Tianzhen Zhang · Youlu Yuan · John Yu Wangzhen Guo · Russell J. Kohel

Molecular tagging of a major QTL for fiber strength in Upland cotton and its marker-assisted selection

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Abstract Fiber is a basic raw material in the textile industry. The changes in spinning technology have in common the requirement of unique and often greater cotton fiber quality, especially strength, for processing. We used a Gossypium anomalum introgression line, 7235, characterized by good fiber quality properties, to identify molecular markers linked to fiber-strength QTLs. By the use of F₂ and F₃ populations derived from a cross between 7235 and TM-1, a genetic standard of Upland cotton, nine molecular markers, three SSRs and six RAPDs, were identified to be linked to two QTLs for fiber strength. One was a major QTL, QTL_{FS1}, detected both in Nanjing and Hainan, China, and the Texas College Station, USA. It was found to be associated with eight markers and explained more than 30% of the phenotypic variation. QTL_{FS1} was mapped to chromosome 10. The major QTL in 7235 was identified to be transferred from an Acala 3080 cotton. The marker-assisted selection revealed that DNA markers linked to this OTL could be used in increasing the fiber strength of commercial cultivars.

Keywords *Gossypium hirsutum* L. · Molecular marker · Fiber strength · Major QTL · Gene mapping

Introduction

Cotton fiber arises from the growth and differentiation of the outer epidermal cells of the ovule at or near the day of anthesis. Cotton is a high-value per acre crop that is produced as a raw material for the textile industry. It is an in-

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T. Zhang (☑) · Y. Yuan · W. Guo National Key Laboratory of Crop Genetics and Germplasm Enhancement, Cotton Research Institute, Nanjing Agricultural University, Nanjing 210095, China e-mail: cotton@njau.edu.cn Fax: 0086-25-4395307

J. Yu · R.J. Kohel USDA ARS, Southern Plain Agriculture Research Center, Crop Germplasm Research Unit, College Station, TX77845, USA dustry in which cotton marketing is based on measurable quality properties and one where technological changes are being rapidly implemented. All the changes in spinning technology require unique and often greater cotton fiber quality, especially strength, for processing. Strong fibers survive the rigors of ginning, opening, cleaning, carding, combing and drafting. However, current genetic information and plant breeding methods can not lead to a quick improvement of fiber quality to meet the rapid advances in the textile industry to ensure high productivity.

The industry needs stronger yarns. Since fiber strength translates directly into the strength of rotor yarns, it must possess a higher average level of strength and, most importantly, a lower variability of strength to cope with ever-increasing processing speeds in spinning, weaving and knitting (Benedict et al. 1999; Deussen 1992).

Advances in the use of DNA markers for marker-assisted selection (MAS) are promising for streamlining plant-breeding programs. Molecular maps constructed in crosses of Upland cotton (*Gossypium hirsutum* L.) with extra-long staple cotton (*Gossypium barbadense* L.) has led to the identification of several quantitative trait loci (QTLs) for fiber strength, fineness and length (Jiang et al. 1998; Yu et al. 1998). More than 100 QTLs associated with agronomic and fiber traits were also mapped in an intraspecific population (Shappley et al. 1998).

In the present paper, we used a *Gossypium anomalum* introgression line, 7235 (Qian et al. 1992), with high quality fiber properties, as a parent to identify molecular markers linked with fiber strength using bulked segregant analysis (BSA) as described by Michelmore et al. (1991). Nine molecular markers linked with two QTLs for fiber strength, one of which was a major QTL, were identified, and could be efficiently used in MAS to increase the fiber strength of commercial cultivars.

