

# Efficacy of *qFL-chr1*, a Quantitative Trait Locus for Fiber Length in Cotton (*Gossypium* spp.)

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## ABSTRACT

In an earlier advanced-backcross quantitative trait locus (QTL) analysis of an interspecific *Gossypium hirsutum* L. × *Gossypium barbadense* L. population, 28 fiber length QTLs were identified including *qFL-chr1* on chromosome 1 of the A-subgenome. The *G. barbadense* allele at this QTL contributed to longer fibers and explained up to 24% of the phenotypic variance. To substantiate the association of this genomic region with fiber length, three BC<sub>3</sub>F<sub>2</sub> plants heterozygous for the genetic markers that delineate the *qFL-chr1* QTL were selected to construct three independent populations of near-isogenic introgression lines (NILs). The efficacy of *qFL-chr1* was evaluated among 140 NILs grown in 2 yr. The results support the positive effect of *qFL-chr1* on fiber length. A single NIL, R01-40-08, had about 94.3% of recurrent genome composition and significantly longer fiber than the recurrent parent when grown in Nanjing, China. Therefore, in addition to confirming the efficacy of *qFL-chr1* to enhance fiber length, this work provides a valuable genetic resource for the improvement of cotton.

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**Abbreviations:** GBS, genetic background similarity; HVI, high volume instrumentation; LOD, logarithm of the odds; NIL, near-isogenic introgression line; QTL, quantitative trait locus; RFLP, restriction fragment length polymorphism; SSR, simple sequence repeat; STS, sequence tagged site; UHM, upper-half mean.

A LONG-TERM CHALLENGE faced by upland cotton (*Gossypium hirsutum* L.) breeding programs is the simultaneous improvement of yield and fiber quality. While lint yields will continue to be the primary objective, increasing emphasis has now been placed on improving fiber quality to meet the demands of the textile industry due to changes in spinning technology and also in response to increasing competition with synthetic fibers for the manufacture of yarn and textile products. In the United States, the pressure to improve fiber quality has also been influenced by a fundamental shift in the cotton fiber market from a primarily domestically consumed product to one in which nearly two-thirds of the U.S. cotton is now exported. Since the international cotton fiber market places greater emphasis on several key fiber quality traits than the domestic market, improvements in fiber quality are needed for U.S. cotton to compete successfully in the world market.

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Fiber quality is defined by properties of cotton fiber that improve its processing into yarn and end products. One of the most important aspects of fiber quality is related to fiber length measurements, consisting of the average length of fibers, length uniformity, and content of short fibers. Longer fibered cotton can be processed at higher efficiencies in the mills and produce finer and stronger and, therefore, higher quality yarns, while short fibered cotton require increased twisting during spinning, causing low-strength, poor-quality yarns (Perkins et al., 1984). Further, low length uniformity and high short-fiber content are both associated with increased manufacturing waste and ends down during yarn processing. As a result of the demand for improved fiber properties, the U.S. cotton marketing system recently imposed premiums and discounts for fiber length and other related qualities (Jost, 2002).

The recent development of saturated genetic maps of cotton has allowed the detection of more than 100 QTLs influencing fiber properties related to fiber length including staple length, length uniformity, and short fiber content (Chee and Campbell, 2009). Collectively, these QTL studies have allowed the estimation of the number of genes, their location in the genome, and, more importantly, the phenotypic and genetic effects of individual QTLs on fiber length. It has commonly been proposed that DNA markers tightly linked to fiber length QTLs could allow breeders to select genotypes in a large heterogeneous population for desired allele combinations. However, it has been documented that a QTL identified in a particular mapping population may not necessarily be effective in different genetic backgrounds (Liao et al., 2001; Draye et al., 2005; Chee et al., 2005a, b). Therefore, validating a QTL's position and efficacy are critical for the enhancement of cotton using predictive breeding linking DNA marker technology and phenotypic assessment.

