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RESEARCH

Assessing the Breeding Potential of Thirteen Day-Neutral Landrace Accessions in an Upland Cotton Breeding Program

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ABSTRACT

An untapped genetic resource available to cotton (*Gossypium hirsutum* L.) breeding programs is represented by the primitive, upland cotton landrace collection. Primarily due to their photoperiodic nature, efforts to utilize these resources have been slow. To complement efforts to develop day-neutral converted germplasm lines, we identified a number of naturally occurring day neutral landrace genotypes and evaluated their breeding potential when crossed to elite upland germplasm lines and cultivars. The mean performance of parental lines and F_2 hybrids along with genetic effect estimates indicate that naturally occurring day-neutral landrace genotypes provided average agronomic performance while increasing fiber quality performance. Results suggest that crosses derived from naturally occurring day-neutral genotypes and elite upland lines result in new allelic combinations that interact in both an additive and nonadditive way. However, it appears that several naturally occurring day-neutral genotypes transmit negatively correlated alleles for agronomic performance and fiber quality that often display opposite additive and nonadditive effects. These negatively correlated allele combinations present a major challenge for cotton breeding programs. Future efforts that determine the percentage of "new" alleles present in the landrace germplasm, along with innovative breeding methods focused on efficiently capturing beneficial alleles, are needed to expand the cotton genetic base.

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Upland cotton (*Gossypium hirsutum* L.) cultivar development programs most often use elite, upland cotton germplasm lines and cultivars as a source of parental lines (Bowman and Gutierrez, 2003). An unintended consequence of these efforts has resulted in a narrowing and erosion of the genetic base (Paterson et al., 2004). Recent studies independently estimate low levels of genetic diversity within the elite upland cotton gene pool. In a survey of 378 upland cotton accessions, Tyagi et al. (2014) estimated that the average genetic distance between accessions was 0.195. Similarly, Hinze et al. (2017) estimated that the genetic diversity within 292 improved, upland cotton accessions was 0.145. Therefore, there is an urgent need to broaden the upland cotton genetic base with new, beneficial alleles from the extensive genetic resources representing >50 species available in *Gossypium* (Campbell et al., 2010). Although artificial hybridization between the tetraploid *Gossypium* species results in fertile offspring, there is typically aberrant segregation and instability after successive generations of inbreeding (Saha et al., 2012). Fertilization barriers have prevented widespread use of artificial hybridization between upland cotton and its diploid relatives.

An untapped genetic resource available to cotton breeding programs is represented by the primitive, upland cotton landrace collection (Campbell et al., 2010). In the US National Cotton Germplasm Collection, there are ~2500 landrace accessions available. Lewis and Richmond (1957) reported that many of the

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G. hirsutum primitive landrace accessions displayed photoperiod sensitivity, requiring short daylength to stimulate flowering. In an effort to overcome their photoperiodic nature, McCarty et al. (1979) initiated a backcross-based conversion program to transfer day-neutral genes from adapted genotypes. McCarty and Jenkins (1993, 2002, 2005a, 2005b) have released >100 backcross-derived, day-neutral conversion lines. A number of studies have assessed their utility in genetic enhancement and cultivar development programs (McCarty et al., 2004a, 2004b, 2007, 2008; Campbell et al., 2014).

To complement these efforts to develop day-neutral converted primitive landrace germplasm, we initiated a program in 2008 to search for naturally occurring day-neutral primitive landrace accessions. In this report, we studied breeding populations derived from crosses among 13 naturally occurring, day-neutral landrace accessions and six elite, upland germplasm lines and cultivars. The objective of this study was to use the exotic × elite breeding populations to estimate genetic variance components and predict genetic effects for agronomic and fiber quality traits.

MATERIALS AND METHODS

Topcross Family Development

A total of 78 topcross families were developed using 13 day-neutral landrace accessions (RACE) and six elite, upland germplasm lines and cultivars (ELITE). A description of the RACE accessions and ELITE lines is provided in Table 1. The RACE accessions and ELITE parents were selected based on day neutrality and previous per se agronomic and fiber quality performance data. In 2012, the ELITE breeding lines were each topcrossed as males onto the RACE lines. The F_1 and parental line seeds were manually self-pollinated for increase at a winter nursery in Tecoman, Mexico.