Materials and methods

G. anomalum introgression germplasm lines were developed by crossing G. anomalum and G. hirsutum, and then backcrossing to cultivars and strains with high fiber strength, such as Acala 3080

Table 1 The performance of fiber properties for parents in Nanjing

Year	Parents	Fiber length mm	Uniformity %	Fiber strength cN/tex	Elongation %	Micronaire
1997 in Hainan	TM-1	28.64 ± 0.57	51.34 ± 0.91	22.46 ± 0.57	8.68 ± 0.19	5.08 ± 0.13
	7235	32.67 ± 0.88	49.96 ± 0.95	30.80 ± 1.52	7.86 ± 0.44	4.19 ± 0.21
1998 in Nanjing	TM-1	30.48 ± 0.58	48.53 ± 1.51	20.69 ± 0.59	5.78 ± 0.27	5.00 ± 0.18
	7235	35.10 ± 0.86	47.60 ± 1.80	28.95 ± 1.17	5.10 ± 0.17	4.14 ± 0.21
1998 in Hainan	TM-1	27.31 ± 1.15	55.99 ± 1.58	19.98 ± 0.62	6.98 ± 0.46	4.81 ± 0.64
	7235	29.57 ± 1.33	54.97 ± 1.81	27.44 ± 1.30	5.58 ± 0.34	3.86 ± 0.42

and PD4381. One of these germplasm lines, 7235, was developed from a backcrossed progeny to Acala 3080 (Qian et al. 1992). It was kindly made available from Jiangsu Academy of Agricultural Sciences. However, we found that it segregated for fiber strength, probably due to mechanical mixing. By pedigree selection three times, homozygous lines for fiber quality were developed at the Cotton Research Institute (CRI), Nanjing Agricultural University (NAU), from a single plant of the original line. The fiber strength of 7235 was on the average 29.06 cN/tex, a fiber length of 32.44 mm, and fineness (Micronaire) of 4.06 grown in Nanjing and Hainan in 1997 and 1998 (Table 1). At the same time, the fiber strength of TM-1 was 21.04 cN/g, the length was 28.81 mm, and a Micronaire of 4.96. TM-1, the genetic standard for Upland cotton (Kohel et al. 1970), was obtained from the USDA ARS, Southern Plains Agriculture Research Center, USA.

Single plants from both TM-1 and 7235 were crossed in 1997. F_1 seeds were sent to Hainan Island to produce an F_2 . One set of the (7235 × TM-1) F_2 was grown in Jiangpu Experiment Farm, NAU, in 1998, and another set of the F_2 was grown in the College Station, Texas, USA, in 1999. Additionally, 88 and 162 F_3 families obtained by selfing each individual of the (7235 × TM-1) F_2 were grown in Hainan Island in 1998 and in Jiangpu Experiment Farm, NAU in 1999, for bulked DNA analysis and an inheritance study. Each individual plant was harvested for the fiber tests from the (7235 × TM-1) F_2 and (7235 × TM-1) F_3 . Fiber samples from each plant in Nanjing were tested in the Supervision, Inspection and Test Center of Cotton Quality, Ministry of Agriculture; China, and those collected in the College Station, USA, were tested in STAR-LAB, Knoxville, Tenn., USA.

DNA was individually extracted as described by Zhao et al. (1994) and Guo et al. (1997) from the (7235 \times TM-1) F₂. DNA pools for high and low fiber strength were bulked respectively from five plant DNAs where the highest fiber strength averaged 29.78 ± 1.91 cN/tex and the lowest fiber strength was 18.86 ± 1.36 cN/tex based on (7235 \times TM-1). The F₂ grown in Nanjing 1998 and the $(7235 \times TM-1)$ F₃ grown in Hainan Island in 1998–1999 were used for QTL mapping by bulked segregation analysis (Michelmore et al. 1991). Positive markers were identified only in 7235, and a highstrength bulked DNA pool were used to screen 186 plants of the $(7235 \times TM-1)$ F₂ grown in Nanjing, China, in 1998, and 189 plants in the College Station, USA, in 1999. SSR primers were purchased from Research Genetics, Inc, Huntsville, USA. The PCR was programmed as follows: 45 cycles of 0.15 min at 94 °C (de-naturation), 0.30 min at 40 °C (annealing), and 1.30 min at 72 °C (extension), followed by a final extension at 72 °C for 5 min, and then held at 4 °C. Amplification was performed in a 10-μl reaction volume containing 0.1 U of *Taq* polymerase and the same buffer and MgCl₂ content as the RAPD reaction (see below). The reaction mixture was run on 3% (w/v) Metaphor agarose gel (FML, Maine, USA) in USDA ARS, while products amplified by SSR primers were surveyed by PAGE/silver staining in CRI, NAU (Zhang et al. 2000). The amplification of both SSR and RAPD-PCR was achieved in a PE9600 thermocycler.