The cultivated form of *Gossypium barbadense* L., also known as pima, Egyptian, Sea Island, and Extra Long Staple cotton, has fiber quality much superior to that of the upland cotton. However, the low yield potential and narrow range of adaptation of this species precludes its use in most of the U.S. Cotton Belt. Nevertheless, the improved fiber quality of *G. barbadense* makes it an ideal candidate to enhance fiber quality in upland cotton. A prior study using the advanced backcross approach (Tankley and Nelson, 1996) successfully identified a fiber length QTL designated *qFL-chr1* on chromosome 1. The *G. barbadense* allele improved fiber length in three independently derived advanced-backcross families and explained 12 to 24% of the phenotypic variance (Chee et al., 2005a). The result suggests that *qFL-chr1* could be a valuable target for improving fiber length. The current project objective is to validate the efficacy and association of *qFL-chr1* with increased fiber length.

## MATERIALS AND METHODS

### Population Development and Field Evaluation

One hundred and forty (140) near-isogenic introgression lines (NIILs) were created to assess the efficacy of the *qFL-chr1* QTL. Initially mapped in an advanced-backcross population (Chee et al., 2005a) derived from *G. hirsutum* cv. Tamcot 2111 (recurrent parent) and *G. barbadense* cv. Pima S6 (donor parent) parentage, both marker genotypes and fiber length phenotypes of all BC<sub>3</sub>F<sub>2</sub> were assessed to create the NIILs. Three BC<sub>3</sub>F<sub>2</sub> plants, R01-40, R03-02, and R05-17, were heterozygous at restriction fragment length polymorphism (RFLP) markers (pGH377 and p9-54) that delineate *qFL-chr1*. Based on the genetic map of Chee et al. (2005a), this introgressed region spanned approximately 50 cM or about one-third of the chromosome. These plants were also fixed (homozygous) for the recurrent or the donor parent at most of the remaining genome regions (Chee et al., 2005a). In addition to *qFL-chr1*, there were only two heterozygous chromosome segments on chromosome 13 and chromosome 24 (near marker pAR338 and pAR571, respectively) in R01-40 and R03-02 and three heterozygous chromosome segments in R05-17 near marker pAR547 on chromosome 23.

Progeny (BC<sub>3</sub>F<sub>3</sub>) families for R01-40, R03-02, and R05-17 were derived from selfing the BC<sub>3</sub>F<sub>2</sub> plants and designated as R01, R03, and R05. Within each family, 24 (R01), 53 (R03), and 63 (R05) NIILs were progressed to the BC<sub>3</sub>F<sub>4</sub> as single plant descendent. To ensure seed purity, the BC<sub>3</sub>F<sub>3</sub> plants were grown in a greenhouse for genetic analysis and the production of BC<sub>3</sub>F<sub>4</sub> seed from each via self pollination. The BC<sub>3</sub>F<sub>5</sub> seed was derived from the 25 boll samples (described below) used for fiber analysis in 2004. The 140 NIILs along with the two parents were planted at the University of Georgia, William Gibbs Research Farm, near Tifton, GA, in 2004 and 2005. Tests were arranged in a randomized complete block design with two replications. The plots were single row plots, 9 by 1 m. Field trials were planted 11 May 2004 and 10 May 2005, respectively. Standard, local production practices were followed in each trial. Twenty-five open bolls from the middle of the fruiting zone were harvested from each plot and then ginned on a 10-saw laboratory gin. The upper-half mean (UHM) length of cotton fiber from each plot was analyzed using the high volume instrumentation (HVI) in the Fiber Quality Laboratory of Cotton Incorporated, Cary, NC.

### Genotyping and Data Analysis

Genomic DNA was isolated using the cetyltrimethylammonium bromide (CTAB) method (Paterson et al., 1993). A total of 41 simple sequence repeat (SSR) markers that mapped to chromosome 1 were selected (Blenda et al., 2006) to genotype Pima S6, Tamcot 2111, and 46 BC<sub>3</sub>F<sub>3</sub> individuals that were randomly selected from the three families. The polymorphic SSR loci were then used to genotype the remaining 94 BC<sub>3</sub>F<sub>3</sub> individuals. In addition to SSRs, 19 sequence tagged site (STS)-polymerase chain reaction (PCR) primers were developed from sequenced RFLP probes that mapped near *qFL-chr1* as described (Chee et al., 2004). Oligonucleotide primers were commercially synthesized by Eurofins MWG Operon (Huntsville, AL). Polymerase chain reaction amplification was performed as described in Chee et al. (2004) and amplicons were separated using 10%

nondenaturing polyacrylamide gel electrophoresis. DNA fragments were visualized by staining with silver nitrate following the procedure of Shen et al. (2006).

