Mapping and Validation of Fiber Strength Quantitative Trait Loci on Chromosome 24 in Upland Cotton

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ABSTRACT

A major fiber strength quantitative trait locus (QTL) has been identified on chromosome 24 in the Chinese germplasm line 'Suyuan 7235'; however, the effects of this QTL have not been tested in different genetic backgrounds. In this study, we confirmed the effects of this QTL by crossing Suyuan 7235 with two U.S. germplasm lines with different fiber strength. This QTL was consistently expressed over generations and years in both populations. The Suyuan 7235 allele explained up to 40% of the total phenotypic variation and accounted for an increase of up to 22.8 kN m kg^{-1}. The effects on fiber strength appear to be greater in Suyuan 7235 × 'Sealand 883' (Pop-883) than in Suyuan 7235 × 'Sealand 542' (Pop-542) despite the Sealand 883 parent having stronger fiber than the Sealand 542 parent. Deoxyribonucleic acid fingerprinting on a collection of elite cotton (*Gossypium hirsutum* L.) lines indicated that this QTL is not present in a survey of elite U.S. public germplasm. These results indicate that this fiber strength QTL could significantly improve the economic value of Upland cottons in the United States. The identification of 27 novel markers tightly linked in this region adds additional tools to allow this QTL to be more efficiently deployed in breeding cultivars with improved fiber strength.

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Abbreviations: LOD, logarithms of odds; MAS, marker-assisted selection; PCR, polymerase chain reaction; Pop-542, Suyuan 7235 × Sealand 542; Pop-883, Suyuan 7235 × Sealand 883; QTL, quantitative trait loci/locus; S-7235, Suyuan 7235; SL-542, Sealand 542; SL-883, Sealand 883; SSR, simple sequence repeat.

Historically, the United States has produced medium grade fiber Upland cotton (*Gossypium hirsutum* L.) primarily for the consumption of domestic mills. Early in the 21st century, technological advances in spinning technology (Felker, 2001) created demand for cotton with greater fiber quality than the standards established for the domestic market. Yet studies have shown that fiber quality of Upland cotton in the United States has declined after 2000 (Bowman and Gutiérrez, 2003) as the U.S. cotton industry shifted from a domestic based market to an export oriented market with nearly two-thirds of the cotton fiber produced in the United States now sold on the world market (Foreign Agricultural Services, 2011). Because the international textile mills impose a more stringent demand for fiber quality than domestic mills, further improvements in fiber quality are needed in order for U.S. cotton to remain competitive with other cotton producing countries.

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Among several physical properties that collectively describe cotton fiber quality, fiber strength is one of the main quality traits that can greatly influence the yarn manufacturing process. Stronger fibers can effectively withstand mechanical impacts of the yarn spinning process better than weaker fiber (Deussen, 1992; Meredith et al., 1991); therefore, it can be spun at a greater speed. In addition, yarn strength is directly influenced by fiber strength; thus, raw cotton with higher tenacity generally produces more durable fabrics and also maintains cotton's natural qualities after chemical processing of the fabric (Deussen, 1992; May, 1999).

Classical genetic studies have shown the polygenic nature of fiber strength (summarized by May, 1999); therefore, improving fiber strength will involve stacking multiple favorable alleles into one genetic background. Although high heritability and additive gene action make phenotypic selection effective for fiber strength improvement (May, 1999), the general inverse correlation between yield and fiber strength hinders simultaneous improvement of both traits (Culp and Green, 1992; Culp and Harrell, 1979). As a result, elite high yielding varieties often have average fiber strength even though some germplasm accessions display excellent fiber strength (Bowman and Gutiérrez, 2003).

More than 80 quantitative trait loci (QTL) for fiber strength have been identified from 17 different QTL mapping studies (summarized by Chee and Campbell, 2009). The number of QTL that were detected in each study ranged from one (Zhang et al., 2003) to 21 (Paterson et al., 2003) and explained from 2.4 to 53.8% of the total phenotypic variation. Therefore, it may now be possible to stack multiple favorable alleles conferring improved fiber strength into a single genotype. However, a majority of the QTL were identified in early generation interspecific hybrid populations, with the favorable alleles originating from *Gossypium barbadense* L. (also known as Pima, Sea Island, or Egyptian cotton) complicating their manipulation in Upland cotton genetic backgrounds. An exception to this is a major QTL for fiber strength located on chromosome 24 in the germplasm line Suyuan 7235. This QTL was identified using F_2, $F_{2:3}$, backcross, and recombinant inbred mapping populations derived from the cross of line Suyuan 7235 × TM-1 (Shen et al., 2007, 2005, 2006; Zhang et al., 2003). This fiber strength QTL from Suyuan 7235 may be a good candidate for improving the fiber strength of the U.S. Upland cotton germplasm.

