

BREEDING AND GENETICS

Evaluation of an Exotic Germplasm Population Derived from Multiple Crosses among *Gossypium* Tetraploid Species

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ABSTRACT

Broadening the genetic base of upland cotton (*Gossypium hirsutum* L.) is essential for continuous genetic improvement of yield and fiber quality through breeding. The objectives of this study were to evaluate a species polycross (SP) population for phenotypic and genotypic variations in yield and fiber quality, investigate morphological variations among the SP lines, and analyze the interrelationships among yield, yield components, and fiber properties. A population was developed by crossing cultivars and strains of *G. hirsutum* with the other tetraploid species in the genus. This SP population underwent 11 yr of random mating by natural pollination in an isolated environment with high bee activity followed by 12 yr of selfing. The experiment was conducted at two field locations with two replicates each. Two hundred and sixty lines of the SP population were evaluated with five commercial cultivars. Genotypic variation was significant ($P < 0.01$) for all characters of yield and fiber quality. Although a highly significant ($P < 0.01$) interaction between genotype and location was identified for fiber strength and most yield parameters, the interaction components were small relative to the genotypic components. There was large variation among the SP lines for nectary size, gland content in leaves, pubescence, leaf cut depth, plant height, leaf area, leaf length, and node number of the first fruiting branch. Span length (50%) contributed more variation to fiber strength than span length (2.5%) in the SP population. Lint yield was negatively correlated with short fiber content. It is concluded that the SP population is a useful germplasm for genetic improvement of lint yield and fiber quality.

The U.S. cotton production and textile industry underwent dramatic changes in recent years under the influence of the global cotton market. Domestic demand for cotton by the U.S. textile industry declined from 11.3 million bales in 1997 to 6.2 million bales in 2004 (USDA-FAS, 2004). Cotton production in the United States has become dependent on exports, which increased from 40% in 1997 to 70% in 2006 (Adams, 2006). The surviving U.S. textile industry faces a challenge to improve its competitiveness and increase domestic demand. In the recent years, the industry integrated new technology, such as open-end and air-jet looms, that increased spinning speed about 3 to 6 times (Felker, 2001). Modernizing equipment will no doubt improve production efficiency and the competitiveness of U.S. textile products. It also raised the requirements for fiber quality to maximize the efficiency of high spinning equipment. The new technology requires stronger and longer fibers and fewer short fibers. The pressure to improve fiber quality of U.S. cotton also comes from international customers who require high fiber quality with less short fiber content. Unfortunately, high yield cultivars in the United States do not possess high fiber quality that can meet these standards. Cotton breeders may not have done enough to improve U.S. cotton in the past. In reference to that lack of improvement, one industrial representative stated, “we have had to compromise on the quality of raw cotton” (Felker, 2001, p. 5).

Fiber quality, especially strength and length, can only be effectively improved through genetic breeding. This is evidenced by high heritability of fiber quality reported in previous studies. In those studies, heritability for fiber strength and length ranged from 0.52 to 0.90 and 0.46 to 0.79, respectively (Al-Jibouri et al., 1958; Miller et al., 1958; Al-Rawi and Kohel, 1969; Baker and Verhalen, 1973). Genetic diversity in cultivated cotton, however, is generally considered limited (May et al., 1995; Esbroeck and Bowman, 1998; McCarty et al., 2005). It is essential to broaden the genetic base in upland cotton for continuous genetic improvement of yield and fiber

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quality. Exploration and introduction of novel genes from exotic germplasm can be a major approach for broadening the genetic base in upland cotton.

Based on the genomic affinities among the species of *Gossypium*, Stewart (1994) classified the germplasm pools within the genus into three categories: primary, secondary, and tertiary. Based on his classification, the primary pool includes the species that can be easily crossed and produce highly fertile hybrids. All tetraploid species belong to this group. The germplasm resources in this group can be relatively easily utilized in the breeding programs in upland cotton. The crosses of the species in secondary and tertiary pools with upland cotton usually generate low fertile hybrids, unless special manipulation is involved. Land races of *G. hirsutum* and wild tetraploid species have been used in breeding to transfer desirable morphological characters, such as nectariless and smooth leaf (Meyer and Meyer, 1961; Percy and Kohel, 1999), and disease and insect resistance genes, such as bacterial blight resistance, boll worm resistance, and Fusarium wilt resistance, into upland cotton (Meredith, 1991; Stewart, 1994).

Overall, the number of successful cultivars with an exotic germplasm background is small. Lack of adaptability to environments and appropriate evaluation of existing germplasm resources are two major reasons for their limited use in breeding (McCarty et al., 1996; Esbroeck and Bowman, 1998). McCarty et al. (1979) incorporated day-neutrality genes into tropical germplasm accessions through back-crossing. The incorporation of day-neutral genes into primitive landraces has facilitated the use of this germplasm; however, the conversion requires many generations of crosses and selection for day-neutral genes and the subsequent recovery of primitive genes. Furthermore, linkage drag could reduce the originality of the landraces during the introgression of day-neutral genes (Zhong et al., 2002). The exploration of regionally adapted germplasm derived from wide crosses could be an alternative approach to the utilization of the exotic germplasm resources in breeding.