The 10-mer oligonucleotides were commercially purchased from the RAPD primers kits [Operon Technologies, Alameda, Calif., USA (referred as simply Operon primers) and University of British-Columbia, Canada (UBC primers)]. One thousand and forty (1,040) Operon primers were used to survey the DNA polymorphism of parents in NAU and 800 UBC primers were used in

USDA ARS. Approximately 20 ng of DNA was used as a template in a 25-µl reaction volume. The PCR procedure included 45 cycles of amplification (94 °C 15 s, 40 °C 30 s, 72 °C 1 min 30 s after an initial denaturing step for 95 °C 2 min), which were carried out in a 25 µl- reaction volume containing 0.5 U of *Taq* polymerase (Sigma), buffer (100 mM Tris-HCl, pH 8.3, 500 mM KCl), 0.5 µM of primer, 100 µM of dNTP (dATP, dTTP, dGTP, dCTP) and 2.5 mM of MgCl₂ supplied by the enzyme manufacturer. MgCl₂ was increased to 3.5 mM for some primers to give good resolution. After PCR, the reaction mixture was run on 1.4% (w/v) agarose-gel electrophoresis and visualized by ethidium bromide staining.

Trait means and correlations were calculated by using the SAS program (SAS 1989). The linkage map was made using MAP-MAKER (Lander 1987). The QTL likelihood map, gene action, and phenotypic variance (PV) explained by individual QTLs were determined by interval mapping using MAPMAKER/QTL. A logarithm of odds (lod) threshold of 3.0 was used.

Hybrids between monosomic lines, H1, H2, H3, H4, H6, H7, H8, H9, H10, H12, H16, H17, H18, H20, H23, H25 and H26, and 3-79, were made by USDA ARS, Crop Germplasm Research Unit in cooperated with Texas A&M University. Monosomic and telosomic TM-1 plants were cytogenetically identified and crossed with 3-79, a genetic standard in *G. barbadense*. DNA was extracted from identified F₁ aneuploid plants for chromosomal mapping of molecular markers associated with the fiber strength QTLs using 3-79, TM-1 and 7235 as controls. If there exist amplified fragments originated from 3-79 and from TM-1 in the F₁ aneuploid plants for one pair of co-dominant markers, it is supposed that the marker is not in this chromosome. While there exists an amplified fragment only from 3-79 and not from TM-1, it is supposed that the marker is on this chromosome.

Results

Molecular tagging of the fiber strength QTL in Upland cotton

Two hundred and seventeen pairs of SSR primers purchased from Research Genetics, Inc, Huntsville, USA, were used for the parental survey. There were 26 pairs of (12.32%) SSR primers with which DNA polymorphisms of the two parents were produced. After the bulked DNA survey and analysis of individuals of 186 plants of the (7235 × TM-1) F₂ grown in Nanjing in 1998, three molecular markers, SSR1521₁₃₀, SSR2961₁₉₀ and SSR3255₂₂₀, linked to fiber strength were found using the SAS program at the 0.05% significance level (data not shown). After 800 RAPD UBC primers were surveyed in USDA ARS, and 1,040 Operon primers were surveyed in NAU, six RAPD molecular markers, UBC301₉₃₃, UBC431₁₉₂₀, UBC757₁₃₂₀, OPAP01₉₈₃, OPAL19₈₂₁ and OPM07₁₀₄₇, linked to high fiber strength

Chromosome 10

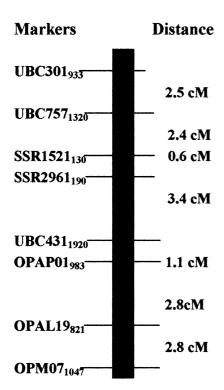


Fig. 1 A chromosome-10 segment showing molecular markers linked to the major QTL for fiber strength in Upland cotton

were identified. Both RAPD and SSR markers identified here produced a normal segregation of 3:1 or 1:2:1 (data not shown). Linkage tests including three SSR markers revealed that, except for SSR3255₂₂₀, these molecular markers could be mapped into one linkage group using MAPMAKER. Their order is illustrated in Fig. 1.