Field Design and Procedures

The 78 F_2 hybrids, 19 parental lines, and one commercial check (cultivar Deltapine 393, PI 635100) were evaluated in three environments during 2013 and 2014. In 2013 and 2014, the trial was conducted at the North Carolina State University Sandhills Research Station near Jackson Springs, NC. Also in 2014, the trial was conducted at the Texas A&M AgriLife Research Farm near College Station, TX. In each trial, entries were randomly assigned to a single replicate of a three-replicate, α-lattice incomplete block field design. Each replicate included 14 incomplete blocks of size seven. In North Carolina trials, plots consisted of a single row 10.6 m long with 96-cm row spacing. In Texas, plots were a single row 12.2 m long with 102-cm row spacing. Trial management followed the established local production practices at each location. Total seed cotton weight was obtained from each plot after harvest with a spindle-type mechanical cotton picker. Prior to machine harvest, a 25-boll sample was hand harvested from each plot to determine yield components and fiber quality properties. Boll weight was determined using the 25-boll sample. All samples from each location were ginned on a common 10-saw laboratory gin. The lint sample obtained after ginning was divided by the weight of the seed cotton sample before ginning to obtain lint percentage. Seed cotton yield was multiplied by lint percentage to obtain lint yield. The lint sample was sent to the Cotton Incorporated Fiber Testing Laboratory (Cary, NC) to determine high volume instrument (HVI) fiber properties. The fiber properties measured included upper-half mean fiber length, fiber strength, uniformity index, and micronaire.

Data Analysis

Phenotypic Data Analysis

Phenotypic data were analyzed using a mixed model and the PROC GLM module with the RANDOM statement of SAS 9.2 (SAS Institute, 2008). First, phenotypic data were analyzed for each individual year-location. After confirming homogenous

Table 1. A description of the thirteen day-neutral landrace accessions (RACE) and six elite lines (ELITE) used as parents to develop topcross populations.

Genotype	PI no.	Country of origin	Type	Reference
TX-1147	PI 273894	Ethiopia	RACE	None
TX-1151	PI 529967	Columbia	RACE	None
TX-1306	PI 381946	Argentina	RACE	None
TX-1321	PI 403928	Cote D`Ivoire	RACE	None
TX-1326	PI 403933	Cote D`Ivoire	RACE	None
TX-1327	PI 403934	Cote D`Ivoire	RACE	None
TX-2074	PI 490391	Mali	RACE	None
TX-2315	PI 377683	Australia	RACE	None
TX-2318	PI 607644	Former Soviet Union	RACE	None
TX-2319	PI 607645	Former Soviet Union	RACE	None
TX-2320	PI 607646	Former Soviet Union	RACE	None
TX-2323	PI 607649	Mexico	RACE	None
TX-2354	PI 607669	Paraguay	RACE	None
Deltapine 90	PI 529529	United States	ELITE	None
DES 119	PI 606809	United States	ELITE	Bridge (1986)
MD 25	PI 659508	United States	ELITE	Meredith and Nokes (2011)
Delta Pearl	PI 614100	United States	ELITE	None
PD 94042	PI 603219	United States	ELITE	May (1999)
UA 48	PI 660508	United States	ELITE	Bourland and Jones (2012)

error variance, the combined data were analyzed using ANOVA where block and environment (each year-location) were considered random effects, and genotypes were considered fixed effects. Fisher's protected LSD was calculated and used to make planned comparisons among least square means.

Genetic Analysis

An additive-dominance genetic model (Jenkins et al., 2006) was used to analyze phenotypic data across locations. Variance components were estimated following the mixed linear model approach described by Zhu (1989). The phenotypic variance was partitioned into components for environment, block, additive, dominance, additive × environment, dominance × environment, and residual; they were expressed as proportions of the total phenotypic variance (Tang et al., 1996, Wu et al., 2010). Genetic effects were predicted by the adjusted unbiased prediction approach (Zhu, 1993). Standard errors of variance components and genetic effects were estimated by randomized 10-fold jackknife resampling technique (Zhu, 1993; Wu et al., 2008, 2012). An approximate one-tailed *t* test was used to detect the significance of variance components. A two-tailed *t* test was used to detect the significance of genetic effects (Miller, 1974).

The significance of predicted genetic effects were tested against zero using a *t* test and represented the additive or homozygous dominance effects for each of the 19 topcross parents. Comparisons among the RACE and ELITE parents were made by comparing the 95% confidence intervals for additive and homozygous dominance effects. Heterozygous dominance effects were estimated for each F_2 hybrid combination. All of these genetic analyses were conducted using the qgtools package in R under the RStudio environment (R Core Team, 2014; Wu, 2014).

RESULTS

Mean Comparisons among Parents and F_2 Hybrids

Tables 2–7 provide mean trait values for each parent and F_2 hybrid combined across three environments. Below, results will be presented for each trait.

Lint Percentage

Overall, the RACE lines produced mean lint percentage similar to the six ELITE lines. Three of the RACE lines produced lint percentage lower than the low-percentage ELITE line DES 119. TX-2354 produced a lint percentage similar to the high-lint-percentage ELITE line PD 94042. Out of all 78 F_2 hybrids, four produced lint percentage equal to PD 94042. Two involved crosses with TX-1151 and two with TX-2354. Five F_2 hybrids produced lint percentage lower than the low-percentage ELITE line DES 119. Four involved crosses with TX-2320 and one with TX-2318.