Yield of cotton can be determined by boll number per unit area, boll size, and lint percentage (Worley et al., 1974; Culp and Harrell, 1975) or by boll number per unit area, seeds per boll, and lint per seed (Coyle and Smith, 1997). Lint percentage is critical for maintaining high lint yield (Culp and Harrell, 1975) and is largely related to boll size and seed size. High lint percentage can be maintained by selecting for maximum seed surface per unit area

(Coyle and Smith, 1997). Yield can be increased by increasing boll number per unit area, seed number per boll, and seed surface per unit seed weight. Interrelationships between lint yield and fiber quality have been studied extensively (Miller et al., 1958; Stewart and Kerr, 1974; Culp and Harrell, 1975; Scholl and Miller, 1976; Wilson et al., 1994; McCarty et al., 1996; Smith and Coyle, 1997). The interrelationships between yield parameters and fiber properties are complicated. Generally, a negative correlation between lint yield and fiber strength has been shown in these studies. The correlation between lint yield and lint percentage, bolls per plant, micronaire, and fiber elongation is positive, while the correlation between lint yield and boll weight and seed index is negative. Genetic correlation of lint percentage with lint yield and bolls per plant was determined to be 0.80 and 0.48, respectively, while that with seed index, boll weight, fiber strength, fiber length, and fineness was -0.60, -0.36, -0.12, -0.52, and -0.31, respectively (Miller et al., 1958). The mechanism underlying genetic correlation could be either linkage or pleiotropy (Meredith, 1984).

The objectives of this experiment were to evaluate the phenotypic and genotypic variation of yield, yield components, and fiber properties; to investigate phenotypic variation of morphological characters; and to analyze interrelationships among yield, yield components, and fiber properties in a regionally adapted exotic germplasm population.

MATERIAL AND METHODS

An exotic germplasm population was obtained from P.A. Miller who initiated the study in 1967. The population was developed by crossing twelve cultivars of *G. hirsutum* and strains with four tetraploid species: *G. barbadense* L., *G. tomentosum* Nutt., *G. mustelinum* Watt., and *G. darwinii* Watt. The entries in *G. hirsutum* include four commercial cultivars, Auburn M., Carolina Queen, Stoneville 213, and Deltapine Smooth Leaf, and eight strains, TH 149-20, PD 2165, Coker 413, Ga. H.T., Atlas (AxC)-261, Deltapine 523, Mo. 61-470, and Stoneville 508-9117. All the strains except Stoneville 508-9117 have genetic background of Beasley's Triple hybrid [(*G. arboreum* L. x *G. thurberi* L.) x *G. hirsutum*] and contributions from *G. barbadense*. All the entries in *G. hirsutum* were evaluated in Regional Variety Tests at multiple locations in the United States during 1965. The exact strains of the four tetraploid species

used in the crosses as parents and the crossing pattern are unknown. All 12 entries of *G. hirsutum* and the other four tetraploid species were involved in the initial crosses and the subsequent development of the population. Seeds of the F₂ were produced in a winter nursery located in Mexico and planted in 1968 in a small isolated field surrounded by woods in Raleigh, NC. Bee activity was known to be high in the area. From 1968 to 1978, the population was maintained by natural pollinations. Observations were made in the field, and natural crosses were estimated to exceed 50%. In 1979, a sub-sample of this population was grown at Stoneville, MS, under a predominately self-pollinating environment. The population (2,000 plants) was maintained and advanced by harvesting one boll from each plant and bulking the harvested bolls for planting the next generation. The population was planted in this way almost every other year until 2004. As a result, the population planted in 2004 underwent random mating for 11 generations and predominantly selfing for 12 generations. In 2004, 260 plants were randomly chosen and 15 to 20 bolls were collected from each plant. The seeds from each plant were planted as one line in 2005 in the evaluation trial.

Two hundred and sixty lines were planted in fields for germplasm evaluation at Stoneville, MS, in the summer of 2005. The experimental design was a randomized complete block with two locations and two replicates at each location. Five cultivars, Deltapine 555BR (DP555BR; Delta Pine and Land Co.; Scott, MA), Stoneville 4892BR (ST4892BR; Stoneville Pedigreed Seed; Memphis, TN), FiberMax 960B₂R (FM960B₂R; Bayer Crop Sciences; Research Triangle Park, NC), Phytogen 72 (PHY72; Phytogen Seed Co.; Indianapolis, IN), and Paymaster 2167R (PM2167R; Delta Pine and Land Co.), used as standards in the National Cotton Variety Trial, were also planted as checks with four replicates at each location. The germplasm lines and cultivars were grown in single-row plots, each 4.57 m long on a 1.0-m row spacing. Soil types were Beulah fine sandy loam (a coarse-loamy, mixed, active, thermic Typic Dystrochrepts) for Location 1 and Bosket fine sandy loam (a fine-loamy, mixed, active, thermic Mollic Hapludalf) for Location 2. Seeds were planted on 19 Apr. 2005 at Location 1 and 5 May 2005 at Location 2. Plant stand of each plot was counted and recorded. The plant stand ranged from 25 to 70 plants plot⁻¹. Plots were thinned to 25 to 40 plants plot⁻¹.