QTL-likelihood maps, gene action, and phenotypic variance explained by individual QTLs, determined using MAPMAKER/QTL based on the (7235 \times TM-1) F_2 grown in Nanjing in 1998, are given in Table 2. We found that all eight markers were associated with one QTL, QTL_{FS1}. In this group, LOD values for all markers were over 5.0, and ranged from 5.23 to 7.72. The mode of gene effects is additive to recessive. Since we could not detect the peak and range, due to not enough markers available in this linkage group, it was supposed that one QTL was responsible for the fiber strength.

Genomic DNA of 188 plants of the $(7235 \times TM-1)$ F_2 , grown in the College Station, USA, in 1999, was screened using five markers including SSR 2961 and SSR 3255. The linkage relationship between SSR2961₁₉₀ and the fiber-strength QTL was also detected in the linkage group using four markers covering 4.2 cM (Table 2). LOD values for five intervals detected in the linkage group were all over 2, and a peak is located between UBC301 and SSR2961. Fiber development in the College Station, was well developed and fiber strength was higher than that grown in Nanjing in 1998 (Table 1). In 1999, the fiber strength of 7235 was 29.19 cN/tex and

Table 2 Inheritance of the major QTL for fiber strength in the $(7235 \times TM-1)$ F₂ and F_{2:3} grown under four environments

QTL	LOD	% Variation	a	d	d/a	Mode
$(7235 \times \text{TM-1})\text{F}_2 \text{ in Nanjing}$						
OPal19s-OPap01	6.69	15.5	-0.913	0.910	-0.99671	
OPap01-OPm07	5.23	25.3	-1.375	-0.567	0.412364	
OPm07-ubc431	6.70	15.5	-0.919	0.898	-0.97715	
ubc431-SSR2961	7.05	20.8	-0.552	1.659	-3.00543	
SSR2961-SSR1521	6.88	31.3	-1.571	-0.508	0.323361	
SSR1521-ubc757	6.73	31.5	-1.574	-0.553	0.351334	
ubc757-ubc301	7.61	33.8	-1.65	-0.484	0.293333	
$(7235 \times \text{TM-1})\text{F}_2 \text{ in USA}$						
OPm07-OPap1	2.71	20.3	-1.503	-1.005	0.668663	
OPap1-OPal19s	2.78	6.6	-0.739	0.755	-1.02165	
OPal 19s-ubc301	3.41	23.9	0.132	2.542	19.25758	
ubc301-SSR2961	3.54	25.6	0.173	2.636	15.23699	ARD
$(7235 \times \text{TM-1})\text{F}_3$ in Hainan						
OPm07-OPap01	4.94	53.3	-1.266	-0.857	0.676935	
OPap01- ubc301	5.08	53.8	-1.289	-0.831	0.644686	D
ubc301-OPal19s	4.79	53.0	-1.249	-0.888	0.710969	
$(7235 \times \text{TM-1})\text{F}_3$ in Nanjing						
OPal19s-OPap01	1.49	3.8	-0.462	0.452	-0.97835	
OPap01-OPm07	1.71	18.5	-1.04	-1.051	1.010577	
OPm07-ubc431	1.49	3.8	-0.465	0.447	-0.96129	
ubc431-SSR2961	1.53	3.9	-0.455	0.468	-1.02857	
SSR2961-SSR1521	1.88	19.0	-1.098	-0.97	0.883424	
SSR1521-ubc757	1.87	19.4	-1.096	-1.011	0.922445	ARD
ubc757-ubc301	1.98	18.5	-1.121	-0.874	0.779661	

that of TM-1 was 22.59 cN/tex in the College Station, much higher than those in Nanjing in 1998. However, we could not detect an association for SSR3255₂₂₀ (P > 0.05) in this population.

Additionally, the combined analysis of molecular markers and the fiber strength of the $(7235 \times TM-1)$ F_3 , grown in Hainan and Nanjing and self-produced from the $(7235 \times TM-1)$ F_2 , confirmed such a close linkage relationship between these eight markers and the fiber-strength QTL (Table 2). QTL mapping using MAP-MAKER/QTL based on the $(TM-1 \times 7235)$ F_3 grown in Hainan revealed that LOD values ranged from 4.79 to 5.08 covering 6.8 cM for four markers. At FSR1₉₃₃ there is the highest LOD value of 5.08 for this QTL. It was inherited dominantly and could explain 53.8% of the phenotypic variation in the population.