Linkage maps were constructed using the MAPMAKER/Exp Version 3.0b Software (Lander et al., 1987) using a 4.0 logarithm of the odds (LOD) score and a 50 cM maximum distance to detect linkages. Composite interval mapping (CIM) (Zeng, 1994) analysis was performed using Windows QTL Cartographer 2.5 (Basten et al., 2001) on three different datasets from each family separately for BC<sub>3</sub>F<sub>4</sub> and BC<sub>3</sub>F<sub>5</sub> generations and then combined across the three families. Composite interval mapping was performed using forward-backward regression with a walk speed of 0.5 cM. Since the number of marker-trait associations tested was limited only to markers on chromosome 1, a 2.0 LOD score was used to declare significance. Each QTL's percentage of phenotypic variance (PV) explained ( $R^2$ ) was estimated at the peak LOD score. Analysis of variance was performed using SAS/STAT software (SAS Institute, 1994).

### Fiber Quality and Genetic Composition of the Near-Isogenic Introgression Line R01-40-08

A single NIIL, R01-40-08, which has the longest fiber among lines in the R01 family in 2004 and 2005, was selected for further fiber quality evaluation. In 2008, 98 randomly selected individuals from the R01-40-08 line (BC<sub>3</sub>F<sub>6</sub> generation) along with five individuals from each of the two parents were planted at the Lihui Experiment Station of the Jiangsu Academy of Agricultural Sciences in Nanjing China. In 2009, a single plant each that was derived from 42 randomly selected individuals from the 2008 season was planted in the same location along with five individual plants for each parent. In both years, boll samples were hand harvested from individual plants and fiber samples were tested using HVI in the Supervision, Inspection, and Test Center of Cotton Quality, Ministry of Agriculture in Anyang, China. Fiber quality traits measured included fiber length, fiber strength, micronaire, fiber elongation, and fiber uniformity ratio.

The genetic composition of R01-40-08 was evaluated using 534 SSR markers evenly spaced across the cotton genome based on the genetic map of Park et al. (2005) and Guo et al. (2007). DNA was collected using two sets of bulked tissues from five BC<sub>3</sub>F<sub>6</sub> plants grown in the 2008 season in Nanjing, China. The genetic composition of R01-40-08 from the levels of Pima S6 introgression was determined by using the genetic background similarity (GBS) formula of  $GBS = N/S \times 100\%$  (Zhao et al., 2010), where  $S$  represents the number of polymorphic markers between donor parent

and recurrent parent and  $N$  represents the number of monomorphic markers between the NIIL R01-40-08 and the recurrent parent.

## RESULTS

### Fiber Quality Performance of Near-Isogenic Introgression Lines and Detection of *qFL-chr1* Effect

The mean and range for UHM length of the donor and recurrent parents and the three BC<sub>3</sub> families are presented in Table 1. The donor parent had a significantly ( $p < 0.01$ ) longer fiber (33.02 and 34.04 mm) than the recurrent parent (27.94 and 28.70 mm) in 2004 and 2005, respectively. The mean UHM length of each family was not significantly different ( $p > 0.05$ ) from the recurrent parent. This was expected because the individual lines in each family were segregating for the QTL. The family means for fiber length of the NIILs were numerically greater than the recurrent parent in all tests with the exception of family R03 in the 2005 test. In addition, a number of NIILs were identified in each family with fiber length superior to that of the recurrent parent.

### Confirmation of Fiber Length Quantitative Trait Locus Effect on Chromosome 1

Of the 60 SSR and STS markers, 12 markers showed polymorphism between the two parents and were used to genotype all the BC<sub>3</sub>F<sub>3</sub> individuals. A linkage map of the *qFL-chr1* QTL interval was constructed that spanned a distance of 8.0 cM (Fig. 1). The linear order of marker loci was consistent with other published maps (He et al., 2007; Guo et al., 2007).