At harvest, 30 bolls from each plot were sampled by hand. The samples from individual plots were ginned separately using a laboratory saw gin. Seed weight and lint weight from the sample of each plot were measured and recorded. Remaining bolls from each plot were also harvested by hand to determine yield. Seed cotton weight of plots was measured and recorded individually. The total seed cotton weight of each plot was calculated as sum of the seed cotton weight of the sampled bolls and the remaining bolls in that plot. Yield parameters were calculated from these measurements: lint percentage = (100) (the lint weight from the sample/seed cotton weight of the sample); boll weight = seed cotton weight per sample/30; lint weight per seed = lint weight per sample/[(seed weight per sample)/(seed index)]; seeds per boll = [(seed weight per sample)/(seed index)]/30; lint yield per plot = (seed cotton weight per plot)(lint percentage). Twenty to twenty-five grams of lint were submitted to StarLab, Knoxville, TN, for Breeder's Analysis of fiber quality. Fiber strength was measured as the force per tex required to break a bundle of fibers. Elongation was the percentage of elongation at the point of break in strength determination. Fiber span lengths were measured as the average length of the longest 50 and 2.5% of the fibers scanned. Fibers were also analyzed for mean short fiber content using the Automated Fiber Information System (AFIS). Mean short fiber content is the percentage by weight of the fibers that are less than 12.7 mm. Fiber fineness and maturity were measured separately using AFIS in that fineness was the weight of fibers per unit of length in millitex, and maturity ratio was the proportion of mature fibers to the immature fibers.

Eight morphological characters, nectary size, gland content in leaf, pubescence, node of the first fruiting branch, cut depth in leaf, plant height, leaf length, and leaf area, were measured in all plots. Gland content in leaf was estimated by counting the number of glands per unit leaf area under a biological microscope at peak flowering. In doing so, a young leaf from the top of the plant was collected from each plot. A field of vision under the microscope was randomly chosen along the main vein on the leaves using a circle with known diameter on a stage micrometer. The glands were counted within the circle. The measurements were conducted the same way on top, middle, and bottom along the main vein of each leaf, respectively. The readings were averaged across the three measurements for each sample. Pubescence was

scored among the plots according to a rating system (Bourland et al., 2003) as follows: 1-pilose, 2-very hairy, 3-hairy, 4, 5-intermediate, 6-nearly smooth, 7-very smooth. The depth of leaf cut was scored among the plots according to a rating system as follows: 1=0 to 25%, 2=25 to 50%, 3=50 to 75%, and 4=75 to 100%. Leaf area was measured on the fourth fully extended leaf from the top of a plant using a Li-3100 Area Meter (LI-COR Inc.; Lincoln, NE) at the stage of peak flowering. Leaf samples of five plants from each plot were scanned as one measurement of leaf area. The readings were averaged for each plot. Nodes of the first fruiting branch were counted as the node number above the cotyledon node on the main stem.

The GLM procedure of the Statistical Analysis System (version 6; SAS Institute; Cary, NC) was used for analysis of variance on all data. A mixed model was used with germplasm lines as the random effect and location as the fixed effect. Correlation between yield and fiber quality was analyzed with a linear regression model. Genetic correlation (R_g) among yield parameters and fiber properties were calculated using the equation described by Kempthorne (1957):

$$\begin{aligned} R_g &= \sigma_{gxy} / (\sigma_{g_x}^2 \sigma_{g_y}^2)^{1/2}, \sigma_{g_x}^2 \\ &= 1/r (V_x - V_{ex}), \sigma_{g_y}^2 \\ &= 1/r (V_y - V_{ey}), \sigma_{gxy} \\ &= 1/r (Cov_{xy} - Cov_{exy}) \end{aligned}$$

where σ_{gxy} is the genetic component of covariance between variable x and y; $\sigma_{g_x}^2$ and $\sigma_{g_y}^2$ are genetic components of variance for x and y, respectively; V_x and V_y are variances of x and y, respectively; V_{ex} and V_{ey} are errors for x and y, respectively; r is the number of replicates. Locations were treated as replicates for the calculation of genetic correlation. Variance and covariance for yield parameters and fiber properties were calculated by creating a matrix using MANOVA statement in PROC GLM procedures (SAS Institute).

The significance of R_g was not determined, because there was no adequate probability table available for a statistical test of genetic correlation. The means of the SP population were compared with the averages of the cultivars using *t*-tests assuming unequal variances in the SP population and cultivars. Mean squares of the G x L interaction in the SP population (df = 1040) and cultivars (df = 40) were used as experiment errors to test significance in the *t*-tests.