There are several challenges that need to be addressed if a breeding program desires to integrate marker-assisted selection (MAS) to improve fiber quality traits. For example, it is important to determine if a QTL will produce similar phenotypic effects in multiple genetic backgrounds and/or environments. Although previous studies have shown that the fiber strength QTL in Suyuan 7235 can be detected over different generations and in different environments in China, this QTL has only been tested in the TM-1 genetic background (Chen et al., 2009; Guo et al., 2003; Shen et al., 2007, 2005, 2006; Zhang et al., 2003). It has been shown in rice (*Oryza sativa* L.) (Liao et al., 2001; Steele et al., 2006), maize (*Zea mays* L.) (Li et al., 2009), tomato (*Solanum lycopersicum* L.) (Lecomte et al., 2004), and cotton (Chee et al., 2005a, b) that QTL detected in genetic populations chosen to maximize phenotypic differences may be less effective in other genetic backgrounds due to interaction with other loci or epistasis (Holland, 2007). The objectives of this study are to validate the presence of a QTL for fiber strength on chromosome 24 of Suyuan 7235 and to determine the efficacy of this QTL in two cotton cultivars with different fiber strength.

MATERIALS AND METHODS

Population Development and Phenotyping

Two genetic populations were developed by crossing Suyuan 7235 to Sealand 542 (PI 528730) and Sealand 883 (PI 528875), designated as Pop-542 and Pop-883, respectively. The germplasm line Suyuan 7235 (designated from here on as S-7235) was released by the Institute of Industrial Crops, Jangsu Academy of Agricultural Sciences, China, because it possessed superior fiber strength (Qian et al., 1992). Suyuan 7235 was developed by crossing *Gossypium anomalum* Wawra with *G. hirsutum* and then backcrossing the progeny to the *G. hirsutum* cultivar Acala 3080 (PI 529543) (Qian et al., 1992). The cultivars Sealand 542 and Sealand 883 (designated from here on as SL-542 and SL-883, respectively) were developed at the Pee Dee experiment station, Florence, SC, and were selected as parents in this study because they are genetically similar but have different fiber strength (Fig. 1). The Sealand cultivars were developed by crossing the Upland cotton line 'Coker Wilds' with the Sea Island cotton (*G. barbadense*) 'Bleak Hall' (PI 608115) followed by backcrossing to Coker Wilds (Bowman et al., 2006; Culp and Harrell, 1974).

The F_1 hybrids for Pop-542 and Pop-883 were grown in the greenhouse and F_2 seeds were collected from a single F_1 plant for each cross combination. The F_2 populations, Pop-542 and Pop-883, comprising 175 individuals each, were planted at the William Gibbs Farm, in Tifton, GA, in the summer of 2005. Seed cotton from the individual F_2 plants was hand picked, ginned on a table-top saw gin, and tested for fiber quality. In 2006, $F_{2:3}$ families along with the three parents were planted as progeny rows in a CRD with two replications in Tifton, GA. All 175 $F_{2:3}$ families were advanced to the $F_{2:4}$ generation in 2007 when they were again planted together with the three parents in a CRD with two replications in Tifton, GA. The plots were single row plots, 9 m by 1 m, planted at four seeds per row foot in early May and harvested in early October. Standard production practices were followed in each test. A sample of 25 bolls was harvested from each $F_{2:3}$ and $F_{2:4}$ progeny row, ginned on a table-top saw gin, and tested for fiber quality. Fiber strength was measured using the high volume instruments at the Cotton Incorporated Textile Services Laboratory. High volume instrument measures of fiber strength are reported as kilonewton meter per kilogram (kN m kg^{-1}), where one newton equals 9.81 kg-force.

