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ORIGINAL PAPER

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Molecular dissection of interspecific variation between *Gossypium hirsutum* and *G. barbadense* (cotton) by a backcross-self approach: II. Fiber fineness

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Abstract A backcross-self population from a cross between *Gossypium hirsutum* and *G. barbadense* was used to dissect the molecular basis of genetic variation governing two parameters reflecting lint fiber fineness and to compare the precision of these two measurements. By applying a detailed restriction fragment length polymorphism (RFLP) map to 3,662 BC_3F_2 plants from 24 independently derived BC_3 families, we were able to detect 32 and nine quantitative trait loci (QTLs) for fiber fineness and micronaire (MIC), respectively. The discovery of larger numbers of QTLs in this study than previously found in other studies based on F_2 populations grown in favorable environments reflects the ability of the backcross-self design to resolve smaller QTL effects. Although the two measurements differed dramatically in the number of QTLs detected, seven of the nine MIC QTLs were also associated with fiber fineness. This supports other data in suggesting that fiber fineness more accurately reflects the underlying physical properties of cotton fibers and, consequently, is a preferable trait for selection. "Negative transgression," with the majority of BC_3F_2 families showing average phenotypes that were poorer than that of the inferior parent, suggests that many of the new gene combinations formed by interspecific hybridization are maladaptive and may contribute to the lack of progress in utilizing *G. barbadense* in conventional breeding programs to improve upland cotton.

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Introduction

This is the second installment of a series of papers describing the results of a backcross-self approach to introgress and map quantitative trait loci (QTLs) for fiber elongation properties from a cultivated *Gossypium barbadense* L. line into Upland cotton (*G. hirsutum*). In the first paper, we described a total of 22 QTLs for fiber elongation. For the majority of these QTLs, the *G. barbadense* alleles contributed improved elongation properties, indicating the potential benefit of introgressing genes from this species to breeding for higher quality Upland cotton.

In this manuscript, we report the results of interspecific introgression and QTL analysis for fiber fineness, an important component of fiber quality because of its direct impact on processing performance and the quality of the end product. Finer mature fibers can be spun into yarns with more fibers per cross-section, resulting in not only stronger and therefore better quality yarns but also less down time in the spinning process (Steadman 1997). Direct determination of the physical properties related

to fiber diameter is now possible with single-fibered microscopic analyses, however the high cost in both time and labor have precluded the routine use of this technique as a cotton-classing process in the textile industry (Bradow and Davidonis 2000). Several fiber-testing instruments have been developed that provide estimates of fiber diameter. Micronaire (MIC) has been the most widely used method of determining fiber diameter. However, MIC reading is a measure of resistance to airflow of a constant weight of fibers and can be confounded by the degree of development of the fiber lumen (Steadman 1997), another important quality trait known as fiber maturity. Therefore, while lower MIC cotton usually indicates the finer fibers that are sought after by textile mills, it could also result from immature fiber that can cause neps and dye defects. Although other, more direct methods for measuring fiber diameter are now available, such as the relatively new advanced fiber information system (AFIS) fineness measurement, MIC is still widely utilized in combination with other fiber properties in the textile industry to blend sets of cotton bales in order to promote consistency of performance in the yarn-manufacturing process (May 2000).

The objectives of the investigation reported here were to determine the chromosomal locations of QTLs for fiber diameter in an interspecific *G. barbadense* × *G. hirsutum* backcross-self population and to investigate the relationship between QTLs associated with MIC and AFIS fineness measurements. The QTLs identified in this study add a new level of information to our understanding of the genetic control of this trait, thanks to the improved resolution afforded by the backcross-self approach. They will also be the foundation for the development of near-isogenic lines valuable for marker-assisted introgression to improve fiber quality and to identify the specific genetic determinants of this important trait.