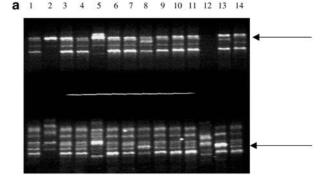
QTL mapping based on the (TM-1 \times 7235) F₃ grown in Nanjing indicated that the LOD value is over 2 but only in the 0.6-cM position of $FSR1_{933}$ between $FSR2_{1320}$ and FSR1₉₃₃. The QTL could explain 19.2% of the phenotypic variation (Table 2). Although there existed a low LOD value for these markers in Nanjing in 1999, great significance was observed between these markers and fiber strength. Due to the low temperature and more rain in Nanjing during fiber development in 1999, fibers did not develop very well, especially for 7235. We were prepared for harvesting fiber samples individually to evaluate the fiber quality of $(7235 \times \text{TM-1}) \text{ F}_3$ plants. However, we had to harvest one boll from each plant of the $(7235 \times$ TM-1) F₃ families and bulk them for a fiber quality test, since we could not harvest enough samples from each plant. The fiber strength of 7235 decreased greatly to an average of 26.0 cN/tex, and that of TM-1 decreased to 19.1 cN/tex in 1999 from that in 1998 (Table 1).

The identified QTL on the average explained 18.5-53.8% of the total phenotypic variance for fiber strength in the F_2 and F_3 populations (Table 2) after a combined analysis of molecular markers and the fiber strength of the (7235 × TM-1) F_2 and $F_{2:3}$. Thus, it is considered as a major gene (QTL) responsible for fiber strength. Additive and/or recessive effects pre-dominate this major QTL for fiber strength in 7235, and it should be a desirable source to increase fiber strength by MAS.

On the other hand, we could not detect any association between $SSR3255_{220}$ and fiber strength in the (7235 × TM-1) F_3 either.

Origin of the major QTL in 7235

Parents such as *G. anomalum* and Acala 3080, used to develop 7235 and some other high fiber-strength strains including PD6992 and HS-427-10, as well as *G. barbadense* cultivars such as Hai 7124 and 3-79, were explored to detect the origin of the major QTL in 7235. It was found that molecular markers such as RAPD-UBC 301₉₃₃ and SSR2961₁₉₀ associated with QTL_{FS1} were present only in Acala 3080 and 7235 (Fig. 2-1,2, see arrow), and not in *G. barbadense* cultivars, *G. anomalum* and other higher fiber



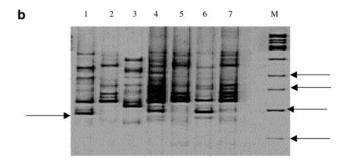


Fig. 2a, b Origin of the super-fiber strength QTL amplified by SSR primer $FSS2_{190}$ and RAPD primer (marked fragment arrow *indicated*). **a** Amplification products by $0PM07_{1047}$ (above) and $UBC301_{933}$ (under). From left to right: 1.194, 2.252, 3.287, 4.359, 5.*G.anomalum*, 6.Xumian 6, 7.PD4381, 8.Acala 3080, 9.235, 10.250, 11.131,12.129,13.7235, 14.TM-1. **b** Amplification products by $SSR2961_{190}$. 1.7235, 2.TM-1, 3.*G.anomulum*, 4.Xumian 6, 5.PD4381, 6.Acala 3080, 7.129, 8.M

strength lines such as PD6992 and HS-427-10. Therefore we suggest that the major tagged QTL for fiber strength in 7235 would be transferred from Acala 3080 rather than *G. anomalum* and other germplasm lines.

Chromosome association of the fiber-strength QTL

DNA polymorphism of the monosomic plant of the (monosomic lines \times 3-79) F_1 , 3-79, TM-1 and 7235, was also surveyed using SSR1521. Monosomic lines used as parents included H1, H2, H3, H4, H6, H7, H8, H9, H10, H12, H16, H17, H18, H20, H23, H25 and H26. We found that around 170-bp, 150-bp, and 130-bp DNA fragments could be amplified from 3-79, TM-1 and 7235 respectively; and they are co-dominant markers. Since only the 150-bp fragment amplified from 3-79 was reproduced from the monosomic plant of the (H10 \times 3-79) F_1 , it could be concluded that SSR1521₁₃₀ as well as SSR1521₁₅₀ was located on chromosome 10 of Upland cotton.