Composite interval mapping detected *qFL-chr1* in the region between BNL2921 and JESPR56 (Fig. 1) in all families except R01 in 2004. The biometrical parameters of *qFL-chr1* are presented in Table 1. The association was more significant in the combined across-family dataset with LOD values of 3.7 and 4.5 for the 2004 and 2005 data, respectively. This QTL explained only 12.14 and 14.48% of the total phenotypic variance in the 2004 and 2005 combined across family dataset, respectively (Table 2); however, the variance explained in different families by year ranged from 13.54 to 43.06%. The gene action was additive with the  $G$ .

**Table 1. Upper half mean length (in millimeters) of Pima S6, Tamcot 2111, original BC<sub>3</sub>F<sub>2</sub> individuals, and their BC<sub>3</sub>F<sub>4</sub> and BC<sub>3</sub>F<sub>5</sub> family.**

Family and parents	BC <sub>3</sub> F <sub>2</sub> †	No. of NIILs ‡	2004 NIIL Trial			2005 NIIL Trial		
			Max.	Min.	Mean	Max.	Min.	Mean
R-01-40	30.23	24	30.99	26.92	29.46	32.00	25.91	29.46
R-03-02	29.46	53	30.23	26.92	28.70	30.23	26.92	28.19
R-05-17	29.97	63	30.73	26.67	29.21	30.99	27.18	29.21
Combined dataset		140	30.99	26.67	28.96	32.00	25.91	28.96
Pima S-6	30.99		33.78	32.26	33.02	34.80	33.53	34.04
Tamcot 2111	27.43		28.96	27.18	27.94	28.96	28.19	28.70

†Data from Chee et al. (2005a).

‡NIIL, near-isogenic introgression line.

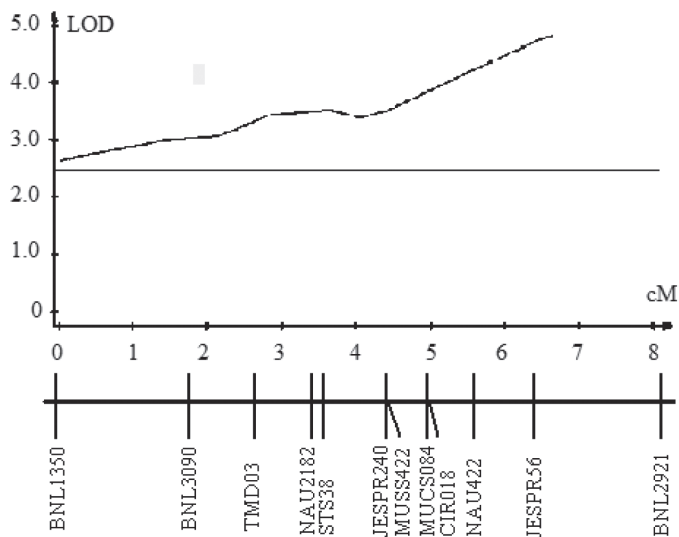


Figure 1. Composite interval mapping of fiber length quantitative trait locus (QTL) from the combined population in 2005. LOD, logarithm of the odds.

**Table 2. Quantitative trait locus (QTL) mapping for fiber length by composite interval mapping.**

Populations	Year	LOD <sup>†</sup>	Additive	Dominance	R <sup>2</sup>
R01	2004	1.57	0.0246	0.0001	24.97
	2005	3.11	0.0410	0.0102	43.06
R03	2004	2.09	0.0206	0.0059	18.42
	2005	2.04	0.0208	0.0040	18.07
R05	2004	2.02	0.0152	0.0029	13.54
	2005	2.24	0.0160	0.0058	14.88
Combined across family	2004	3.7	0.0179	0.0023	12.14
	2005	4.5	0.0211	0.0016	14.48

<sup>†</sup>LOD, logarithm of the odds.

*barbadense* allele contributing increased length by 0.73 mm to 1.45 mm in the different families.