Materials and methods

Population development and phenotyping

A backcross-self mating design was used in this study. Approximately 100 *Gossypium hirsutum* cv. Tamcot 2111 plants were pollinated by *G. barbadense* cv. Pima S6 to produce F_1 hybrid plants. One interspecific hybrid plant from each cross was then backcrossed three times to Tamcot 2111 to yield BC_3F_1s. A total of 24 lineages led to the production of at least one BC_3F_1 plant, which was self-pollinated to generate 24 BC_3F_2 families ranging in size from 33 to 191 plants per family, for a grand total of 3,662 BC_3F_2 progeny. The BC_3F_2 progenies were space planted together with ten entries of each parent as checks in the field near College Station, Texas, under fertilization and irrigation regimes consistent with commercial cotton production (for more detail, see Chee et al. 2005). Although all progeny were grown to maturity and DNA was sampled, a number of plants were lost due to sterility or otherwise produced insufficient lint for fiber analysis. Fiber samples were harvested only from 2,976 progenies, ranging in size from 22 to 172 plants per family. Seed cotton from all bolls of an individual BC_3F_2 plant was hand harvested and ginned on a saw gin.

The fiber samples were sent to the Cotton Incorporated Textile Services Laboratory (Cotton Incorporated, Cary, N.C.) where two measurements were made that reflect the diameter of cotton fibers. MIC readings were obtained from a high-volume precision instrument (Zellweger-Uster, Knoxville, Tenn.) comparable to those used in the US cotton classing. The AFIS mean fiber fineness reading was obtained from the diameter module of the advanced fiber information system instrument. It measures the diameters of individualized fibers expressed in millitex (the weight, in milligrams, of 1 km of the fiber). A fiber fineness of one millitex would equal 1,000 m of fibers with a mass of 1 mg. For both traits, a lower reading would indicate finer fiber and, therefore, more desirable fiber quality.

Genotyping and data analysis

Laboratory techniques were as described in Jiang et al. (2000). The genome composition of the BC_3F_1 plants was inferred based on genotyping the pooled DNA of 20–30 BC_3F_2 plants with 262 restriction fragment length polymorphism (RFLP) markers selected for even representation of the cotton genome map (Reinisch et al. 1994; Jiang et al. 1998). The markers that detected introgression in the BC_3F_1 were then used to evaluate the entire BC_3F_2 family for which they were segregating. A subset of 127 RFLP markers proved sufficient to identify all of the introgressed regions found in the BC_3 families. Regions containing *G. barbadense* introgression that were segregating in each BC_3F_2 family were monitored by graphical genotypes (Young and Tanksley 1989) with the construction based on a detailed genetic map comprising over 2,500 loci (Rong et al. 2004).

One-way ANOVA (SAS, ver. 8, GLM; SAS Institute 1999), the modes of gene action (*a* and *d*) and the proportion of phenotypic variance explained by a QTL were calculated for every marker locus segregating within each BC_3F_2 family as described in Chee et al (2005). For loci that were segregating in two or more families, a two-way mixed model variance analysis was also performed, using the MIXED procedure (SAS Institute 1999). The variance analysis model included genotype (G) as a fixed factor and family (F) and genotype × family (G×F) interaction as random factors. Model parameters were estimated using the residual maximum likelihood (REML) method. The marker-trait association (genotype factor) was tested with an F statistic, using a general Satterthwaite approximation for the denominator degrees of freedom (SAS Institute 1999). A likelihood-ratio statistic (ChiSq) was performed for the GxF interaction (Self and

Liang 1987). G effects and G×F effects were considered to be significant if $P < 0.001$.

Results

Measures and correlations

A skewed phenotypic distribution toward the coarser fibered *G. hirsutum* parent was evident for both traits (Fig. 1). Although a few individual plants appeared to be transgressive, none of the BC_3 families had a mean fiber fineness or MIC value less than that of the *G. barbadense* parent. The family means for both traits were greater than that of the coarser fibered *G. hirsutum* parent in 18 of the 24 BC_3 families. Fiber fineness and MIC were positively correlated at $r = 0.61$ ($P < 0.00001$, $n = 2{,}977$). The moderately strong correlation between the two traits was expected as they both measure similar physical properties; however, because the two measurements could be influenced by different genes, the QTL analyses for both traits are presented.