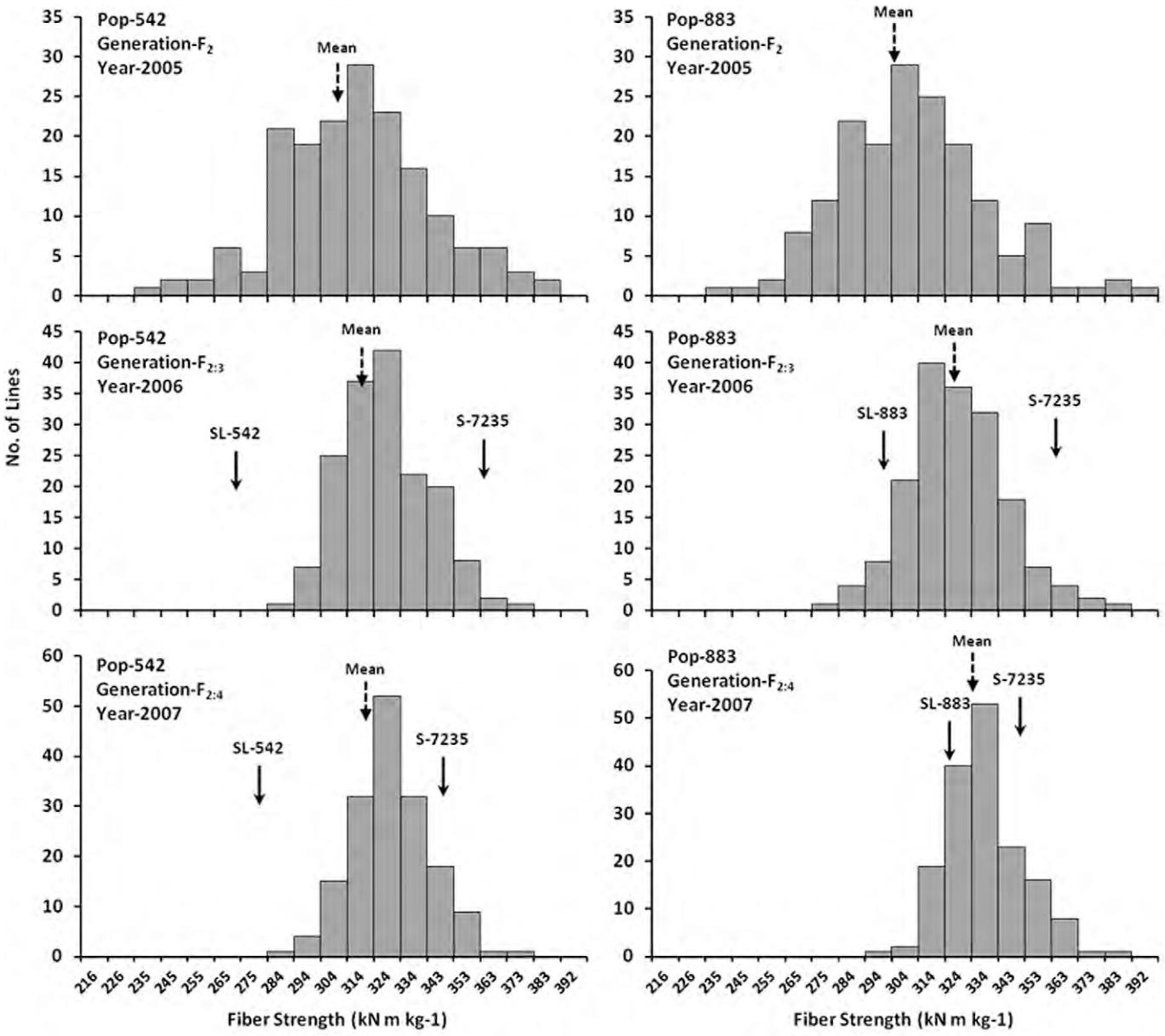

Figure 1. Distribution of fiber strength in F_2, $F_{2:3}$, and $F_{2:4}$ generations of Suyuan 7235 (S-7235) × Sealand 542 (SL-542) (Pop-542) and Suyuan 7235 × Sealand 883 (SL-883) (Pop-883).