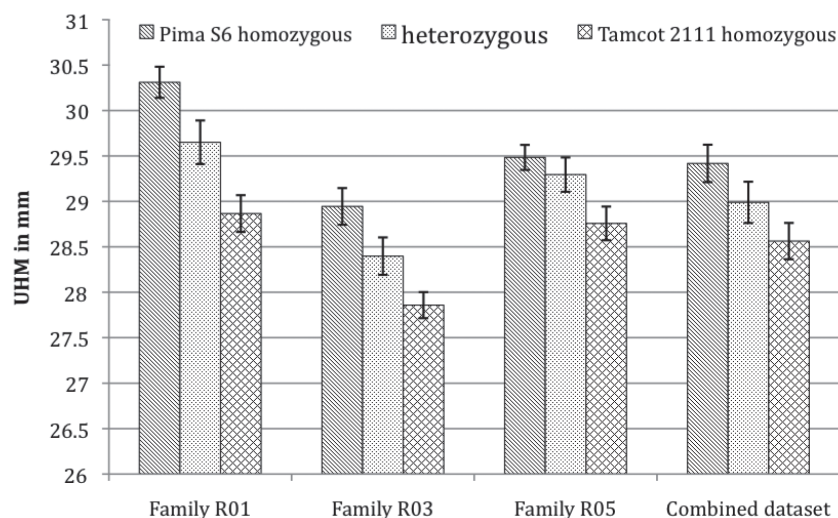


Figure 2. Mean fiber lengths (2004 and 2005) of near-isogenic introgression lines (NILs) with different genotypic classes for the region between JESPR56 and BNL2921. The error bars represent standard error of the means for each genotypic class. UHM, upper-half mean.

Based on the markers JESPR56 and BNL2921, which delineate the target QTL region, we identified 29 BC<sub>3</sub>F<sub>3</sub> plants homozygous for the Pima S6 allele and 34 BC<sub>3</sub>F<sub>3</sub> plants homozygous for the Tamcot 2111 allele. Sixty-eight BC<sub>3</sub>F<sub>3</sub> plants were heterozygous at this QTL interval. Chi-square analysis indicated that the transmission of this chromosome region does not significantly deviate from Mendelian inheritance of 1:2:1 ratio ( $\chi^2 = 0.75, p > 0.5$ ). The mean fiber length of the three genotypic classes is shown in Fig. 2. In the datasets of the individual families and in the combined dataset, the mean fiber length of the NIILs derived from plants homozygous for the Pima S6 introgressed segment was significantly longer than those homozygous for the recurrent parent Tamcot 2111 segment (Fig. 2). In the combined dataset, the NIILs with the Pima S6 introgression displayed a fiber length mean of 29.42 mm compared to 28.56 mm for those without the introgression. Although the heterozygous class also had longer fiber than the NIILs homozygous for the Tamcot 2111 segment, the fiber length of these lines was not significantly different from the homozygous Pima S6 class in the R05 family and in the combined dataset. Finally, the mean fiber length of the NIILs without the introgressed segment was no different from that of the recurrent parent Tamcot 2111.

### Development of Near-Isogenic Introgression Lines

Among the 29 NIILs homozygous for the Pima S6 introgressed segment at the target QTL region, the line R01-40-08 produced longer fiber in all tested environments. For example, at the Tifton location in 2004 and 2005, the mean fiber length of R01-40-08 was 30.48 mm and 31.88 mm, respectively, which was significantly longer ( $p < 0.01$ ) than that of recurrent parent (28.32 mm and 28.96 mm respectively). This line was selected for further testing at Nanjing, China, in 2008 and 2009. Genotyping was also conducted to determine the precise amount of donor

introgression. In 2008, the mean fiber length of 98 BC<sub>3</sub>F<sub>6</sub> plants was 29.45 mm, which was significantly longer ( $p < 0.05$ ) than that of the recurrent parent (27.7mm). Forty-two plants were randomly selected and subsequently advanced to BC<sub>3</sub>F<sub>7</sub> in 2009. Again, the mean fiber length of these plants (29.42 mm) was significantly longer ( $p < 0.05$ ) than the recurrent parent (28.22 mm).

Of the 534 SSR markers tested, 413 were polymorphic between the parents. Genotyping of the two DNA pools of five plants each from the NIIL R01-40-08 revealed 23 markers that detected the donor parent allele. The GBS estimate indicated that the genome of R01-40-08 shared 94.43% similarity to that of the recurrent parent, which was much higher than the expected value of 87.5% for a BC<sub>3</sub> generation.