Lint Yield

None of the RACE lines produced lint yield equivalent to the high-yielding ELITE line Delta Pearl. However, five of the RACE lines produced lint yield equivalent to the lowest yielding ELITE line, MD 25. Thirty-seven F_2 hybrids produced lint yields equal to the high-yielding ELITE line Delta Pearl, and nine F_2 hybrids produced lint yields lower than the lowest yielding ELITE line, PD 94042. Two F_2 hybrids involving Delta Pearl (TX-1326 and TX-1327) produced the lowest lint yields, which highlights differences often observed among specific cross combinations. Other F_2 hybrids involving Delta Pearl produced competitive lint yield. Five of the six hybrids from each of the crosses involving TX-1306, TX-1327, and TX-2354 produced lint yields equal to Delta Pearl.

Fiber Strength

Two of the RACE lines (TX-2318 and TX- 2320) produced fiber strength equivalent to the high-strength ELITE line UA-48. Six additional RACE lines produced fiber strength greater than the lowest strength ELITE line, Deltapine 90. Eleven F_2 hybrids produced fiber strength equal to the high ELITE line UA-48. Forty-four F_2 hybrids produced fiber strength greater than the lowest

Table 2. Lint percentage of F_2 hybrids derived from crosses of 13 day-neutral landrace lines and six elite lines. The LSD between means at the two-tailed 95% probability level is 2.4%.

RACE parent	RACE parent mean	ELITE parent: DES 119	Delta Pearl	Deltapine 90	MD 25	PD 94042	UA-48	RACE parent hybrid mean
				%				
ELITE parent mean		37.0	39.9	38.0	38.1	41.0	37.2	
TX-1147	33.7	36.4	37.5	36.4	35.8	37.5	34.9	36.4
TX-1151	35.4	37.3	40.6	37.1	37.0	38.8	36.5	37.9
TX-1306	35.3	36.2	37.5	36.6	35.6	38.3	37.5	37.0
TX-1321	37.8	38.3	36.2	36.9	37.3	37.1	35.0	36.8
TX-1326	35.1	37.3	36.3	36.0	36.5	35.1	35.0	36.0
TX-1327	38.5	37.6	35.3	37.1	36.8	36.7	37.1	36.7
TX-2074	35.2	35.3	34.6	34.6	34.8	36.4	35.6	35.2
TX-2315	36.6	36.0	35.4	35.7	–	36.5	35.1	35.7
TX-2318	33.6	35.4	35.7	35.4	35.1	36.1	33.7	35.2
TX-2319	35.3	36.7	36.8	36.5	–	35.5	35.7	36.2
TX-2320	26.7	33.2	33.8	33.0	31.4	34.8	36.4	33.8
TX-2323	36.7	36.5	36.4	35.6	37.3	36.1	36.3	36.4
TX-2354	38.6	38.5	38.2	38.2	39.0	39.7	37.5	38.5
ELITE parent hybrid mean		36.5	36.5	36.1	36.0	36.8	35.9	

Table 3. Lint yield of F_2 hybrids derived from crosses of 13 day-neutral landrace lines and six elite lines. The LSD between means at the two-tailed 95% probability level is 179 kg ha^{-1}.

RACE parent	RACE parent mean	ELITE parent DES 119	Delta Pearl	Deltapine 90	MD 25	PD 94042	UA-48	RACE parent hybrid mean
		kg ha^{-1}						
ELITE parent mean		962	1091	961	301	937	1012	
TX-1147	740	1005	518	840	827	991	832	835
TX-1151	796	1014	1018	1091	899	842	949	969
TX-1306	853	916	941	850	917	1118	973	953
TX-1321	681	962	901	971	1072	977	908	965
TX-1326	740	1062	271	959	757	651	906	768
TX-1327	326	949	219	1021	941	949	1087	861
TX-2074	682	789	863	999	795	904	881	872
TX-2315	893	952	980	863	–	958	898	930
TX-2318	585	805	791	612	762	791	684	741
TX-2319	829	998	1006	1039	–	743	566	870
TX-2320	561	796	816	899	905	836	889	857
TX-2323	740	918	974	621	966	823	866	861
TX-2354	821	1000	600	1016	951	1176	1057	967
ELITE parent hybrid mean		936	761	906	890	904	884	

Table 4. Fiber strength of F_2 hybrids derived from crosses of 13 day-neutral landrace lines and six elite lines. The LSD between means at the two-tailed 95% probability level is 20 kg ha^{-1}.

RACE parent	RACE parent mean	ELITE parent DES 119	Delta Pearl	Deltapine 90	MD 25	PD 94042	UA-48	RACE parent hybrid mean
		kN m kg^{-1}						
ELITE parent mean		309	300	289	331	300	353	
TX-1147	326	322	316	317	327	317	349	325
TX-1151	307	319	313	318	323	294	335	317
TX-1306	320	317	308	306	325	315	338	318
TX-1321	311	298	319	315	310	305	330	313
TX-1326	308	323	331	323	345	320	345	331
TX-1327	308	315	323	317	316	316	321	318
TX-2074	325	289	290	290	290	279	298	289
TX-2315	291	299	316	308	–	304	327	311
TX-2318	345	312	307	332	328	345	338	327
TX-2319	314	310	313	299	–	313	326	312
TX-2320	343	333	333	329	350	328	337	335
TX-2323	298	294	320	320	311	306	321	312
TX-2354	312	313	307	296	322	299	317	309
ELITE parent hybrid mean		311	315	313	323	311	329	

Table 5. Fiber length of F_2 hybrids derived from crosses of 13 day-neutral landrace lines and six elite lines. The LSD between means at the two-tailed 95% probability level is 1.3 mm.