QTL detection for each trait

Although only 127 loci were segregating in the BC_3F_2, many of these loci were segregating in more than one family (see section Materials and methods). We tested all 319 possible marker-trait associations for the two traits. The number of underlying QTLs was estimated conservatively by assuming that blocks of linked markers all associated with the same trait represented a single QTL. The chromosomal location and subgenomic distributions of QTLs are shown for chromosomes 12 and 14 in Fig. 2 (as examples), with plots for the remaining chromosomes available on-line in the supplementary

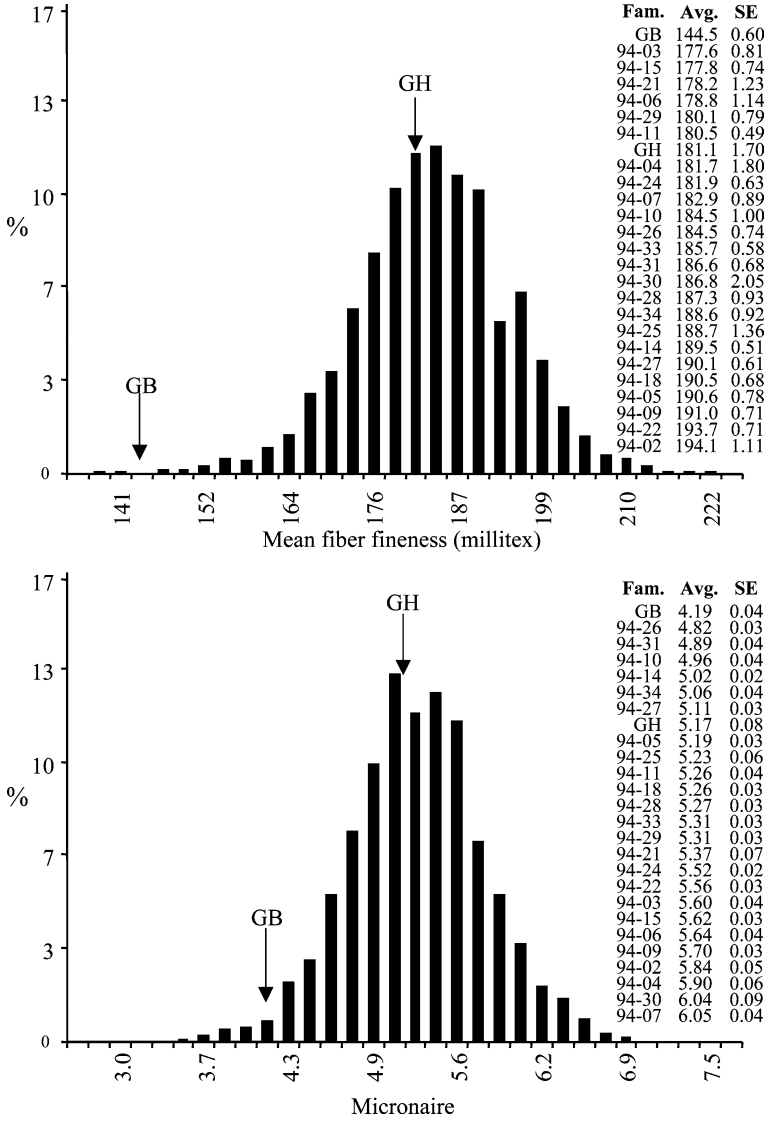

Fig. 1 Frequency distribution of the individual BC_3F_2 plants and the tabulated family means of the BC_3 families for the traits fiber fineness and micronaire. *GH Gossypium hirsutum*, *GB G. barbadense*