## DISCUSSION

Among the different properties of cotton fibers that constitute fiber quality, fiber length has more QTLs mapped than any other fiber trait. Specifically, 107 QTLs have been detected for fiber length from 18 different QTL studies (summarized in Chee and Campbell, 2009). Confirming the QTL efficacy and genetic markers associations is particularly important for the utilization of QTL knowledge in breeding. A small number of QTLs detected in different populations appear to co-localize in common genomic regions thus suggesting they may be allelic (Rong et al., 2007). However, validation of both the efficacy and marker association of cotton fiber QTLs has not been published in advanced breeding generations.

Herein, the *qFL-chr1* QTL shows that it enhances fiber length and is localized in a predicted region of the cotton genome previously reported in an initial QTL mapping analysis (Chee et al., 2005a). The biometrical parameters were consistent with the previous observation that the gene action was additive with the Pima S6 allele contributing to increased fiber length. These results support the notion that the advanced backcross approach, which allows recombination and segregation to break the donor genome into smaller components and permits QTL analysis to be conducted along small nonoverlapping segments of introgressed chromosomes, has enabled individual genetic loci to be more clearly resolved and their effects better estimated.

The magnitude of the genetic effect of *qFL-chr1* is only modest as the Pima S6 allele provides a maximum increase in fiber length of only 1.45 mm (1.54 mm in the advanced backcross study). However, the genetic resource and DNA markers toolkit developed have two significant contributions to the fiber quality improvement of upland cotton. First, the NIILs carrying the positive *G. barbadense* alleles of *qFL-chr1* locus represent a new genetic source for improving fiber length in the upland germplasm. This is important because upland cotton has a very narrow gene pool resulting from its evolutionary history, domestication, and modern plant breeding (Paterson et al., 2004). A high degree of relatedness

within cultivated germplasm suggests that many favorable genes, especially those related to yield and fiber quality, might have reached fixation in the elite gene pool. Therefore, while some degree of transgressive segregation in fiber length will continue to be discovered from crossing among elite parents, the use of interspecific gene combinations such as the *G. barbadense* allele at the *qFL-chr1* locus offer an important source of new genetic variation in the upland cotton gene pool to ensure continued genetic gain in fiber length improvement.

Simple sequence repeat markers linked to *qFL-chr1* will be a valuable tool for deploying this QTL in breeding programs. Classical genetics (May, 2000) and recent QTL mapping studies (Chee and Campbell, 2009) have shown that fiber length is governed by multiple genes with small effects; therefore, breeding to improve fiber length would require stacking the favorable alleles of multiple genetic loci. Historically, phenotypic selection has improved fiber length for crosses within the upland or pima germplasm (May, 2000); however, interspecific breeding and selection has not produced great improvements. Due to hybrid breakdown and skewed chromatin transmission that are prevalent in interspecific *G. barbadense* × *G. hirsutum* crosses (Stephens, 1949; Jiang et al., 2000), the fiber quality attributes from *G. barbadense* have been difficult to recover in breeding populations. As a result, despite *G. barbadense* having appeared in the pedigree of many germplasm lines, most do not exhibit fiber properties greatly different from those of other modern upland cultivars suggesting that phenotypic selection has not been effective in introgressing favorable alleles from *G. barbadense* into the upland germplasm. Therefore, the SSR markers linked to *qFL-chr1* could assist breeders in transferring and maintaining this during cultivar development.

Classical quantitative genetic studies have indicated a strong genetic correlation among different fiber quality traits (Kloth, 1998). For example, fiber length tends to be positively correlated with fineness, elongation, and strength (May, 2000). In the original advanced-backcross population, Draye et al. (2005) reported that this region of chromosome 1 also was associated with a QTL for fiber elongation. Interestingly, our data indicated that the region near the *qFL-chr1* locus was not associated with other HVI fiber properties. Since the three NIIL families retained only a small segment of chromosome 1, estimating to be around 8 cM (Fig. 2), it is therefore possible that the genetic association between fiber length and fiber elongation at *qFL-chr1* region is due to linkage rather than pleiotropy.

The QTL-NIILs developed in this study are estimated to carry as little as 5.57% of the donor genome (R01-40-08). Efforts are now underway to advance a number of the QTL-NIILs to complete homozygosity. Once developed, we expect these lines to not only benefit fiber quality improvement but also represent a valuable resource for future use in fine mapping and perhaps even in map-based cloning of the *qFL-chr1* locus.

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