RACE parent	RACE parent mean	ELITE parent DES 119	Delta Pearl	Deltapine 90	MD 25	PD 94042	UA-48	RACE parent hybrid mean
		mm						
ELITE parent mean		28.2	28.1	27.1	29.1	27.1	31.2	
TX-1147	29.1	29.0	28.6	28.9	29.1	28.5	30.1	29.0
TX-1151	29.0	29.4	28.0	29.4	29.7	27.4	30.5	29.1
TX-1306	28.5	29.2	28.0	28.1	29.3	28.7	29.7	28.9
TX-1321	28.5	27.9	29.9	29.2	28.8	28.3	30.8	29.2
TX-1326	27.8	28.6	29.2	29.0	29.6	28.0	29.2	28.9
TX-1327	27.9	29.3	30.1	29.1	29.7	28.9	30.3	29.6
TX-2074	28.9	26.3	27.1	26.0	26.3	26.0	26.6	26.4
TX-2315	27.7	28.9	29.7	29.1	–	28.1	30.6	29.3
TX-2318	31.6	29.3	29.1	29.5	30.3	30.2	31.1	29.9
TX-2319	28.1	28.2	28.3	28.3	–	28.7	29.4	28.6
TX-2320	30.4	30.2	29.8	29.5	30.4	29.3	29.6	29.8
TX-2323	28.0	27.2	29.9	28.8	28.3	27.2	29.9	28.6
TX-2354	27.6	27.9	28.2	28.0	28.8	27.3	28.6	28.1
ELITE parent hybrid mean		28.6	28.9	28.7	29.1	28.2	29.7	

Table 6. Uniformity index of F_2 hybrids derived from crosses of 13 day-neutral landrace lines and six elite lines. The LSD between means at the two-tailed 95% probability level is 1.3%.

RACE parent	RACE parent mean	ELITE parent DES 119	Delta Pearl	Deltapine 90	MD 25	PD 94042	UA-48	RACE parent hybrid mean
		%						
ELITE parent mean		82.5	82.2	82.6	84.0	82.9	84.6	
TX-1147	83.2	83.5	83.4	82.6	83.8	83.6	83.9	
TX-1151	82.7	83.5	83.9	83.7	84.1	82.3	83.7	83.5
TX-1306	84.2	83.5	83.1	82.9	84.1	83.9	84.0	83.6
TX-1321	83.2	82.8	83.9	83.0	83.6	82.6	83.7	83.3
TX-1326	83.6	83.1	83.5	83.3	84.5	83.5	84.4	83.7
TX-1327	82.6	83.3	84.0	82.8	83.3	83.6	83.6	83.4
TX-2074	83.8	82.0	82.5	82.4	82.1	82.2	82.9	82.3
TX-2315	82.1	82.8	83.0	83.3	–	82.8	84.0	83.2
TX-2318	84.3	83.0	82.3	83.3	83.5	83.8	84.0	83.3
TX-2319	83.5	82.2	82.9	82.8	–	83.6	83.7	83.0
TX-2320	84.0	83.8	83.1	83.2	84.3	83.4	84.4	83.7
TX-2323	83.4	82.1	83.7	82.7	83.2	83.3	83.7	83.2
TX-2354	83.4	82.6	83.5	83.1	83.8	83.2	83.4	83.3
ELITE parent hybrid mean		82.9	83.3	83.0	83.7	83.2	83.8	

Table 7. Micronaire of F_2 hybrids derived from crosses of 13 day-neutral landrace lines and six elite lines. The LSD between means at the two-tailed 95% probability level is 0.42 units.

RACE parent	RACE parent mean	ELITE parent DES 119	Delta Pearl	Deltapine 90	MD 25	PD 94042	UA-48	RACE parent hybrid mean
		units						
ELITE parent mean		4.31	4.61	4.76	4.43	4.73	4.94	
TX-1147	3.96	4.40	4.43	4.23	4.29	4.53	4.36	4.37
TX-1151	3.91	4.37	4.57	4.48	4.18	3.87	4.40	4.31
TX-1306	4.41	4.44	4.67	4.48	4.54	4.78	4.51	4.57
TX-1321	4.03	4.62	4.48	4.26	4.29	4.32	4.46	4.40
TX-1326	4.44	4.72	4.46	4.57	4.48	4.64	4.88	4.62
TX-1327	3.63	4.64	4.31	4.64	4.61	4.41	4.72	4.56
TX-2074	4.80	4.54	4.59	4.73	4.61	4.74	4.66	4.65
TX-2315	4.60	4.50	4.34	4.57	–	4.47	4.54	4.48
TX-2318	4.02	4.49	4.64	4.38	4.26	3.99	4.31	4.34
TX-2319	4.56	4.27	4.75	4.43	–	4.54	4.71	4.54
TX-2320	3.42	3.97	4.16	4.53	4.30	4.06	4.43	4.24
TX-2323	4.49	4.80	4.46	4.63	4.58	4.83	4.76	4.68
TX-2354	4.58	4.61	4.37	4.62	4.40	4.47	4.62	4.51
ELITE parent hybrid mean		4.49	4.48	4.50	4.41	4.43	4.57	

