higher than Sealand 542. For fiber strength, converted racestocks had higher inbreeding depression effects compared to PD 2164, PD 97072, and PD 99041 while being similar to Sealand 542. The lone exception was M237-3, which displayed inbreeding depression effects not different than PD 97072. For fiber length, converted racestocks had higher inbreeding depression effects than PD 2164 and PD 97072 and lower effects compared to PD 99041. Among the converted racestocks, M327-3 displayed the lowest inbreeding depression. For micronaire, converted racestocks displayed inbreeding depression effects equal to or higher than the Pee Dee breeding lines.

For each trait and cross combination, heterozygous dominance effects were predicted and their standard errors estimated (Table 13). 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 converted racestock × Pee Dee breeding line cross combination.

Discussion

Primitive racestock accessions maintained and curated in global cotton germplasm collections represent an underutilized genetic resource for contemporary cotton breeding programs. To date, efforts to utilize these exotic accessions have focused mostly on developing day-neutral converted germplasm lines. Limited studies focused on the breeding potential of the collection of day-neutral converted racestocks have been conducted. In this study, our goal was to evaluate the breeding potential of a selected group of day-neutral converted racestocks when crossed to a selection of unique, high fiber quality Pee Dee germplasm.

Overall, converted racestocks and derived hybrids had low lint percent, average to below average agronomic performance, and good fiber quality. Compared with the Pee Dee germplasm lines included in this study, converted racestocks and hybrids derived from them were equal to or lower than Pee Dee germplasm for lint yield, boll weight, seed index, and bolls m^{-2}. However, the mean performance of

Table 11 Additive effects for agronomic and fiber quality traits expressed as deviations from the grand mean

Parent	Lint percent	Lint yield	Seed Index	Boll weight	Bolls m^{-2}	Fiber strength	Fiber length	Micronaire
M-0044-149	−1.43 ± 0.04**	−76.13 ± 4.79**	0.07 ± 0.02*	−0.08 ± 0.01**	−0.25 ± 0.35	−2.86 ± 1.10	−0.03 ± 0.05	0.09 ± 0.01**
M1388-2	−2.48 ± 0.03**	−102.52 ± 5.59**	−0.02 ± 0.01	−0.29 ± 0.02**	−0.13 ± 0.20	1.94 ± 0.78	−0.01 ± 0.01	−0.04 ± 0.01**
M237-1	−1.73 ± 0.06**	−71.74 ± 4.00**	−0.06 ± 0.02	−0.07 ± 0.01**	−0.13 ± 0.17	2.84 ± 1.10	0.00 ± 0.01	0.13 ± 0.01**
M237-3	−1.05 ± 0.03**	−39.89 ± 5.96**	−0.06 ± 0.02*	−0.02 ± 0.01	−0.06 ± 0.13	1.99 ± 0.76	−0.01 ± 0.01	0.09 ± 0.01**
PD 2164	0.68 ± 0.04**	−40.65 ± 4.97**	0.55 ± 0.03*	0.21 ± 0.01**	−0.60 ± 0.82	−0.22 ± 0.19	0.03 ± 0.05	−0.18 ± 0.01**
PD 97072	0.61 ± 0.04**	62.49 ± 7.06**	0.10 ± 0.02*	0.06 ± 0.01**	0.38 ± 0.52	−0.62 ± 0.30	0.00 ± 0.01	−0.07 ± 0.01**
PD 99041	0.85 ± 0.03**	49.48 ± 5.55**	−0.06 ± 0.01**	0.04 ± 0.01**	0.27 ± 0.38	−0.75 ± 0.32	−0.02 ± 0.03	0.22 ± 0.01**
Sealand 542	−0.95 ± 0.04**	−23.57 ± 7.42*	0.11 ± 0.01**	−0.10 ± 0.01*	−0.11 ± 0.17	−1.24 ± 0.45	0.02 ± 0.03	−0.28 ± 0.01**

Significant effects are different than zero

* Significantly different at the 0.05 level of probability

** Significantly different at the 0.01 level of probability

converted racestocks was similar to Pee Dee germplasm for fiber quality. Hybrids derived from converted racestocks had fiber strength and length equal to or greater than Pee Dee germplasm derived hybrids. Agronomic and fiber quality performance of converted racestocks and their hybrids was similar to those reported in previous studies (McCarty et al. 1996, 2004a, b, 1998a, b, 2006, 2007, 2008). In those studies, hybrids derived from crosses with commercial cultivars (no Pee Dee germplasm) also reported low lint percent, below average to average lint yield, and good fiber quality.