Molecular Marker Analysis

Genomic DNA from each of the F_2 plants and parents was extracted following an established procedure (Paterson et al., 1993). Quantity and quality of extracted DNA was checked on a 0.8% agarose gel before diluting for polymerase chain reaction (PCR) amplification. Sequences of simple sequence repeat (SSR) primers were downloaded from the Cotton Marker Database (Blenda et al., 2006) and were commercially synthesized by Operon (Eurofins MWG Operon). A total of 68 SSR markers mapping to either chromosome 24 or its homeolog chromosome 8 were selected from the genetic maps available at Cotton Marker Database (Blenda et al., 2006). Polymerase chain reaction amplification was performed as described (Chee et al., 2004) and the PCR products were electrophoretically separated using 10% nondenaturing polyacrylamide gel electrophoresis. The DNA fragments were visualized by staining with silver nitrate (Zhang et al., 2002). The SSR primer pairs were first screened for polymorphism between the parents and then the polymorphic primers were tested on the mapping populations.

Data Analysis

The phenotypic distribution of fiber strength in both mapping populations was calculated with SAS version 9.1 (SAS Institute, 1989). Linkage maps of both populations were constructed using Mapmaker EXP (Lander et al., 1987) software. Logarithms of odds (LOD) score of 5.0 and maximum recombination fraction of 30 cM were set as grouping thresholds. Recombination units were converted into genetic distances by using the Kosambi mapping function (Kosambi, 1944). Detection of QTL and estimation of genetic parameters were performed with composite interval mapping (CIM) function of the software WinQTL Cartographer version 2.5 (Wang et al.,

2005). The phenotypic data from the F_2, $F_{2:3}$, and $F_{2:4}$ generations in each population were analyzed separately. However, since the error mean squares for fiber strength from the $F_{2:3}$ and $F_{2:4}$ were homogeneous in the Pop-883 dataset (Levene, 1960), marker-trait association was also analyzed using the pooled data in this population. One thousand permutations at the 0.05 significance level was used to calculate the appropriate likelihood ratio threshold values for each phenotypic dataset. Forward regression with a walk speed of 0.5 cM was used for scanning the region for QTL.

RESULTS

Population Biometrical Parameters

The three parents had significantly different fiber strength in 2006 and 2007 (Fig. 1). Suyuan 7235 had a mean fiber strength of 363.8 kN m kg^{-1} in 2006 and 350.1 kN m kg^{-1} in 2007. Among the Sealand parents, SL-883 had higher mean fiber strength of 301.1 and 324.6 kN m kg^{-1} in 2006 and 2007, respectively, than SL-542, which had fiber strength of 271.5 kN m kg^{-1} in 2006 and 277.5 kN m kg^{-1} in 2007. The fiber strength of both Pop-542 and Pop-883 populations were normally distributed in F_2, $F_{2:3}$, and $F_{2:4}$ generations (Fig. 1). In both populations, transgressive segregation was observed in all generations; however, a greater number of transgressive segregants were detected in Pop-883. The range of phenotypes and population means differed among populations, with Pop-883 displaying a higher population mean in all generations (Fig. 1).

Confirmation of Fiber Strength Quantitative Trait Locus on Chromosome 24

Fifty-two of the 68 SSR markers were polymorphic between S-7235 and the Sealand parents and were genotyped on both F_2 populations. We were able to establish linkage for 49 loci in Pop-542 and 50 loci in Pop-883. The SSR marker NAU3954 was polymorphic only in Pop-883 and therefore mapped only in this population. In both F_2 populations, with the exception of markers BNL3860 and NAU1369, all loci were mapped to a single linkage group at a LOD score of 7.0. The two unlinked markers were not included in further analysis. The linkage map of Pop-542 had an overall length of 8.7 cM with an average distance between markers of 0.18 cM. Similarly, the genetic linkage map of Pop-883 covered a distance of 11.0 cM with an average distance between markers of 0.22 cM. The maps developed from the two populations were nearly identical. However, the map order was not resolved for a number of markers due to the population size of only 175 individuals. Therefore, the two maps were compared to prior published maps (Chen et al., 2009; Shen et al., 2007) and a consensus map was developed using individuals from both populations (Fig. 2). In comparison to the complete linkage maps of chromosome 24 available at the Cotton Marker Database (Blenda et al., 2006), the most probable localization of this region is on the second quartile of chromosome 24, covering approximately 11 cM or 9.8% of the total recombinational length of the chromosome (Guo et al., 2007).