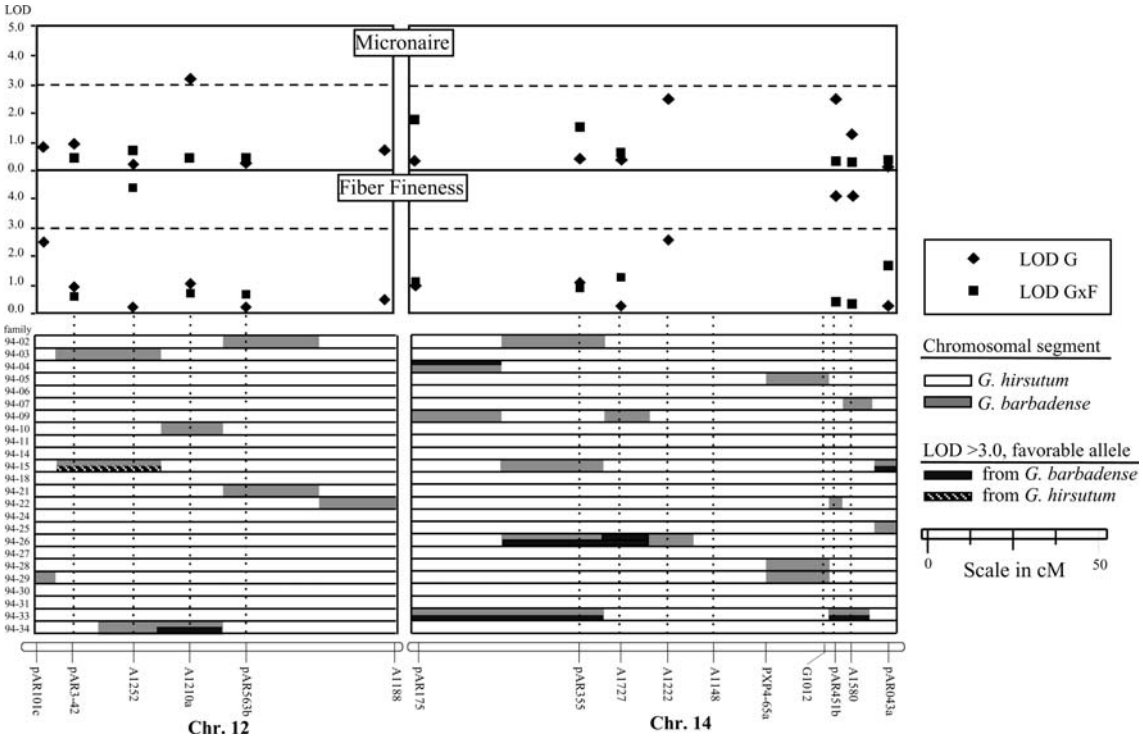

Fig. 2 Graphical genotype (*bottom section*) and significance plot of marker-trait associations (*top section*) for chromosomes 12 and 14 (with the remaining chromosomes across the cotton genome available in the ESM Fig. S1). For the graphical genotype, each *horizontal bar* represents the indicated chromosome for each of the 24 BC_3F_2 families, with *shaded areas* depicting regions containing *G. barbadense* introgression. For each introgressed region, significant ($P < 0.001$) marker-trait associations detected within each family are indicated by *solid black* or *hatched bars* that represent *G. barbadense* or *G. hirsutum* favorable alleles, respectively. The *top half* of the *horizontal bars* indicates significant marker-trait association for MIC, while the *bottom half* is for fiber fineness. For the significance plot, *box symbols* represent the G×F interaction and *diamond symbols* represent the G effects obtained from either among-family (two or more families) or single-family associations. *LOD*: Negative log 10 of the *P* value. By convention, cotton chromosomes 1–13 and linkage groups with the *prefix A* are part of the A-subgenome; similarly, chromosomes 14–26 and linkage groups with the *prefix D* are from the D-subgenome

material (ESM), Fig. S1. A summary of the QTLs detected for each trait follows.

Fiber fineness

A total of 51 significant marker-trait associations were detected, involving 17 linked groups (referred to as *FF01.1-FFD08.4*, Table 1) and one unknown locus (pAR792n, a new polymorphism that was not mapped in Rong et al. 2004). These associations appeared to represent only 32 non-overlapping QTLs (ESM Fig. S1), of which 3 (*FF01.1*, *FF14.1*, *FF14.2*) were reiterated in two BC_3 families and one (*FF06.2*) was reiterated in three BC_3 families. Thirteen of the non-overlapping QTLs were located in the A-subgenome and 18 in the D-subgenome. The percentage of variance explained by individual associations ranged from 7% (*FF14.1-2*) to 36% (*FF05.1*). In 18 of the non-overlapping QTLs (56%), the *G. barbadense* allele contributed finer fiber, which was consistent with the parental phenotypes.