MAS efficiency of QTL_{FS1} to increase fiber strength

Our primary MAS revealed that the major QTL for fiber strength in 7235 is genetically stable in 243 plants, in-

Table 3 The performance of fiber strength in segregating populations

Marker	Genotype	No. plants	Fiber strength (cN/tex)	Difference	Variation	T	P
FSR1 ₉₃₃	+ -	129 35	25.68 24.03	1.65	7.74 2.48	4.48	2.1×10^{-5}
FSR4 ₁₀₄₇	+	110 54	26.14 23.66	2.48	6.66 3.56	6.97	1.21×10^{-10}
FSS1 ₁₃₀	++ -	95 35	25.94 24.03	1.91	7.49 2.64	4.86	4.31×10^{-5}
	++ + -	95 34	25.94 24.94	1.00	7.49 7.37	1.85	0.07
	+ - 	34 35	24.94 24.03	0.91	7.37 2.64	1.67	0.19

cluding 206 in the (Simian 3×7235) BC₁F₅, 8 in the (Zhongmiansuo 35×7235) BC₁F₁, 16 in the (Sumian 16 \times 7235) BC₁F₂, and 13 in the (TM-1 \times 7235) F₄ using two RAPD markers, FSR1₉₃₃ and FSR4₁₀₄₇, and a SSR marker, FSS1₁₃₀. The QTL for fiber strength associated with three markers was inherited steadily in different backgrounds and segregating generations. The mean difference of fiber strength between individuals marked with FSR1₉₃₃ and FSR4₁₀₄₇ was not decreased after several generations of selfing and backcrossing. There was a significant difference, 25.68 cN/tex //24.03 cN/tex and 26.14 cN/tex //23.66 cN/tex, in the mean of fiber strength with and/or without FSR1₉₃₃ and FSR4₁₀₄₇, respectively (Table 3). Additionally, the fiber strength means of homozygous plants with and without the FSS1₁₃₀ SSR marker were 25.94 cN/tex 24.03 cN/tex. Their difference was highly significant too. The fiber-strength mean of heterozygotes identified with SSR marker FSS1₁₃₀, was 24.94 cN/tex (Table 3). The difference between the heterozygote and other genotypes was not significant. It was concluded that the marker-assisted selection to increase fiber strength is efficient, especially using this SSR marker associated with the major QTL, since it could identify the homozygous genotype.

Discussion

Inheritance of fiber strength in cotton

Fiber strength is a typical quantitatively inherited trait (see review by May 1999). Additive gene action predominates, and five (Self and Henderson 1954) to as many as 14 (Tipton et al. 1964) genes were measured to influence fiber strength. However, some data suggest that fiber strength may not always segregate in a quantitative manner, especially in the inheritance analysis of some introgression lines. Richmond (1951) indicated that recovery of high strength segregated from a small backcross population during introgression of strength from the triple hybrid *Gossypium thurberi* × *Gossypium arboreum* × *G. hirsutum* as evidence for only a few major genes controlling strength. Meredith (1977, 1992)

came to a similar conclusion. Two further backcrossings were made to nectariless Deltapline 16 to produce a nectariless strain, MD65-11, which had a strength about 10% higher than that of Deltapine 16. MD 65-11 was crossed with Deltapine 90 followed by two backcrosses to Deltapine 90 with selection first for nectariless and then for bundle strength. Genetic analysis of variance components suggested that a single gene may control a 9% increase in fiber strength. However, subsequent analysis with greater population sizes indicated that two major genes, which might be linked, were responsible for the high-strength trait. From our genetic (presented elsewhere) and molecular-tagging results, we concluded that the higher fiber-strength trait in 7235 was controlled by one major gene and minor modifiers. This gene was most likely transferred from the Acala-type cultivars.