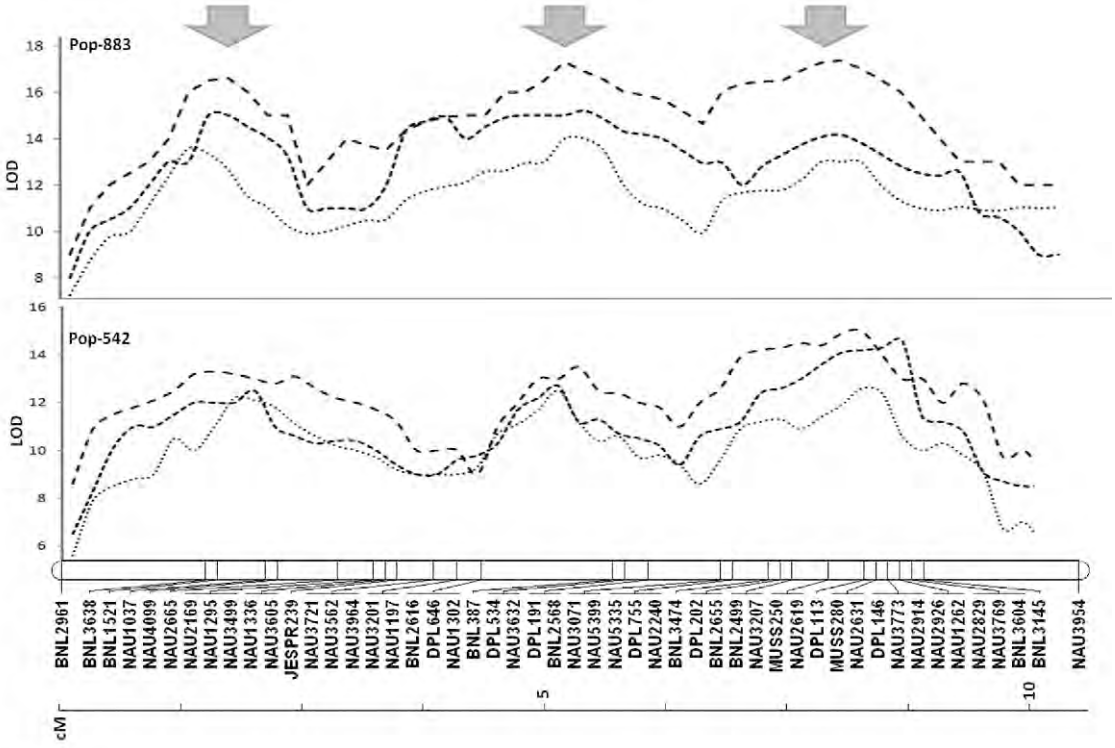

Figure 2. Consensus genetic linkage map of chromosome 24 with logarithms of odds (LOD) score profile for fiber strength in Suyuan 7235 × Sealand 542 (Pop-542) and Suyuan 7235 × Sealand 883 (Pop-883). Arrows indicate the likely peak of putative quantitative trait loci.

Table 1. Biometrical parameters of quantitative trait loci (QTL) for fiber strength on chromosome 24.

Population	Generation (year)	LOD†	Additive	Dominance	R2
Pop-542 (Suyuan 7235 × Sealand 542)	F_2 (2005)	12.5	19.02	–1.34	22.0
	$F_{2:3}$ (2006)	15.0	10.63	–2.89	24.9
	$F_{2:4}$ (2007)	15.1	9.35	1.37	18.2
Pop-883 (Suyuan 7235 × Sealand 883)	F_2 (2005)	14.1	22.82	–1.24	30.9
	$F_{2:3}$ (2006)	15.3	11.97	–2.58	40.1
	$F_{2:4}$ (2007)	17.4	11.99	–3.32	36.3
Combined across generations	$F_{2:3}$ and $F_{2:4}$	16.6	11.17	–3.39	44.5

† LOD, logarithms of odds.

Composite interval mapping detected a major fiber strength QTL between markers BNL2961 and BNL3145 (LOD > 12.5) in both populations (Fig. 2). The percent of phenotypic variance explained by this QTL differed across populations and between generations within a population, ranging from 18.2 to 22.0% in Pop-542 and from 30.9 to 40.1% in Pop-883 (Table 1). In Pop-883, association analysis performed on the pooled dataset across $F_{2:3}$ and $F_{2:4}$ generations detected this QTL at a higher LOD of 16.6 explaining 44.5% phenotypic variance. In all generations of both populations, the allele from S-7235 conferred positive additive effects, increasing fiber strength from 9.4 to 19.0 kN m kg^{-1} in Pop-542 and from 12.0 to 22.8 kN m kg^{-1} in Pop-883 (Table 1). It is interesting to note that while the efficacy of each QTL appears to be consistent across generations, the effects on fiber strength appear to be greater in Pop-883 than in Pop-542 despite the SL-883 parent having stronger fiber than the SL-542 parent.