strength ELITE line Deltapine 90. Four of the six hybrids with TX-2320 produced fiber strength equal to the high strength ELITE line UA-48.

Fiber Length

Two of the RACE lines (TX-2318 and TX-2320) produced fiber length equivalent to the high-length ELITE line UA-48. The remaining RACE lines produced fiber length greater than (five) or equal (six) to the low-length ELITE lines (Deltapine 90 and PD 94042). Fourteen F_2 hybrids produced fiber lengths equal to the high-length ELITE line UA-48. The remaining F_2 hybrids produced fiber length equal to or greater than the lowest length ELITE lines, Deltapine 90 and PD 94042. Three of the six F_2 hybrids with TX-2320 produced fiber lengths equivalent to UA-48.

Uniformity index

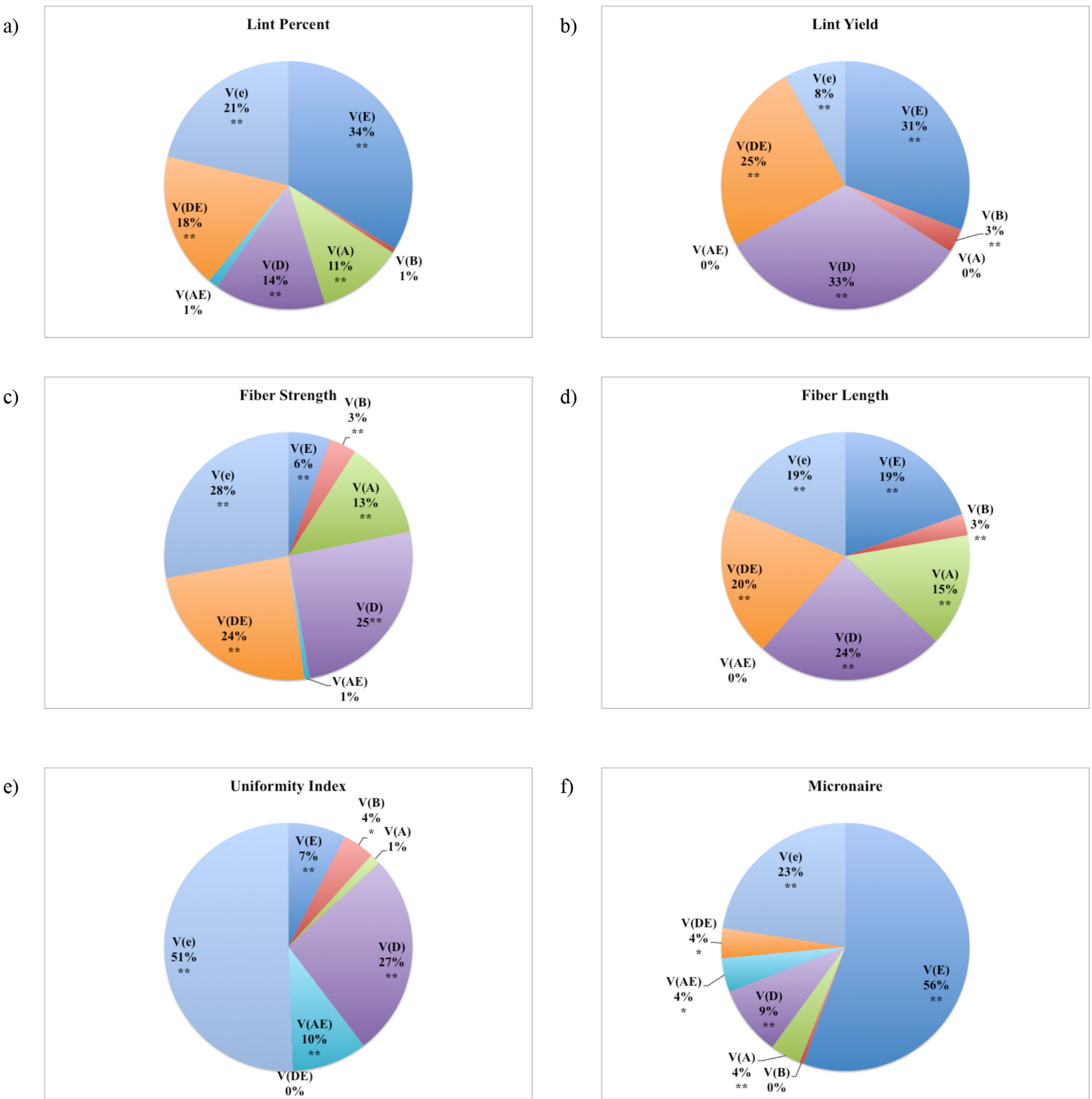
Eight of the RACE lines produced uniformity index equivalent to the high-uniformity ELITE line UA-48. The remaining RACE lines produced uniformity index equivalent to the lowest uniformity ELITE line, Delta Pearl. The majority of F_2 hybrids (53) produced uniformity index equivalent to UA-48. Five of the six F_2 hybrids with TX-1326 produced uniformity index equivalent to UA-48.