RESULTS

Mean squares for yield, yield components, and fiber properties of the SP population are given in Table 1. Genotype (G) effects were highly significant ($P < 0.01$ or 0.001) for all characters. Mean squares of location (L) were large relative to the G and G x L interaction for yield and yield components except lint percentage. The G x L interaction was highly significant ($P < 0.01$ or 0.001) for yield, lint percentage, lint/seed, and seed weight. The mean squares of location for fiber properties were similar to those for genotype except micronaire, which was over 80 times greater than that of genotype. The G x L interaction was not significant for most fiber properties, but was highly significant ($P < 0.01$) for fiber strength. The G x L interaction for fiber strength, however, was small relative to the genotype, only 0.15 times as large as the genotypic effect.

The averages of lint yield and fiber properties for the five cultivars are given in Table 2. The two Mid-south cultivars, DP555BR and ST4892BR, averaged 395.5 g/plot for yield, 201 kN m kg⁻¹ for fiber strength, 13.8 for 50% span length, 28.4 mm for 2.5 % span length, and 5.93% for short fiber content. The average yield of the two high fiber quality cultivars, FM960B₂R and PHY72, was 247 g/plot, 38% less than the average between DP555BR and

Table 1. Mean squares of genotype and location for yield and fiber properties in species polycross (SP) population

| Source | df | Fiber properties and yield ^z | | | | | | | | | | | |
|--------------|-----|---|----------|-------------|--|--|-------------|-------------|------------|----------|--------------------------------|---------------------------------|-------------|
| | | Yield (x10 ⁻³) | Lint (%) | Boll weight | Lint seed ⁻¹ (x10 ⁻²) | Seeds boll ⁻¹ (10 ⁻²) | Seed weight | Micro-naire | Elongation | Strength | 50% length (x10 ²) | 2.5% length (x10 ²) | Short fiber |
| Location (L) | 1 | 970** | 3.8 | 2.8* | 14** | 12** | 80** | 68.6** | 0.02 | 21.8** | 0.22* | 2.00** | 0.20 |
| Genotype (G) | 259 | 13** | 28** | 1.5** | 1.3** | 0.29** | 4.3** | 0.82** | 2.7** | 11** | 0.14** | 1.08** | 3.2* |
| G x L | 259 | 4.2** | 3.3** | 0.33 | 0.29** | 0.10 | 0.53* | 0.12 | 0.48 | 1.6* | 0.03 | 0.08 | 2.2 |
| Error | 518 | 3.0 | 2.4 | 0.32 | 0.21 | 0.10 | 0.42 | 0.10 | 0.52 | 1.2 | 0.03 | 0.07 | 2.4 |

^zValues followed by *, ** are significantly different at $P < 0.01$, $P < 0.001$, respectively.

ST4892BR. The fiber strength of these two cultivars averaged 242 kN m kg⁻¹, 20% higher than the two Mid-south cultivars. Fiber length of the two high quality cultivars averaged 14.3 and 29.9 mm for 50% span length and 2.5% span length, respectively. Short fiber content averaged 5.17 % between the two high quality cultivars, 12.8 % less than the average of the two Mid-south cultivars. Moderate lint yield and low fiber strength and span length were observed in Acala type cultivar, PM2167R. These results indicated a general negative association between lint yield and fiber quality. Yield parameters and fiber properties in the SP population were compared with the cultivars using *t*-tests assuming unequal variances in SP population and cultivars (Table 2). The means of the SP population for micronaire, fiber strength, and 50% span length were significantly ($P \leq 0.01$) different from the averages of the five cultivars. There was a

significant ($P \leq 0.01$) difference between SP population and the cultivars for all lint yield characters except seeds per boll. There was a wide variation among SP lines for these parameters. Lint percentage was significantly lower in the SP population than the average of the standards, while seed weight and boll weight were significantly higher than the standards. Generally, wide ranges were identified for all the characters analyzed in the SP population.

Seven of the SP lines with lint yield greater than 300 g plot⁻¹ and fiber strength greater than 230 kN m kg⁻¹ were identified as elite genotypes (Table 3). All these lines performed good with yield ranging from 301 to 379 g plot⁻¹ and fiber strength ranging from 231 to 242 kN m kg⁻¹. Among them, SP-103 performed the best with 379 g plot⁻¹ for yield, 38% higher than FM960B₂R, and 242 kN m kg⁻¹ for fiber strength, 4% higher than FM960B₂R.