Based on all the markers mapped within the BNL2621 and BNL3145 region, which flanked the fiber strength QTL, we identified 20 lines homozygous for the S-7235 allele, 74 lines heterozygous, and 31 homozygous for the SL-542 allele in Pop-542 and 17 lines homozygous for the S-7235 allele, 79 lines heterozygous, and 30 homozygous for the SL-883 allele in Pop-883. Figure 3 shows the mean fiber strength of the three genotypic classes. In both populations, a significant difference in fiber strength (LSD at $p < 0.05$) was observed between the three genotypic classes. In population Pop-542, the difference in mean fiber strength between the two homozygous genotypic classes ranged from 18.3 to 36.3 kN m kg^{-1}. Again, the difference in mean fiber strength was consistently larger in Pop-883, ranging from 22.0 to 43.0 kN m kg^{-1}. These results strongly support the QTL analysis that the substitution of an S-7235 allele in this QTL region will result in significant improvement in fiber strength.

DISCUSSION

Previous QTL mapping studies have reported the presence of a major QTL for fiber strength on chromosome 24 (previously referred as LGD03) in the high fiber strength germplasm line S-7235 (Guo et al., 2003; Shen et al., 2007, 2005; Yuan et al., 2001; Zhang et al., 2003). In the present study, we confirmed the association of chromosome 24 with fiber strength in the germplasm line S-7235. In both mapping

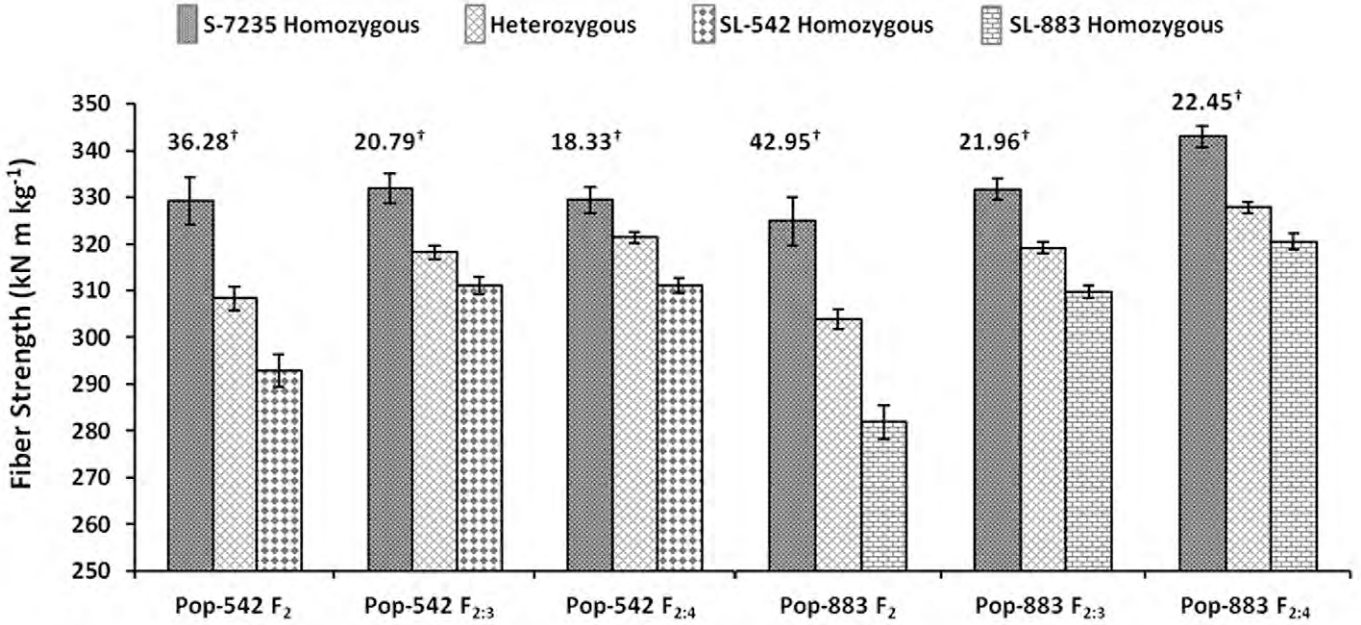

Figure 3. Mean fiber strength of different genotypic classes over three generations of Suyuan 7235 (S-7235) × Sealand 542 (SL-542) (Pop-542) and Suyuan 7235 × Sealand 883 (SL-883) (Pop-883). Error bars are standard error of the means. †Difference in fiber strength (kN m kg^{-1}) between the homozygous genotypic classes.