Micronaire

Two of the RACE lines (TX-1327 and TX-2320) produced micronaire lower than the lowest micronaire ELITE line, DES 119. None of the RACE lines or F_2 hybrids produced micronaire higher than the highest micronaire ELITE line, UA-48. Only one F_2 hybrid (TX-1151/PD 94042) produced micronaire lower than DES 119.

Variance Components

Variance components were estimated and expressed as proportions of the phenotypic variance (Fig. 1). Variance components for environment, dominance, and residuals were significant ($p < 0.01$) for all phenotypic traits. Additive effects were significant for lint percentage, fiber strength, fiber length, and micronaire. Additive × environment interactions were significant only for uniformity index and micronaire; however, dominance × environment interactions were significant for lint percentage, lint yield, fiber strength, fiber length, and micronaire. Additive effects



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

Fig. 1. Variance components for, environment [V(E)], block [V(B)], additive [V(A)], dominance [V(D)], additive × environment [V(AE)], dominance × environment [V(DE)], and residual [V(e)], expressed as proportions of the phenotypic variances for agronomic and fiber quality traits collected in three environments in 2013 and 2014.

accounted for between 4 (micronaire) and 15% (fiber length) of the total variance. Dominance effects accounted for between 9 (micronaire) and 33% (lint yield) of the total variance. Dominance × environment interactions accounted for between 4 (micronaire and 25% (lint yield) of the total variance. Environment accounted for between 6 (fiber strength) and 56% (micronaire) of the total variance. Residuals accounted for between 8 (lint yield) and 51% (uniformity index) of the total variance. Consistent with other recent cotton combining ability studies, additive × environment interactions were negligible (Jenkins et al., 2009; Zeng and Wu, 2012). Not surprisingly, the proportion each variance component contributed to the total variance differed from previous studies (Jenkins et al., 2009; Zeng and Wu, 2012). Zeng et al. (2011) noted that variance component proportions often differ due to differences in the genotypes being evaluated.

Predicted Genetic Effects

To assess the breeding potential of the 13 RACE lines used in this study, we predicted additive and dominance effects for each trait. The genetic effect predictions can be translated as follows: (i) additive effects represent general combining ability, (ii) homozygous dominance effects represent inbreeding depression, and (iii) heterozygous dominance effects represent specific combining ability (Jenkins et al., 2009). We tested if each genetic effect was different than zero. Predicted genetic effects were also compared between the 13 RACE lines and the six ELITE lines.

Additive and dominance effects and their SEs were predicted on a per trait basis and are provided in Fig. 2. For lint percentage, three RACE lines (TX-1151, TX-1306, and TX-2354) displayed positive additive effects, and six (TX-1321, TX-1327, TX-2074, TX-2315, TX-2318, and TX-2319) displayed positive dominance effects. Seven RACE lines displayed negative additive effects, and three displayed negative dominance effects. Five RACE lines (TX-1151, TX-2074, TX-2315, TX-2318, and TX-2319) displayed additive and dominance effects in the opposite direction. TX-2320 displayed negative additive and dominance effects for lint percentage. In comparison, the ELITE lines showed positive additive and dominance effects for lint percentage. The lone exception was DES-119, which displayed a negative dominance effect.

Additive and dominance effects for lint yield were negligible. None of the RACE or ELITE lines displayed significant additive effects. Among the RACE lines, TX-1326 and TX-2319 showed positive dominance effects for lint yield, whereas five (TX-1151, TX-1321, TX-1327, TX-2074, and TX-2323) displayed negative dominance effects. In comparison, three of the six ELITE lines showed negative dominance effects for lint yield.

For fiber strength, four RACE lines (TX-1147, TX-1326, TX-2318, and TX-2320) displayed positive additive effects, and two (TX-2074 and TX-2354) displayed positive dominance effects. Six RACE lines displayed negative additive effects and four displayed negative dominance effects. TX-1147, TX-1326, TX-2074, TX-2320, and TX-2354 displayed additive and dominance effects in the opposite direction. Considering ELITE lines, two (MD-25 and UA-48) showed positive additive effects and one (UA-48) showed positive additive and dominance effects. Three of the six ELITE lines showed negative dominance effects, and two displayed negative additive effects.