Table 2. Means and ranges of yield parameters and fiber properties in species polycross (SP) population and cultivars

| Source | Fiber properties and yield parameters ^z | | | | | | | | | | | |
|-----------------------|--|----------|-----------------|------------------------------|--------------------------------|------------------|------------|----------------|-----------------------------------|-----------------|------------------|-----------------|
| | Yield (g plot ⁻¹) | Lint (%) | Boll weight (g) | Lint seed ⁻¹ (mg) | Seeds boll ⁻¹ (no.) | Seed weight (mg) | Micronaire | Elongation (%) | Strength (kN m kg ⁻¹) | 50% Length (mm) | 2.5% Length (mm) | Short fiber (%) |
| DP555BR | 427 | 41 | 4.6 | 54 | 35 | 76 | 4.5 | 5.3 | 199 | 13.5 | 28.5 | 6.28 |
| ST4892BR | 364 | 38 | 4.8 | 61 | 30 | 102 | 4.4 | 6.2 | 203 | 14.0 | 28.2 | 5.58 |
| PM2167R | 291 | 36 | 5.0 | 52 | 34 | 95 | 4.5 | 6.5 | 202 | 13.2 | 25.7 | 5.26 |
| FM960B ₂ R | 275 | 35 | 5.2 | 58 | 32 | 106 | 3.9 | 5.1 | 232 | 14.0 | 29.5 | 4.94 |
| PHY72 | 219 | 36 | 4.8 | 53 | 33 | 94 | 4.1 | 7.0 | 252 | 14.5 | 30.2 | 5.39 |
| Cultivars | 315 | 37.2 | 4.9 | 55.6 | 32.8 | 95 | 4.3 | 6.0 | 218 | 13.7 | 28.5 | 5.49 |
| SP | 279*** | 32*** | 5.5*** | 53** | 33 | 113*** | 4.1** | 6.1 | 211*** | 14.0*** | 28.5 | 5.52 |
| SP range | 161-479 | 25-42 | 3.8-9.3 | 39-80 | 26-42 | 90-140 | 3.1-5.9 | 4.3-8.5 | 177-255 | 12.5-15.3 | 24-33 | 3.9-8.5 |

^z Values followed by **, *** are significantly different at $P < 0.01$, $P < 0.001$, respectively, in *t*-test comparisons for SP mean vs. cultivar average. Mean squares of the G x L interaction in the SP population (df = 1040) and cultivars (df = 40) were used as variances in the *t*-tests.

Table 3. Means of yield, yield components, and fiber properties in seven SP lines^z

| Genotype | Yield (g plot ⁻¹) | Lint (%) | Boll weight (g) | Lint seed ⁻¹ (mg) | Seeds boll ⁻¹ (no.) | Seed weight (mg) | Micronaire | Elongation (%) | Strength (kN m kg ⁻¹) | 50% Length (mm) | 2.5% Length (mm) | Short fiber (%) |
|----------|-------------------------------|----------|-----------------|------------------------------|--------------------------------|------------------|------------|----------------|-----------------------------------|-----------------|------------------|-----------------|
| SP-103 | 379 | 32 | 6.6 | 58 | 36 | 125 | 4.6 | 4.8 | 242 | 15.2 | 30.7 | 5.65 |
| SP-156 | 318 | 35 | 4.9 | 67 | 26 | 124 | 4.8 | 5.1 | 235 | 14.7 | 30.0 | 4.83 |
| SP-170 | 317 | 29 | 5.0 | 49 | 29 | 123 | 3.8 | 7.2 | 231 | 14.7 | 29.5 | 6.78 |
| SP-177 | 335 | 35 | 4.9 | 62 | 27 | 116 | 4.7 | 5.4 | 231 | 14.5 | 30.0 | 4.98 |
| SP-192 | 339 | 35 | 4.8 | 51 | 32 | 96 | 4.6 | 6.3 | 232 | 14.0 | 27.9 | 7.70 |
| SP-205 | 349 | 35 | 4.8 | 51 | 33 | 96 | 4.7 | 7.7 | 232 | 15.0 | 30.7 | 3.88 |
| SP-206 | 301 | 34 | 6.1 | 61 | 35 | 117 | 3.8 | 5.3 | 237 | 14.7 | 30.2 | 5.03 |

^z The lines were chosen with strength greater than 230 kN m kg⁻¹ and lint yield greater than 300 g plot⁻¹.

Correlation and genetic correlation between yield parameters and fiber properties are given in Table 4. Lint yield was positively correlated with all yield components analyzed except seed weight. Highly significant ($P < 0.001$) negative correlation was identified between lint yield and fiber strength. Lint yield was also negatively correlated with micronaire and short fiber content at $P < 0.05$ and 0.01 , respectively. Lint percentage was negatively correlated with boll weight and seed weight, but positively correlated with lint per seed. Negative correlation between lint percentage with fiber strength and with fiber lengths was also highly significant ($P < 0.001$). Although fiber strength was positively correlated with both properties of span lengths, higher correlation was observed with 50% span length than 2.5% span length. Genetic correlation of fiber strength with 50% span length was nearly double of that with 2.5% span length. Micronaire was significantly ($P < 0.001$) negatively correlated with 2.5% span length, but not correlated with 50% span length. There was no correlation between span length and short fiber content.