Variance component analysis showed that both additive and dominance main effects contributed to the total variation for lint percent, lint yield, seed index, boll weight, and micronaire (Table 10). These results were in good agreement with phenotypic observations (Tables 1, 2, 3, 4, 5, 6, 7, 8, 9). For bolls m^{-2}, fiber strength, and fiber length, environmental variance explained a large part of the total variation, while dominance was the only significant genetic effect. In terms of interactions with the environment, dominance × environment interactions explained a portion of the total variation for lint yield, seed index, boll weight, bolls m^{-2}, fiber strength, and micronaire. This was especially true for lint yield and bolls m^{-2} in which dominance × environment interactions explained 56 and 69 % of the total variation, respectively. Although proportionally different with respect to the total variation, the identification of primarily additive, dominance, and dominance × environment interactions is consistent with previously reported variance components using different topcross parents (McCarty et al. 2004a, 2007). Using three of the four converted racestocks used in this study and a different set of elite topcross parents, McCarty et al. (2004a) reported similar variance component estimates which demonstrated the importance of dominance effects when considering the use of these specific converted racestocks in cotton breeding programs. Evidently, many of the alleles present in these converted racestocks and elite upland germplasm interact with one another in a non-additive way.

On average, the genetic effects predicted in this study indicated that converted racestocks transmitted negative additive effects for lint percent and additive effects similar to or less than zero for lint yield and other yield component traits. In terms of homozygous dominance effects, converted racestocks transmitted

Table 12 Homozygous dominance effects for agronomic and fiber quality traits expressed as deviations from the grand mean

Parent	Lint percent	Lint yield	Seed index	Boll weight	Bolls m^{-2}	Fiber strength	Fiber length	Micronaire
M-0044-149	−1.91 ± 0.18**	−55.91 ± 12.90**	0.02 ± 0.03	0.03 ± 0.04	−2.31 ± 0.65*	−0.44 ± 0.87	0.15 ± 0.12	−0.07 ± 0.05
M1388-2	2.16 ± 0.17**	35.66 ± 11.81	−0.80 ± 0.06**	−0.04 ± 0.05	0.58 ± 0.54	1.47 ± 1.16	−0.35 ± 0.10*	−0.01 ± 0.04
M237-1	−1.63 ± 0.20**	−5.48 ± 10.77	−0.45 ± 0.04**	−0.32 ± 0.04**	1.52 ± 0.38**	2.19 ± 1.59	−1.06 ± 0.07**	−0.11 ± 0.03*
M237-3	−1.01 ± 0.20**	−35.01 ± 17.90	0.04 ± 0.06	−0.15 ± 0.04*	−0.69 ± 0.86	−3.24 ± 0.70**	1.12 ± 0.11**	−0.44 ± 0.04**
PD 2164	0.97 ± 0.23**	8.12 ± 12.84	−0.56 ± 0.08**	0.19 ± 0.04**	0.18 ± 0.56	−14.26 ± 1.80**	−2.33 ± 0.15**	0.26 ± 0.04**
PD 97072	1.91 ± 0.14**	99.90 ± 23.95**	−0.95 ± 0.04**	−0.34 ± 0.04**	3.34 ± 1.06*	−8.49 ± 1.05**	−1.15 ± 0.07**	0.36 ± 0.04**
PD 99041	0.01 ± 0.16	175.00 ± 18.87**	0.02 ± 0.06	−0.13 ± 0.04*	7.19 ± 1.32**	−15.92 ± 1.43**	1.90 ± 0.17**	−0.30 ± 0.04**
Sealand 542	0.53 ± 0.14*	−73.74 ± 13.96**	0.76 ± 0.08**	0.60 ± 0.04**	−7.18 ± 0.86**	−5.34 ± 1.32**	0.09 ± 0.14	−0.06 ± 0.04

Significant effects are different than zero

* Significantly different at the 0.05 level of probability

** Significantly different at the 0.01 level of probability

lower inbreeding depression effects for agronomic traits. For fiber strength and length, additive effects were not significant and effects of inbreeding depression were negligible.