Feasibility of QTL detection using the BSA method

Detailed RFLP maps in a cross between cultivars of allotetraploid (AADD) G.hirsutum L. and G.barbadense L. was used to identify QTLs associated with agronomic and fiber traits, and to determine the chromosomal locations and subgenomic distributions of QTLs. Four QTLs (Yu et al. 1998) and three QTLs (Jiang et al. 1998) for fiber strength were identified collectively to explain 68.8% and 30.90% of the phenotypic variance (PV), respectively. We used more than 2,000 PCR primers (SSRs and RAP-Ds) for mapping of fiber quality traits including fiber strength, length and fineness (data no shown). However, only one major QTL and two minor QTLs could be tagged in our mapping populations (data not shown for another QTL for fiber fineness). The synthesis of "DNA pools" from segregating populations is an efficient strategy for identifying DNA markers closely linked to simply inherited-genes. Michelmore et al. (1991) identified three RAPD markers in lettuce linked to a gene for resistance to downy mildew. Giovannoni et al. (1991) identified two RAPD markers tightly linked to loci affecting ripening and the jointless stem in tomato. In cotton, a RAPD-PCR marker linked to a fertility restoration gene was identified for the first time using a "DNA pools" strategy (Guo et al. 1997). However, theoretical estimates (Wang and

Paterson 1994) suggested that phenotype-based DNA pools can be reliably used to tag QTLs of very large effect, but may frequently fail to tag many QTLs of smaller effects that collectively explain a large portion of the genetic variation in a trait. The present paper supported this theoretical prediction. Additionally, a major QTL may also affect other types of QTL tagging. A major QTL can overshadow the effects of minor independently segregating QTLs by increasing the total phenotypic variation, and thus genes with lesser effects might fall below the threshold of detection. In many instances it was found that a large portion of the phenotypic variation for the measured traits could be explained by the segregation of a few major QTLs. For example, 33–37% of the PV for seed weight in cowpea and mungbean was explained by a single QTL (Fatokun et al. 1992). A QTL for glume hardness explained 42% of the variation in a maize-teosinte cross (Doebley and Stec 1991).

Improvement of fiber strength by MAS

There are several reasons for the continued demand for stronger cotton fibers. First of all, the technology used to convert raw fibers into yarns and fabrics continues to demand higher strength fibers. This is because of higher processing and production speeds. A second important reason is that high-strength fibers are in demand because of higher specifications of the breaking strength for yarns and the tear strength for fabrics. Many of the cotton fabrics sold in the apparel and home furnishings market have some type of resin finish applied to them to give a smooth or wrinkle-free appearance. These resin finishes weaken the fabrics and lower the abrasion resistance.

Spinning speeds in terms of yarn delivery in meters/minute have been plotted for the last 20 years. We have progressed from 20 m/min in ring spinning to more than 150 m/min in rotor spinning, a strength or lack thereof being the limiting factor for the exploitation of higher machine speeds. Again, productivity and costs are the motives driving these developments, while at the same time maintaining or improving yarn quality. Some new spinning technologies, such as friction spinning, have failed in part due to a lack of yarn strength.

Breeders have long recognized a strong negative association between lint yield and fiber strength. The simultaneous improvement of the lint yield and fiber strength of cotton has become a major breeding consideration because genetic linkages between these two characters have been broken and favorable recombinations have been found. In the PD cotton-breeding program, the highly significant negative correlation between lint yield and fiber strength has been reduced from r = -0.97 to a positive (but not significant) r = 0.45 through intermating and selection. Three cultivars with high yield potential and extra-fiber strength, SC-1, PD-1 and PD-3, have been released. This ARS program has been a source of useful genetic variability for much of the applied cotton breeding programs in the USA. This program consisted

of repeated crossing and intercrossing of Upland cotton, *G. hirsutum*, with introgressions of *G. arboreum*, *G. thurberi* and *G. barbadense*. Since additive and/or recessive effects pre-dominate for this major QTL for fiber strength in 7235, the DNA markers associated with the QTL should be a desirable source to increase fiber strength by MAS in cotton breeding programs.