Eight morphological characters, nectary size, gland content in leaf, leaf pubescence, node number of the first fruiting branch, plant height, leaf area, leaf length, and leaf cut depth, were analyzed in the SP population (Table 5; Fig. 1). The means of the individual lines were calculated across locations and replicates. There were nine lines identified as nectariless (Fig. 1A). Although the mean of gland content in the SP population was 121 glands/cm², a wide range of densities was identified among the lines (Table 5). The gland content in one line was as low as 29 glands/cm², and another one as high as 175 glands/cm². Most lines were scored 4 to 5 for pubescence (intermediate pubescent), while nine lines scored greater than 6.5 (very smooth) (Fig. 1B). Most lines were scored as normal (25-50% depth of leaf cut), while 29 were scored as okra leaf (> 50% depth of leaf cut) (Fig. 1C). Wide variations were also identified for plant height, ranging from 119 to 175 cm, leaf area of 4th fully extended leaf, ranging from 79 to 196 cm², leaf length, ranging from 10.1 to 17.9 cm, and node number of the first fruiting branch, ranging from 5.5 to 11.8 (Table 5).

Table 4. Correlation and genetic correlation coefficients between yield parameters and fiber properties in SP population

| | Yield parameters and fiber properties ^x | | | | | | | | | | |
|--------------------------|--|-------------------|-------------------------|--------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|------------------|
| | Lint % | Boll weight | Lint seed ⁻¹ | Seeds boll ⁻¹ | Seed weight | Micronaire | Elongation | Strength | Length (50%) | Length (2.5%) | Short fiber |
| Yield | 0.38*** 0.46 | 0.23*** 0.24 | 0.31*** 0.50 | 0.22*** 0.13 | -0.11** -0.04 | -0.07* 0.08 | 0.03 -0.01 | -0.19*** -0.28 | 0.02 -0.11 | 0.06 -0.02 | -0.11** -0.12 |
| Lint % | | -0.16*** -0.23 | 0.69*** 0.70 | -0.14*** -0.17 | -0.47*** -0.56 | 0.27*** 0.32 | -0.02 -0.06 | -0.24*** -0.30 | -0.15*** -0.22 | -0.20*** -0.22 | 0.00 0.01 |
| Boll weight | | | 0.25*** 0.31 | 0.74*** 0.73 | 0.52*** 0.66 | -0.08* -0.13 | -0.19*** -0.23 | 0.03 0.02 | 0.17*** 0.14 | 0.26*** 0.25 | 0.02 -0.07 |
| Lint seed ⁻¹ | | | | -0.25*** -0.14 | 0.31*** 0.19 | 0.30*** 0.14 | -0.14** -0.22 | -0.10 -0.18 | 0.05 -0.02 | 0.04 0.03 | 0.00 0.03 |
| Seeds boll ⁻¹ | | | | | -0.12** 0.07 | -0.20*** -0.30 | -0.08* -0.08 | -0.04 -0.03 | 0.04 -0.01 | 0.11* 0.04 | 0.02 -0.09 |
| Seed weight | | | | | | 0.03 -0.27 | -0.15*** -0.19 | 0.17*** 0.19 | 0.25*** 0.28 | 0.30*** 0.33 | 0.01 -0.01 |
| Micronaire | | | | | | | -0.07* -0.15 | 0.07* 0.01 | 0.04 -0.05 | -0.31*** -0.41 | 0.04 0.04 |
| Elongation | | | | | | | | -0.05 -0.07 | 0.09** 0.12 | -0.01 -0.02 | 0.02 0.11 |
| Strength | | | | | | | | | 0.46*** 0.62 | 0.32*** 0.37 | 0.00 -0.02 |
| Length (50%) | | | | | | | | | | 0.73*** 0.75 | 0.00 0.03 |
| Length (2.5%) | | | | | | | | | | | -0.04 -0.02 |

^x Values followed by *, **, *** are significantly different at $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively, $df = 1038$ (error).

Upper values are correlation coefficients, and lower values are genetic correlation coefficients, based on Kempthorne's equation (1957).

Table 5. Means, standard deviations, and the ranges of five morphological characters in the species polycross population

| | Plant height (cm) | Leaf area (cm ²) ^x | Leaf length (cm) | Node number ^y | Gland content (no. cm ⁻²) ^z |
|-------|-------------------|---|------------------|--------------------------|--|
| Means | 149 ± 14 | 142 ± 25 | 13.0 ± 1.8 | 7.92 ± 1.86 | 121 ± 33 |
| Range | 119 - 175 | 79 - 196 | 10.1 - 17.9 | 5.5 - 11.8 | 29.2 - 175 |

^x Leaf area was measured from the fourth fully extended leaf on the top of the main stem.

^y Node number above the cotyledon and below the first fruiting branch.

^z Gland content in leaf was measured as the number of glands in the third fully extended leaf on the top of the main stem at peak flowering.