Overall, the results of this study indicated that decreased agronomic performance should be expected when using converted racestocks in cotton breeding programs. However, decreased agronomic performance is not accompanied by a dramatic decrease in fiber quality. Liu et al. (2000) reported that many converted racestocks were found to have more than 75 % shared alleles at marker loci with typical upland cotton. In this study, the large portion of the total variance explained by environmental variation relative to other variance components for fiber strength and fiber length support their conclusions that converted racestocks and upland cotton likely share many alleles associated with quantitative traits. On the other hand, the identification of significant dominance effects for fiber strength and fiber length suggest that the converted racestocks likely transmit novel alleles. Although not directly tested in this study, it is probable that converted racestocks transmit alleles associated with agronomic and fiber quality performance that are negatively correlated. The negative relationship between agronomic performance and fiber quality has been well documented and continues to impede breeding progress (Campbell et al. 2013). Hence, it is likely that negative linkages between agronomic performance and fiber quality alleles present in converted racestocks will present a major challenge to cotton breeders. Breeding methods designed to break negative linkages between agronomic performance and fiber quality will be required to transfer new and favorable allelic combinations derived from converted racestocks. In addition, as noted by Liu et al. (2000), future efforts that incorporate DNA based selection methods to identify and fix introgressed segments in converted racestocks and their offspring will help efforts to more effectively use genetic variation present in the primitive racestock germplasm. With advances in DNA sequencing technology coupled with an increased knowledge of cotton genome structure and organization (Paterson et al. 2012), these efforts should be pursued sooner rather than later.

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Table 13 Heterozygous dominance effects for agronomic and fiber quality traits expressed as deviations from the grand mean