populations, the markers associated with fiber strength indicated that the QTL we identified was the same locus as previously reported by Shen et al. (2007). By utilizing three overlapping recombinant inbred lines developed from the same S-7235 × TM-1 cross, Chen et al. (2009) showed that this fiber strength QTL region may harbor as many as five distinct QTL clustered within a 14 cM region. A close examination of our association analysis revealed three subregions separated by "dips" of more than 2 LOD value from the likelihood peaks in both populations (Fig. 2), suggesting the presence of more than one QTL within this interval of chromosome 24 (Lynch and Walsh, 1998). We note that the populations studied here are too few and too small to provide the genetic resolution necessary to rigorously test for multiple QTL in such a small genetic interval. However, the current data lend credence to prior results that this region of chromosome 24 may contain more than one QTL for fiber strength (Chen et al., 2009).

Numerous studies have shown interactions between QTL and genetic backgrounds and suggested the need to test the efficacy of a QTL in multiple genetic backgrounds before its utilization in MAS (Lecomte et al., 2004; Li et al., 2009; Sebolt et al., 2000). For example, Lecomte et al. (2004) introgressed five QTL controlling fruit quality into three tomato lines and found that the breeding efficiency of each QTL varied according to the recipient parent. Sebolt et al. (2000) introgressed a QTL conferring high seed protein concentration into three soybean [*Glycine max* (L.) Merr.] lines with varying levels of protein content and detected the effects in only two of the three genetic backgrounds; the effect of this QTL was not detected in the line having the highest seed protein concentration. In this study, we selected SL-883 and SL-542 as parents because they are genetically distinct from TM-1, the sole genetic background in which this fiber strength QTL has been tested (Guo et al., 2003; Shen et al., 2007, 2005; Yuan et al., 2001; Zhang et al., 2003). In addition, SL-883 and SL-542 differ significantly in fiber strength, which indicates that they contain different sets of alleles for this phenotype, offering the opportunity to validate both the efficacy and marker association of the chromosome 24 region from S-7235 with fiber strength. Both SL-883 and SL-542 cultivars were marketed commercially as extra-long staple Upland varieties in late 1940s (Culp and Harrell, 1974). Sealand 542 was more widely planted due to higher yield potential, with approximately 1000 acres grown in South Carolina, Georgia, and Florida in 1948 (Jenkins, 1948).

In an earlier study, Shen et al. (2007) indicated that the genetic effects of this QTL in TM-1 background improved fiber strength by 6.1 to 12.2 kN m kg^{-1}. Using recombinant inbred lines derived from the same TM-1 genetic background, Chen et al. (2009) later reported that they observed a similar effect for this QTL region, accounting for an additive increase in fiber strength from 7.4 to 13.6 kN m kg^{-1}. Our results indicated that the effects of this QTL region in both the SL-883 and SL-542 cross combinations were similar to that observed in the TM-1 background as reported by Shen et al. (2007) and Chen et al. (2009). However, the efficacy of this QTL region appears to be slightly greater in Pop-883 than in Pop-542 in all tested generations despite the SL-883 parent having stronger fiber than the SL-542 parent. For example, the genetic effects based on replicated data in the $F_{2:3}$ and $F_{2:4}$ generations indicated that the S-7235 alleles increased fiber strength by 9.4 to 10.6 kN m kg^{-1} in Pop-542 compared to 12.0 kN m kg^{-1} in Pop-883 (Table 1). Furthermore, the mean fiber strength for progenies homozygous for the S-7235 alleles at the QTL region ranged from 18.3 to 36.3 kN m kg^{-1} in Pop-542, but the range was relatively higher from 22.0 to 43.0 kN m kg^{-1} in Pop-883 (Fig. 3). Because the differences we observed in the two genetic backgrounds were small, further evaluation of the QTL region is needed to confirm the interactions with genetic backgrounds.