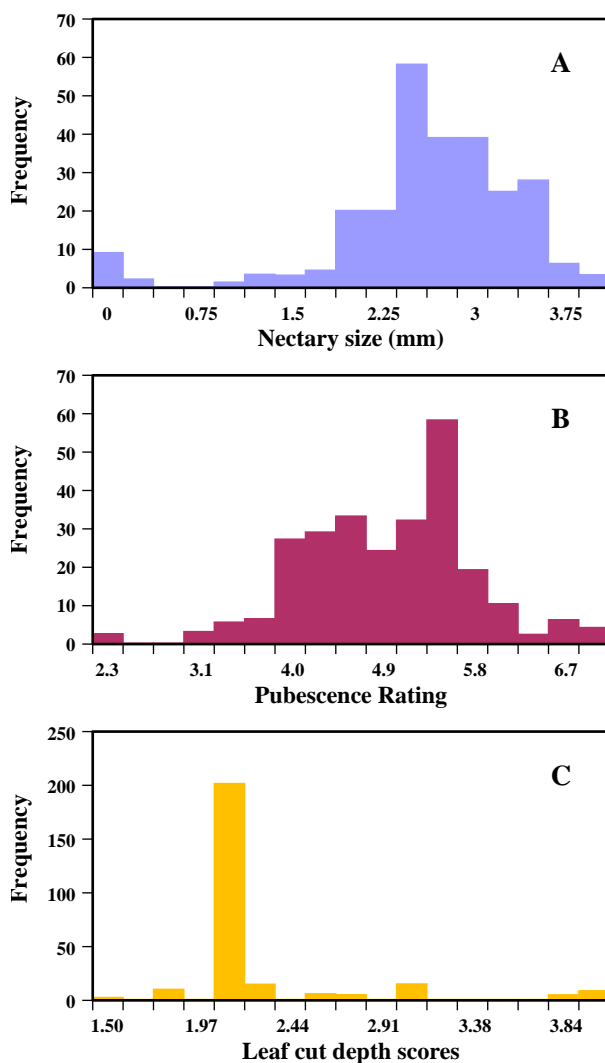


Fig. 1. Means of nectary size (A), pubescence (B), and scores of leaf cut depth (C), and their distribution among species polycross lines. Pubescence was scored according to a rating system: 1-pilose, 2-very hairy, 3-hairy, 4, 5-intermediate, 6-nearly smooth, 7-very smooth. Leaf cut depth was scored according to a rating system: 1=0-25%, 2=25-50%, 3=50-75%, and 4=75-100%

DISCUSSION

The highly significant genotypic effects for all characters analyzed in the SP population indicate large genetic variability exists in this germplasm. SP germplasm is a unique population with contribution of genes from all tetraploid species in *Gossypium* and from commercial cultivars and strains in *G. hirsutum* with genetic backgrounds from a triple hybrid. The purpose of inter-crosses in creating this population was to break linkage blocks that have limited the success of simultaneous improvement of yield and fiber quality. The population underwent a period of random mating followed by a period of selfing. It is expected that a random mating population has been established after 11 generations of extensively natural crosses, and homozygosity has been nearly completed within lines after years of selfing. Visual observation of plants in fields showed a high degree of uniformity within a progeny row.

Lack of a significant G x L interaction for most fiber properties in this study is consistent with previous studies (Miller et al., 1959; Abou-El-Fittouh, et al., 1969; Bridge et al., 1969; Murray and Verhalen, 1970; May and Taylor, 1998; May and Jividen, 1999). Even for the significant G x L interaction for fiber strength, the effect is only 15% of that for genotypic effect. Environments at the two locations were different as evidenced by the difference in lint yield between locations, averaging 309 and 248 g plot⁻¹ for Location 1 and Location 2, respectively. A highly significant G x L interaction was observed for lint yield and most yield components in this population. The significant G x L interaction for yield indicates that the two environments resulted in differential growth and development across genotypes. The interaction components, however, were small compared with the genotypic components for these characters, so it would be reasonable to emphasize general adaptability in the development of cultivars when this germplasm resource is used in breeding. Although the interactions between genotype and year were not estimated in this study, the variations in these interactions may be similar to the variations observed in the G x L interaction within one year (Meredith, 1984), since highly significance differences ($P < 0.001$) between locations were identified for all characters. Considering the cost and time, evaluation at multiple locations in one year should provide enough information on the total variation in this germplasm.

Yield components and fiber properties in the SP population were compared with a group of standard cultivars used in the National Variety Test. Means of most fiber properties analyzed in the SP population were significantly different from the averages of the standard cultivars. Fiber strength in the SP population was higher than in the high yielding standard cultivars. More importantly, there were wide ranges of mean values among SP lines for yield components and fiber properties. The ranges were 161 to 479 g plot⁻¹ for lint yield, 177 to 255 kN m kg⁻¹ for fiber strength, and 12.5 to 15.3 mm for 50% span length, and 24 to 33 mm for 2.5% span length. Although the mean of yield in the SP population was lower than the high yielding cultivars, DP555BR and ST4892BR, it was 27% higher than PHY72 and not different from FM960B₂R. These results suggest that the SP population is a useful germplasm resource for genetic improvement of both lint yield and fiber quality.