Micronaire

Twelve significant marker-trait associations were detected, covering five linkage groups (referred to as *MIC01.1-MICD08.3*; Table 2). These associations appeared to represent only nine non-overlapping QTLs (ESM Fig. S1). Only one QTL (*MIC06.1*) was reiterated in two BC_3 families. Eight QTLs were detected in the D-subgenome, while only one was detected in the A-subgenome. The percentage of variance explained by individual associations ranged from 9% (*MIC26.1*) to 25% (*MIC14.1, MICD08.1*). Of the nine non-overlapping QTLs, the *G. barbadense* allele contributed lower MIC, and therefore finer fiber at eight (89%) loci while the *G. hirsutum* allele contributed lower MIC at only one locus (11%).

Consistency of QTLs across measurements and families

Among the nine non-overlapping QTLs for MIC, seven (78%) were also associated with fiber fineness. Four of the corresponding QTLs were detected in the same family (*FF06.2* = *MIC06.1*, *FF14.1* = *MIC14.2*, *FF17.1* = *MIC17.2*, *FFD08.4* = *MICD08.3*), while three were detected in different families (*FF26.1* = *MIC26.1*, *FFD08.1* = *MICD08.1*, *FFD08.3* = *MICD08.2*). The finer fibered *G. barbadense* alleles reduced fiber diameter at five cor-

Table 1 Biometrical parameters of QTLs affecting mean fiber fineness. Each row corresponds to a one-way analysis for a single locus and a single family