The potential value of this QTL region for improving U.S. Upland cotton is significant because cotton fiber with strength above 304.0 kN m kg^{-1} receives a premium price (AMS, 2011), but Upland cotton fiber produced in the United States seldom exceeds this threshold. For example, none of the high yielding varieties from the 2009 statewide multilocation cotton varietal trials in Georgia (Day, et al., 2009) or Texas (Hague et al., 2009), the two top cotton producing states in the United States, had fiber strength higher than 294.0 kN m kg^{-1}. Introgression of this QTL cluster into a suitable Upland cotton genetic background could potentially improve fiber strength by up to 20.0 kN m kg^{-1} when present in a suitable background and therefore may result in an improved cultivar with sufficient fiber strength to receive a premium price in both domestic and international markets.

The possibility that this region of chromosome 24 from S-7235 may harbor multiple QTL for fiber strength suggests that the most feasible approach for marker assisted backcrossing would be to introgress the QTL region as a single unit. The mapping of 27 additional markers in this QTL region, expanding it from 35 loci (Chen et al., 2009; Shen et al., 2007) to a total of 50 loci, has provided new SSRs for tagging this QTL region. Our data suggests that BNL2621 and BNL3145 are the best candidate flanking markers within this interval to facilitate foreground selection for this QTL region as a single unit. While linkage drag is always a concern given that this QTL region is quite large, it does not affect other important fiber quality traits such as length, elongation, and micronaire (data not shown). Therefore, the use of this QTL region for improving fiber strength is not expected to penalize other components of fiber quality.

To further evaluate the utility of this QTL region for improving the U.S. cotton germplasm, we tested 10 markers within the BNL2621 and BNL3145 flanking region on a panel of elite germplasm lines that were

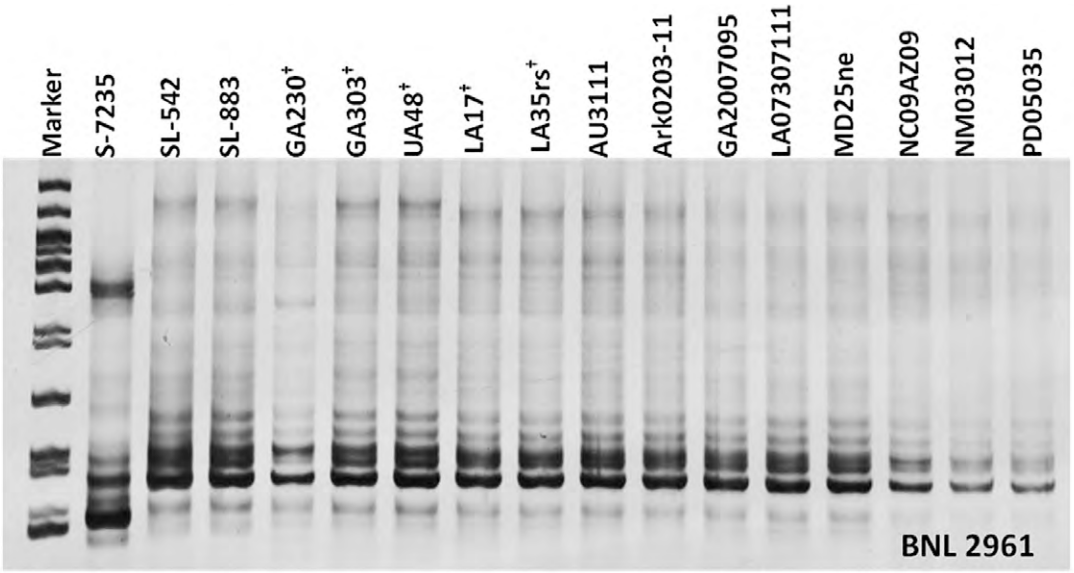

Figure 4. Polymorphism analysis of marker BNL2961 on a panel of elite cultivars and germplasm lines. Individuals from AU3111 through PD05035 are entries from 2010 Regional Breeders Testing Network tests planted in Tifton, GA. †Recently released cultivars.

submitted to the 2010 Regional Breeders Testing Network (RBTN, 2009). These lines represent the most elite breeding materials in the U.S. public cotton breeding programs and include five recently released cultivars (Fig. 4). The result shows that the alleles linking the fiber strength QTL from S-7235 are absent in all the lines in the test panel. Therefore, the markers could be employed for MAS in segregating populations involving S-7235 and any of the elite germplasm lines tested.

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