For fiber length, seven of the RACE lines (TX-1147, TX-1151, TX-1321, TX-1327, TX-2315, TX-2318, and TX-2320) displayed positive additive effects, whereas two displayed positive dominance effects. TX-2318 and TX-2320 displayed positive additive and dominance effects for fiber length. Six of the thirteen RACE lines displayed negative dominance effects. TX-1151, TX-1321, TX-2074, and TX-2315 displayed additive and dominance effects in the opposite direction. Considering ELITE lines, only two (Delta Pearl and UA-48) showed positive additive and/or dominance effects.

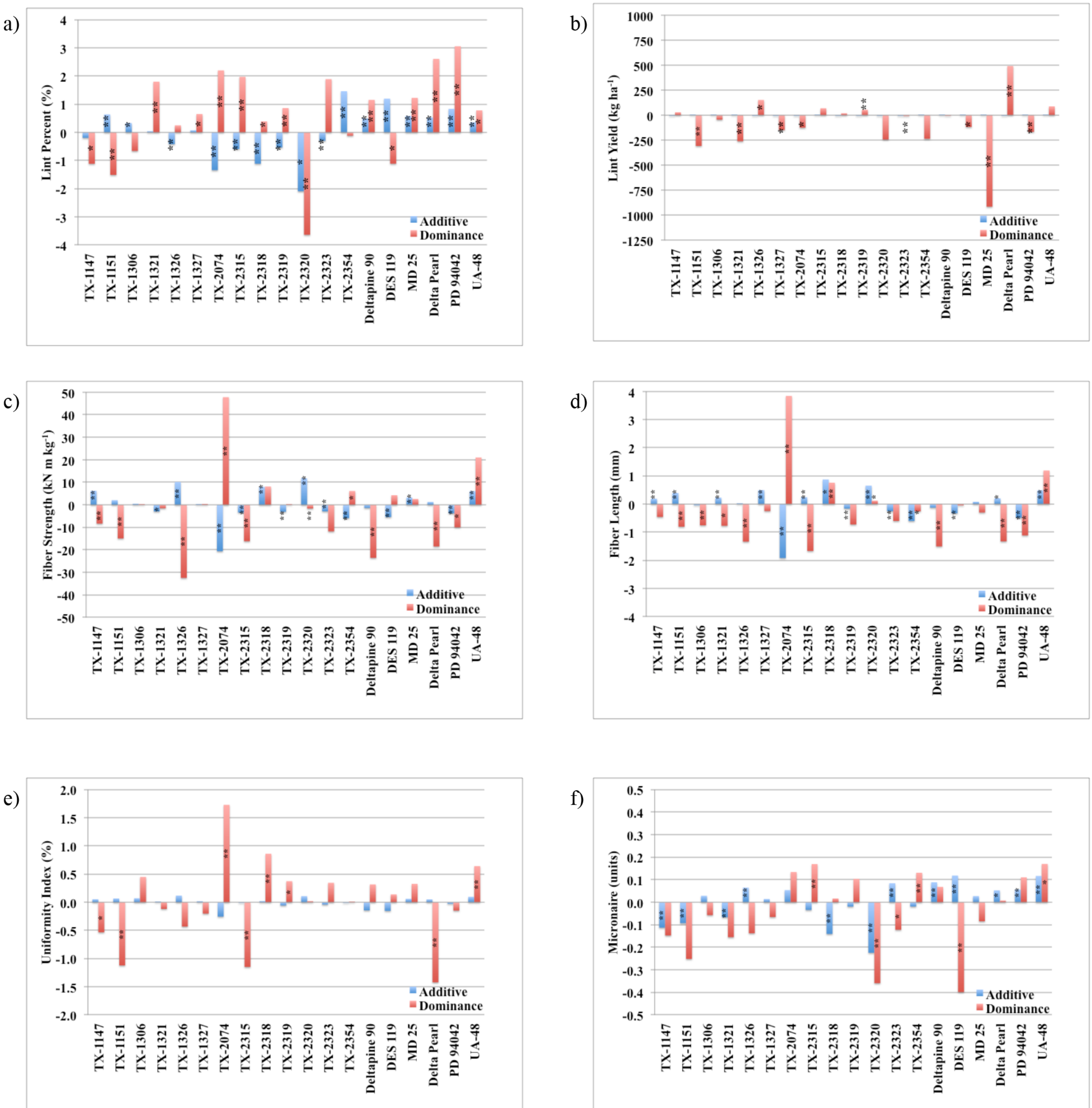
For uniformity index, additive and dominance effects were negligible. None of the RACE or ELITE lines displayed significant additive effects. Three RACE lines (TX-2074, TX-2318, and TX-2319) and one ELITE line (UA-48) showed positive dominance effects for uniformity index. Three RACE lines (TX-1147, TX-1151, and TX-2315) and one ELITE line (Delta Pearl) showed negative dominance effects for uniformity index.