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References

- Benedict CR, Kohel RJ, Lewis HL (1999) Cotton fiber quality. In: Smith WC (ed) Cotton: origin, history, technology, and production. John Wiley and Sons, Inc, pp 269–288
- Deussen H (1992) Improved cotton fiber properties: the textile industry's key to success in global competition. In: Proc Cotton Fiber Cellulose: Structure, Function and Utilization Conference. Memphis, National Cotton Council of America, Tennessee, pp 43–64
- Doebley J, Stec A (1991) Genetic analysis of the morphological difference between maize and teosinte. Genetics 129:285–295
- Fatokun CA, Menancbo-Haltea DI, Danesh D, Young ND (1992) Evidence for orthologous seed weight genes in cowpea and mung bean based on RFLP mapping. Genetics 132:841–846
- Giovannoni JY, Wing RA (1991) Isolation of molecular markers from specific chromosomal intervals using DNA pools from existing mapping populations. Nucleic Acids Res 19: 6553–6558
- Guo WZ, Zhang TZ, Pan JJ, Kohel RJ (1997) Identification of RAPD marker linked with fertility restoring gene of cytoplasmic male-sterile lines in upland cotton. Chinese Sci Bull 43: 52–54
- Jiang CX, Wright RJ, El-Zik KM, Paterson AW (1998) Polyploid formation created unique avenues for response to selection in *Gossypium* cotton. Proc Natl Acad Sci USA 95:4419–4424
- Kohel RJ, Richmond TR, Lewis CF (1970) Texas marker-1. Description of a genetic standard for *Gossypium hirsutum* L. Crop Sci 10:670–671
- Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1: 174–181
- May OL (1999) Genetic variation in fiber quality. In: Basra AS (ed) Cotton fibers, developmental biology, quality improvement and textile processing. Food Products Press, New York, pp 183–230
- Meredith WR Jr (1977) Backcross breeding to increase fiber strength of cotton. Crop Sci 17:172–175
- Meredith WR (1992) Improving fiber strength through genetics and breeding. In: Proc Cotton Fiber Cellulose: Structure, Function and Utilization Conference. National Cotton Council of America, Tennessee, pp 289–302
- Michelmore RW, Paran I, Kesseli RV (1991) Identification of markers linked to disease-resistance genes by bulked segregant analysis: a rapid method to detect markers in specific genomic regions by using segregating populations. Proc Natl Acad Sci USA 88:9828–9832
- Qian SY, Huang JQ, Peng YJ, Zhou BL, Ying MC, Shen DZ, Liu GL, Hu TX, Xu YJ, Gu LM, Ni WC, Chen S (1992) Studies on the hybrid of *G.hirsutum* L. and *G.anomalum* Wawr. & Peyr. and application in breeding (in Chinese). Sci Agric Sinica 25:44–51

- Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721–726
- Richmond TR (1951) Procedures and methods of cotton breeding with special reference to American cultivated species. Adv Genet 4:213–245
- SAS institute (1989) SAS/STAT user's guide version 6, 4th edn. SAS Institute, Cary, North Carolina
- Self FW, Henderson MT (1954) Inheritance of fiber strength in a cross between the Upland cotton varieties AHA 50 and Half. Agron J 46:151–154
- Shappley ZW, Jenkins JN, Zhu J, McCarty JC Jr (1998) Quantitative trait loci associated with agronomic and fiber traits of Upland cotton. J Cotton Sci 2:153–163
- Tipton KW, El-Sharkawy MAA, Thomas BM, Jones JE, Henderson MT (1964) Inheritance of fiber strength in two seperate crosses of Upland cotton having a common parent. In: Pate JB (ed) Proc Sixteenth Annual Cotton Improvement Conference. Memphis, Tenn. National Cotton Council, pp 20–27
- Wang GL, Paterson AH (1994) Assessment of DNA pooling strategies for mapping of QTLs. Theor Appl Genet 88:355–361
- Yu ZH, Park YH, Lazo GR, Kohel RJ (1998) Molecular mapping of the cotton genome: QTL analysis of fiber quality properties. Proc Beltwide Cotton Res Prod Conf, p 485
- Zhang J, Wu YT, Guo WZ, Zhang TZ (2000) Fast screening of microsatellite markers in cotton with PAGE silver staining. Acta Gossypii Sinica 12:267–269
- Zhao X, Zhang HB, Wing RA et al. (1994) A simple method for isolation of megabase DNA from cotton. Plant Mol Biol Rep 12:126–131