QTL	Chromosome/linkage group	Nearest locus	Family	R^{2a}	a^a	d^a	d/a ratio[a]	Gene action[b]	Homeolog[c]
FF01.1	Chr01	G1097	94-21	24	−4.01	−5.60	1.40	–	Chr15: pAR077a* pGH468b
FF01.1	Chr01	pGH468a	94-11	9	−3.05	0.26	−0.09	A	Chr15: pAR077a* pGH468b
FF01.1	Chr01	A1204	94-11	9	−2.94	1.53	−0.52	A	
FF01.2	Chr01	A1593	94-26	17	−3.67	−3.55	0.97	A	
FF01.2	Chr01	pAR449b	94-26	18	−3.50	−4.20	1.20	A	
FF01.2	Chr01	A1686a	94-26	22	−3.83	−4.63	1.21	A	
FF01.2	Chr01	A1794	94-26	18	−3.70	−4.02	1.09	A	
FF01.3	Chr01	A1485	94-26	12	−2.34	−4.24	1.82	–	
FF02.1	Chr02	pGH399a	94-07	24	7.55	−0.87	−0.12	A	Chr17: pGH399b
FF02.1	Chr02	pAR390	94-07	21	5.88	2.43	0.41	A	
FF05.1	Chr05	pGH530	94-04	36	−9.65	−4.04	0.42	A	LGD08: P2-3
FF05.2	Chr05	pAR1-28	94-15	14	−4.96	0.42	−0.08	A	LGD08: pGH239*
FF06.1	Chr06	A1152	94-26	20	−3.76	−3.71	0.99	A	
FF06.2	Chr06	pAR988	94-06	22	−8.40	−2.33	0.28	–	
FF06.2	Chr06	P1-34b	94-07	15	−4.16			–	Chr25: G1099a
FF06.2	Chr06	M16-147	94-07	15	−7.25	1.06	−0.15	A	
FF06.2	Chr06	pAR988	94-07	18	−5.65	−2.75	0.49	A	
FF06.2	Chr06	P1-34b	94-26	13	−3.71			–	Chr25: G1099a
FF10.1	Chr10	pVNC163b	94-21	25	−4.86	4.60	−0.95	A	Chr20: P5-57*
FF12.1	Chr12	pAR3-42	94-15	10	3.77	1.22	0.32	A	Chr26: pAR101b
FF12.1	Chr12	A1252	94-15	12	4.32	−2.23	−0.52	A	Chr26: A1310a; pGH413*
FF12.2	Chr12	A1210a	94-34	13	−4.47	−2.56	0.57	A	
FF14.1	Chr14	A1727	94-26	10	−3.10	−2.19	0.71	A	
FF14.1	Chr14	pAR355	94-26	11	−2.74			–	
FF14.1	Chr14	pAR355	94-33	7	−1.96			–	
FF14.1	Chr14	pAR175	94-33	11	−3.28	−0.30	0.09	A	
FF14.2	Chr14	pAR043	94-15	7	−3.67			–	Chr02: pAR451a
FF14.2	Chr14	pAR451b	94-33	9	−3.17	−0.49	0.15	A	Chr02: pAR451a
FF14.2	Chr14	A1580	94-33	9	−3.02	−0.77	0.26	A	Chr02: pAR451a
FF15.1	Chr15	pAR077a	94-03	10	−4.52	0.02	0.00	A	Chr01: G1097*; pGH468a*
FF17.1	Chr17	pAR172a	94-10	13	−7.80	6.39	−0.82	A	Chr03: pAR172b
FF18.1	Chr18	pAR788a	94-06	19	9.97			–	LGA01: pAR338b
FF18.2	Chr18	P9-53b	94-29	9	3.19			–	
FF20.1	Chr20	A1163b	94-03	11	−4.33	−0.95	0.22	A	Chr10: A1158a
FF20.2	Chr20	P5-57	94-24	10	−5.40	2.03	−0.38	A	Chr10: pVNC163b*
FF20.3	Chr20	G1104	94-15	12	−3.31			–	
FF25.1	Chr25	pAR969	94-31	19	−3.98	0.75	−0.19	A	Chr06: PXP4-8
FF25.1	Chr25	PXP1-47	94-31	21	−4.26	0.71	−0.17	A	Chr06: PXP4-8
FF25.1	Chr25	pGH309	94-31	18	−3.82	1.06	−0.28	A	Chr06: PXP4-8
FF26.1	Chr26	pGH413	94-28	10	−4.58	−1.95	0.43	A	Chr12: A1252*
FFA03.1	LGA03	pAR864	94-31	16	−3.32	3.92	−1.18	A	
FFA03.2	LGA03	A1672	94-29	8	3.40			–	LGD02: A1174; pGH505
FFD02.1	LGD02	pAR038	94-21	32	−6.15	−2.42	0.39	A	
FFD02.1	LGD02	A1296	94-21	32	−6.15	−2.42	0.39	A	
FFD02.2	LGD02	A1413	94-06	14	−6.00			–	
FFD03.1	LGD03	pAR571b	94-28	11	7.29	0.54	0.07	A	
FFD08.1	LGD08	pAR482	94-15	10	−3.77	−3.25	0.86	A	
FFD08.2	LGD08	G1112e	94-07	12	−3.52	−3.59	1.02	A	Chr05: A1318b; G1112a
FFD08.3	LGD08	pGH239	94-04	20	−16.17			–	Chr05: pAR1-28*
FFD08.4	LGD08	pAR3-41	94-34	11	0.66	8.03	12.26	–	Chr05: A1318b; G1112a
FfpAR792.1	Unlinked	pAR792n	94-31	15	2.61			–	

[a] Quantitative parameters: R^2, percentage of phenotypic variation explained by the marker genotype at the corresponding marker and family (missing where a significant association was not detected); *a*, additive; *d*, dominance; *d*/*a* ratio, overdominance effect

[b] Modes of gene action are indicated by: A, additivity; D, dominance; H, overdominance. Missing values correspond to dominant or severely distorted DNA marker loci

[c] Homeologous loci, if present, are always shown, with an asterisk (*) indicating that at least one family segregating at the homeologous loci gave a significant genotype effect.

responding loci, suggesting that the significant marker-trait associations may reflect variation at the same genetic loci. However, two QTLs showed opposite allelic effects for MIC and fiber fineness, suggesting that the associations may reflect variation at different genetic loci.