F^2 hybrid	Lint percent	Lint yield	Seed index	Boll weight	Bolls m^{-2}	Fiber strength	Fiber length	Micronaire
M-0044-149/PD 2164	−0.41 ± 0.3	26.5 ± 15.17	−0.40 ± 0.12*	−0.25 ± 0.08*	2.89 ± 0.59**	−5.02 ± 1.80	−0.71 ± 0.07**	0.13 ± 0.05
M-0044-149/PD 97072	0.04 ± 0.16	15.82 ± 30.25	0.48 ± 0.08**	0.31 ± 0.03**	0.29 ± 1.57	−2.37 ± 1.77	0.49 ± 0.16	−0.35 ± 0.05**
M-0044-149/PD 99041	−2.2 ± 0.20**	−116.1 ± 21.72**	0.53 ± 0.08**	−0.15 ± 0.07	−2.95 ± 1.03	21.33 ± 1.61**	1.15 ± 0.17**	0.021 ± 0.04
M-0044-149/Sealand 542	4.53 ± 0.21**	109.95 ± 19.42**	−0.56 ± 0.08**	−0.09 ± 0.06	2.89 ± 1.07	−21.18 ± 1.76**	−2.49 ± 0.22**	0.47 ± 0.06**
M1388-2/PD 2164	−3.70 ± 0.19**	−127.08 ± 10.85**	0.91 ± 0.10**	−0.12 ± 0.06	−4.98 ± 0.67**	8.52 ± 1.32**	2.17 ± 0.17**	−0.3 ± 0.04**
M1388-2/PD 97072	−4.11 ± 0.24**	−38.7 ± 25.17	0.94 ± 0.06**	−0.03 ± 0.04	2.25 ± 1.31	11.27 ± 1.64**	0.53 ± 0.08**	−0.01 ± 0.04
M1388-2/PD 99041	2.68 ± 0.24**	50.22 ± 22.84	0.11 ± 0.07	0.12 ± 0.05	0.94 ± 0.80	−11.87 ± 1.80**	−0.78 ± 0.11**	0.40 ± 0.04**
M1388-2/Sealand 542	−2.41 ± 0.16**	−57.72 ± 17.1*	−0.40 ± 0.06**	−0.29 ± 0.03**	−0.14 ± 0.87	−5.45 ± 1.92	−1.44 ± 0.15**	−0.13 ± 0.04
M237-1/PD 2164	0.33 ± 0.25	21.95 ± 18.92	0.51 ± 0.07**	0.12 ± 0.03**	−0.22 ± 0.90	8.16 ± 2.00**	0.93 ± 0.15**	0.05 ± 0.07
M237-1/PD 97072	6.90 ± 0.26**	103.65 ± 32.67*	0.73 ± 0.09**	0.56 ± 0.06**	−2.45 ± 1.12	−17.78 ± 1.58**	2.65 ± 0.19**	−0.18 ± 0.04**
M237-1/PD 99041	−1.90 ± 0.20**	−255.54 ± 19.35**	0.01 ± 0.04	0.57 ± 0.03**	−12.52 ± 1.36**	−2.50 ± 2.23	−2.27 ± 0.11**	0.57 ± 0.04**
M237-1/Sealand 542	−4.40 ± 0.17**	69.49 ± 12.58**	−0.44 ± 0.04**	−0.71 ± 0.04**	11.22 ± 1.36**	15.81 ± 1.35**	0.68 ± 0.13**	−0.03 ± 0.02
M237-3/PD 2164	1.34 ± 0.28**	78.49 ± 22.76*	1.10 ± 0.12**	0.47 ± 0.08**	1.00 ± 1.10	15.42 ± 2.41**	1.08 ± 0.18**	0.34 ± 0.05**
M237-3/PD 97072	1.06 ± 0.11**	180.4 ± 22.2**	−1.07 ± 0.08**	−0.13 ± 0.05	8.78 ± 1.32**	−8.42 ± 1.42**	−3.85 ± 0.17**	0.54 ± 0.05**
M237-3/PD 99041	−1.70 ± 0.14**	2.00 ± 23.18	−0.20 ± 0.07	−0.01 ± 0.05	2.32 ± 1.41	17.01 ± 1.55**	−2.48 ± 0.09**	0.62 ± 0.06**
M237-3/Sealand 542	0.01 ± 0.14	−230.46 ± 22.39**	0.00 ± 0.11	−0.06 ± 0.05	−11.10 ± 1.64**	−11.83 ± 2.68**	2.80 ± 0.08**	−0.49 ± 0.04**
PD 2164/PD 97072	−2.11 ± 0.11**	−106.82 ± 12.478**	0.26 ± 0.04**	−0.01 ± 0.07	−3.48 ± 0.46**	3.10 ± 3.32	1.17 ± 0.14**	−0.15 ± 0.06
PD 2164/PD 99041	2.42 ± 0.21**	31.98 ± 25.67	−0.21 ± 0.06*	−0.08 ± 0.04	−0.13 ± 1.05	−1.64 ± 2.92	0.60 ± 0.14**	−0.52 ± 0.04**
PD 2164/Sealand 542	1.28 ± 0.15**	18.41 ± 26.5	−0.25 ± 0.06**	−0.21 ± 0.05**	0.74 ± 1.15	−0.60 ± 2.60	0.55 ± 0.13**	−0.31 ± 0.03**
PD 97072/PD 99041	−0.71 ± 0.17**	−259.91 ± 31.71**	0.02 ± 0.07	−0.05 ± 0.04	−10.83 ± 1.57**	3.24 ± 1.98	0.07 ± 0.18	−0.41 ± 0.04**
PD 97072/Sealand 542	−3.81 ± 0.18**	−32.17 ± 18.29	0.68 ± 0.11**	0.11 ± 0.02**	1.10 ± 0.76	26.21 ± 3.11**	1.42 ± 0.20**	−0.26 ± 0.05**
PD 99041/Sealand 542	2.71 ± 0.11**	246.46 ± 20.63**	−0.38 ± 0.08**	−0.08 ± 0.04	10.39 ± 1.39**	4.10 ± 2.05	−0.88 ± 0.14**	0.23 ± 0.05**

Significant effects are different than zero

* Significantly different at the 0.05 level of probability

** Significantly different at the 0.01 level of probability

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