For micronaire, five RACE lines (TX-1147, TX-1151, TX-1321, TX-2318, and TX-2320) displayed negative additive effects (lower micronaire, preferred), and two (TX-2320 and TX-2323) displayed negative dominance effects (lower micronaire, preferred). Two RACE lines (TX-1326 and TX-2323) displayed positive additive effects (higher micronaire, not preferred), and two (TX-2315 and TX-2354) displayed positive dominance effects (higher micronaire, not preferred). TX-2320 displayed negative additive and dominance effects for micronaire. TX-2323 displayed additive and dominance effects in the opposite direction. Considering ELITE lines, DES-119 displayed additive and dominance effects in the opposite direction for micronaire. Three ELITE lines (Delta Pearl, PD 94042, and UA-48) displayed positive additive effects for micronaire.

Heterozygous dominance effects were predicted and their SEs were estimated; however, no strong trends were evident (data not shown). This suggests heterozygous dominance effects differed depending on the specific RACE × ELITE line cross combination.

DISCUSSION

In general, landrace accessions represent unexploited genetics within cotton improvement. Up to the present time, they have been used to develop day-neutral converted



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

Fig. 2. Predicted additive and nonadditive effects for (a) lint percentage, (b) lint yield, (c) fiber strength, (d) fiber length, (e) uniformity index, and (f) micronaire expressed as deviations from the grand mean for three environments in 2013 and 2014.

germplasm lines from photoperiod sensitive landrace accessions followed by studies to assess their breeding potential (McCarty et al., 2004a, 2004b, 2007, 2008).

In this study, our goal was to evaluate populations derived from a number of naturally occurring day-neutral landrace (RACE) genotypes when mated with a number of elite upland germplasm lines and cultivars. Overall, RACE genotypes and hybrids derived from them demonstrated excellent fiber quality and average agronomic performance, similar to previous studies using day-neutral converted germplasm lines (McCarty et al. (1996, 1998a, 1998b, 2004a, 2004b, 2006, 2007, 2008). In those studies, RACE-ELITE populations showed low lint percentage, average lint yield, and good fiber quality.

Considering main effects, additive and dominance were present for lint percentage, fiber strength, fiber length, and micronaire, whereas only dominance was present for lint yield and uniformity index (Fig. 1). Phenotypic observations supported these genetic effect estimates (Tables 2–7). Environment explained a large part of the total variation for lint percentage, lint yield, and micronaire. Additive × environment interactions explained a small portion of the total variation for uniformity index and micronaire. Dominance × environment interactions explained a portion of the total variation for lint percentage, lint yield, fiber strength, fiber length, and micronaire. This was especially true for lint percentage, lint yield, fiber strength, and fiber length, for which dominance × environment interactions explained 18 to 25% of the total variation. The presence of additive, dominance, and dominance × environment interactions is similar to previous reports using day-neutral converted germplasm lines and different topcross parents (McCarty et al., 2004a, 2007). In the current study, relative to the additive component, dominance explained a much larger proportion of the total variation for lint yield, fiber strength, fiber length, uniformity index, and micronaire. This finding supports the idea that many alleles present in landrace genotypes and elite upland germplasm interact with one another in a nonadditive way (Campbell et al., 2014).

On average, predicted genetic effects indicated that RACE genotypes transmitted both negative and positive additive effects for lint percentage, fiber strength, fiber length, and micronaire. Negligible additive effects were predicted for lint yield and uniformity index, although positive and negative dominance effects were predicted for both traits. For lint percentage, fiber strength, and fiber length, several RACE genotypes displayed additive and dominance effects in the opposite direction. Of the RACE genotypes, TX-2074 showed significant dominance (positive) and additive (negative) effects in the opposite direction for lint percentage, fiber strength, and fiber length. This likely indicates that TX-2074 has poor general combining ability as offspring performance was inconsistent across ELITE line combinations.

Overall, this study demonstrated that decreased agronomic performance is not accompanied by a large decrease in fiber quality. However, in comparison with a study using day-neutral converted germplasm lines (Campbell et al., 2014), breeding populations derived from the RACE genotypes used in the current study appear to have a lessened negative impact on agronomic performance with the exception of TX-2320. Moreover, the significant genetic effects identified in this study indicate that these RACE genotypes contain and transmit new, beneficial alleles. Liu et al. (2000) reported that many day-neutral converted germplasm lines shared >75% alleles at marker loci with typical upland cotton. It is unclear whether the high percentage of shared alleles is a result of the backcrossing scheme used to develop the converted lines or is a consequence of high genetic similarity between the specific landraces and upland lines used in the study. Shared alleles between the RACE lines used in this study and upland cotton were not assayed, but this knowledge would be beneficial to quantify their genetic similarity. Similar to the findings presented by Campbell et al. (2014) using day-neutral converted germplasm lines, it is likely that RACE genotypes transfer negatively correlated alleles for agronomic and fiber quality performance. Therefore, using these germplasm in contemporary breeding programs will require methods designed to break negative linkages between agronomic performance and fiber quality.

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