Of the 127 loci that detected introgression, 81 linked and two unlinked loci (in total, 65%) were segregating in two or more families; therefore, we performed two-way ANOVA to test for marker-trait associations among families. Among 83 loci studied, we would expect less than

Table 2 Biometrical parameters of QTLs affecting micronaire. For explanation of parameters, see footnotes for Table 1

QTL	Chromosome/linkage group	Nearest locus	Family	R^2	*a*	*d*	*d*/*a* ratio	Gene action	Homeolog
MIC06.1	Chr06	pAR988	94-06	20	−0.38	0.05	−0.13	–	
MIC06.1	Chr06	pAR988	94-07	15	−0.31	0.03	−0.10	A	
MIC14.1	Chr14	pAR175	94-04	25	−0.34	−0.12	0.35	–	
MIC14.2	Chr14	A1727	94-26	10	−0.14	−0.09	0.67	A	
MIC17.1	Chr17	pAR1-56a	94-34	11	−0.23	0.02	−0.09	A	Chr03: pAR1-56b
MIC17.2	Chr17	pAR172a	94-10	18	−0.37	0.34	−0.93	A, D	Chr03: pAR172b
MIC17.2	Chr17	pAR250	94-10	19	−0.28	0.46	−1.64	A, D	Chr03: pAR172b
MIC17.2	Chr17	pGH399b	94-10	16	−0.30	0.40	−1.36	A, D	Chr02: pGH399a
MIC26.1	Chr26	A1310b	94-24	9	0.08	0.13	1.73	–	Chr12: A1252
MICD08.1	LGD08	pAR482	94-06	25	−0.08	−0.39	4.88	–	
MICD08.2	LGD08	pGH239	94-07	11	−0.31	0.06	−0.19	–	Chr05: pAR1-28
MICD08.3	LGD08	pAR3-41	94-34	11	−0.12	0.51	−4.43	-	Chr05: A1318b; G1112a

one association that is significant at the 1% level by chance alone. A significant ($P < 0.001$) among-family G effect was detected at one and six loci for MIC and fiber fineness, respectively (ESM, Table S1). For fiber fineness, the six loci appear to represent only three non-overlapping genomic regions, of which QTLs were detected in all regions in the within-family analysis (*FF14.1*, *FF15.1*, *FF20.2*). No MIC QTLs were detected in the within-family analysis in the region significant for among-family G effect; however, this region was associated with a QTL for fiber fineness (*FF12.2*).

A total of 11 loci were significant ($P < 0.001$) for G×F interactions for fiber fineness (ESM Table S2). Six of these loci (*FF01.3*, *FF05.1*, *FF06.2*, *FF12.1*, *FF18.1*, *FF26.1*) also detected QTLs in one or more segregating families, while the other five loci had a $P <$ F value of less than 0.005 for some families but did not reach the $P < 0.001$ threshold for declaring a QTL. None of the 83 loci tested showed G×F interactions for MIC, although the locus *MIC06.1* had a $P <$ F value that was narrowly above the $P < 0.001$ threshold.

Discussion

The theoretical benefits of using an advanced-generation backcross were realized in this study in that a substantially larger number of QTLs for fiber fineness were detected than in prior QTL mapping studies conducted with F_2 populations (Jiang et al. 1998; Kohel et al. 2001; Mei et al. 2004). However, using a large F_2 population and a second year of progeny testing in field trials that included two irrigation regimes, Paterson et al. (2003) reported nearly threefold the number of MIC QTLs detected in the BC_3F_2 population. Since the BC_3F_2 populations were only studied under relatively favorable conditions and many of the QTLs reported by Paterson et al. (2003) were detected only in water-limited conditions, the discrepancy is likely due to the presence of QTLs which interact with environmental factors such as growing season (year) and irrigation treatment (well watered vs. dryland). This reiterates the point made by Paterson et al. (2003) that breeding high-quality cotton for either well-watered or dryland conditions may require different breeding programs targeted at these different conditions.

The detection of QTLs at corresponding chromosomal locations across various populations further support the likelihood that these QTLs are real and not an analytical artifact. In this analysis, QTLs mapping to the same chromosomal regions (either associated with the same RFLP locus or were overlapped by common markers) and having the same effect across different families were inferred to be allelic. Among the nine MIC QTLs identified in the BC_3F_2 population, three (33%) were in common with the MIC QTLs mapped in the F_2 population of Paterson et al. (2003). For all three of these QTLs (*MIC14.1*, *MIC17.1*, *MICD08.1*), the *G. barbadense* allele contributed reduced fiber diameter. Interestingly, ten (31%) QTLs for fiber fineness detected in the BC_3F_2 population fell in the same region where Paterson et al. (2003) reported a QTL for MIC. This includes the three QTLs that also corresponded to MIC QTLs mentioned above.