Lint yield and fiber strength are two major goals in upland cotton breeding; however, the association between these two traits is generally negative (Miller and Rawling, 1967; Meredith and Bridge, 1971; Smith and Coyle, 1997). It appears that the continuing improvement of fiber strength would be limited by the yield compensation. The exploration of novel genes in exotic germplasm and further incorporation of these genes into cultivars will help breeders improve genetic potentials for both lint yield and fiber quality in upland cotton. Seven SP lines have shown good performance in both yield and fiber quality. These lines averaged 334 g plot⁻¹ for lint yield, 234 kN m kg⁻¹ for fiber strength, 29.9 mm for span length (2.5%), and 5.55% for short fiber content. The seven lines are comparable with high yielding cultivars, ST4892BR and DP555BR, in yield and high quality cultivars, FM960B₂R and PHY72, in fiber quality. These facts indicate that 11 generations of random intermating may have broken linkage blocks to some degrees in the SP population.

The positive correlation between lint yield with lint percentage, boll weight, lint per seed, and seeds per boll in this study are in agreement with previous reports (Worley et al., 1974; McCarty et al., 1996; Wu et al., 2004). The results indicate that these yield components are major contributors to the total variation of lint yield. The interrelationship between yield parameters and fiber properties is complicated. As expected, the correlation between

lint yield and fiber strength is negative. In contrast, a significant negative relationship between lint yield and fiber span length was not detected. This may be explained by the complicated relationship of fiber length with different yield components. Fiber span length is negatively correlated with lint percentage, but positively correlated with boll weight, so the relation between lint yield and fiber length is confounded by the different relation of the two yield components with fiber length. Lint percentage was negatively correlated with fiber strength and span length. The mean of lint percentage in the SP population was significantly lower than the average of the standard cultivars, while boll weight and seed weight are higher than the cultivars. This phenomenon is in agreement with a previous study (Blanche et al., 2006) in which lower lint percentage was identified in the genotypes with higher seed size. These results suggest that lint percentage should be emphasized in the breeding programs for genetic improvement of fiber quality when a SP population is used. Span length (50%) contributed more to the variation of fiber strength than span length (2.5%). The genetic correlation of strength with span length (50%) is almost twice of that with span length (2.5%). Micronaire is negatively correlated with 2.5% span length, while not significantly correlated with 50% span length. Since micronaire is an important criterion for selection, 50% span length should be emphasized more than 2.5% span length in the breeding with the SP germplasm. Although the correlation is not high, the negative correlation between lint yield and short fiber content is interesting. This implies that there would be no yield penalty, if SP germplasm is used to improve this fiber property. The lack of correlation between span lengths and short fiber content implies that the selection on one of these characters would not affect the other one, so both of these properties should be included in breeding. Although the underlying physiological and genetic basis is unknown, it is assumed that the partition of carbohydrate among yield components in SP population may be different from that in most Mid-south cultivars.

Contributions of the morphological traits, such as nectariless, gland content, smooth-leaf, and okra-leaf, to yield in cotton have been studied for decades and results were documented and incorporated into cotton breeding programs (Kohel, 1974; Wilson and George, 1982; Wilson, 1987; Wilson, 1989; Calhoun, 1997; Bourland et al., 2003). In summary of these reports,

contributions of nectariless and gland content to yield are mainly due to insect resistance in plants possessing these genes. The improvement of yield related to smooth-leaf is due to reduction in trash during ginning and lower populations of *Bemisia tabaci* Genn., while those of okra-leaf are due to earliness and resistance to boll rots and pink bollworm. The other four characters, plant height, leaf area, leaf length, and node number of the first fruiting branch, analyzed in this study are related to characteristics of crop canopy and earliness. Tremendous variations were identified in SP population for all morphological characters analyzed. It is known that nectariless in *G. hirsutum* was transferred from *G. tomentosum* (Percy and Kohel, 1999). It is also known that exotic alleles of Gl₂ and Gl₃ controlling the glandless or the glanded trait could be transferred from multiple sources, such as *G. hirsutum*, *G. barbadense*, *G. raimondii* Ulbr., *G. thurberi* Todaro, or *G. arboreum* (Calhoun, 1997; Percy and Kohel, 1999). Although most parental strains of *G. hirsutum* have complicated genetic backgrounds of triple hybrids, the nectariless, glandless, and high gland content traits are not present in the 12 strains of *G. hirsutum*. The identification of nectariless and low and high gland content lines in the SP population are evidence of interspecific introgression.

In conclusion, large phenotypic variations of yield parameters and fiber properties exist among the SP lines. Genotypic components for yield parameters and fiber quality were large relative to the interaction components. This suggests emphasis on general adaptability in the development of cultivars when SP population is used in breeding. Span length (50%) contributed more variation to fiber strength than span length (2.5%). There was a negative correlation between yield and short fiber content. Variations in morphological characters, such as nectariless, and low and high gland content in leaves, were identified. The results provide evidence that SP population is a useful germplasm resource for genetic improvement of lint yield and fiber quality.

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DISCLAIMER

Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation by the US Department of Agriculture.

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