Despite the fact that both MIC and fiber fineness are commonly used in the cotton fiber industry to measure fiber diameter, the two traits are correlated only at a moderate level. The correlation coefficient of $r = 0.61$, while statistically significant ($P < 0.001$), indicates that the two traits have different levels of accuracy and precision in measuring fiber diameter. The larger number of QTLs detected for fiber fineness support previous research that suggests this measurement captured more genetic than non-genetic variance for fiber thickness parameters (Meredith et al. 1996). The opposite is true for MIC (Meredith 1994), which may have accounted for a lesser number of QTLs being detected using this method.

The genetic variance explained by each trait may be related to the manner in which measurements were performed. The AFIS instrument measures the light blocked by an individual fiber as it travels perpendicularly at high speed through a beam of light. The light-attenuation signal is then used to calculate the

cross-sectional area of individual fibers based on the AFIS length and diameter module (Bradow and Davidonis 2000). The MIC reading, on the other hand, measures the amount of resistance to airflow of a constant weight of fiber (Steadman 1997). Comparison of the two methods to microscopic imaging of fiber cross section, which serves as the most direct determination of fiber diameter and cell-wall thickness, clearly indicated that the AFIS method correlated more closely with fiber parameters estimated by imaging (Hequet and Wyatt 2001). The MIC reading also is confounded with other fiber properties such as maturity (Meredith 1994), therefore the degree of cell-wall thickening affected by fiber maturity likely accounts for a portion of the unmapped genetic effects and explains the less accurate reflection of fiber thickness. For example, low MIC fibers could indicate mature fiber with small diameter that will spin efficiently into high-quality yarn, or it could indicate immature fiber that can cause neps and dye defects (May 2000). Nonetheless, the cotton industry still relies extensively on MIC readings to assess fiber fineness because of its speed and low cost. The finding of five corresponding QTLs in which the *G. barbadense* alleles conferred decreased fiber diameter in both traits suggests that MIC reading is a meaningful, albeit coarse, assessment. However, the extent to which the genetic variation of MIC reading is influenced by fiber maturity is not well understood. We will further address the complex relationship between the two fiber diameter traits when we examine their relationships to QTL analysis of fiber maturity in another installment of this series.

The number of QTLs detected per family ranged from zero to five for fiber fineness and from zero to two for MIC. Also, a total of 17 and 7 families detected at least one QTL for fiber fineness and MIC, respectively. Since the *G. barbadense* allele conferred finer fiber at a majority of the QTLs, the mean fiber diameter for the 24 BC_3 families would expected to be either superior to or approaching that of the recurrent parent. However, this was not the case, as 18 of the 24 BC_3 families have coarser fiber (higher MIC and fiber fineness reading) than the recurrent parent. A similar pattern of transgressive segregation has been reported in advanced backcross populations from tomato for a host of morphological characters (Monforte and Tanksley 2000). This ''negative'' transgression, yielding a phenotype that is poorer than the poorer parent, suggests that many new allelic combinations arising after introgression are undesirable.

It is interesting to note that all six families in which the means for fiber fineness were superior to that of the recurrent parent contained at least one QTL with the favorable allele contributed by the *G. barbadense* parent. On the opposing side, no QTLs for fiber fineness were detected for the eight families that ranked with the coarsest fibers. This supports the hypothesis that improvement of fiber diameter for Upland cotton may be achieved by introgressing QTLs from *G. barbadense*. Although a majority of the QTLs detected for both traits accounted for only small portions of the phenotypic variance, about 33% of the QTLs detected for MIC and 31% of those detected for fiber fineness explained more than 20% of the phenotypic variance. Further, several of the QTLs were consistently expressed across different BC_3 families, showing similar effects. This suggests that they may continue to function when transferred to other *G. hirsutum* genetic backgrounds; however this remains to be proven. Efforts are now underway to build a set of near-isogenic introgression lines that carry these QTLs, which will allow the *G. barbadense* alleles to be more readily accessible in breeding programs for improving fiber quality.

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