Theor Appl Genet (2005) 111: 757–763
DOI 10.1007/s00122-005-2063-z

ORIGINAL PAPER

Peng Chee · Xavier Draye · Chun-Xiao Jiang
Laura Decanini · Terrye A. Delmonte
Robert Bredhauer · C. Wayne Smith
Andrew H. Paterson

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

Received: 9 November 2004 / Accepted: 2 May 2005 / Published online: 28 June 2005

Abstract The current study is the first installment of an effort to explore the secondary gene pool for the enhancement of Upland cotton (*Gossypium hirsutum* L.) germplasm. We developed advanced-generation backcross populations by first crossing *G. hirsutum* cv. Tamcot 2111 and *G. barbadense* cv. Pima S6, then independently backcrossing F_1 plants to the *G. hirsutum* parent for three cycles. Genome-wide mapping revealed introgressed alleles at an average of 7.3% of loci in each BC_3F_1 plant, collectively representing *G. barbadense* introgression over about 70% of the genome. Twenty-four BC_3F_1 plants were selfed to generate 24 BC_3F_2 families of 22–172 plants per family (totaling 2,976 plants), which were field-tested for fiber elongation and genetically mapped. One-way analysis of variance detected 22 non-overlapping quantitative trail loci (QTLs) distributed over 15 different chromosomes. The percentage of variance explained by individual loci ranged from 8% to 28%. Although the *G. barbadense* parent has lower fiber elongation than the *G. hirsutum* parent, the *G. barbadense* allele contributed to increased fiber elongation at 64% of the QTLs. Two-way analysis of variance detected significant ($P < 0.001$) among-family genotype effects and genotype×family interactions in two and eight regions, respectively, suggesting that the phenotypic effects of some introgressed chromosomal segments are dependent upon the presence/absence of other chromosomal segments.

Introduction

Growing concerns about genetic vulnerability in many crop species have stimulated renewed interest in utilizing the secondary gene pool as a source of genetic variation in breeding programs. Closely related species often contain novel alleles, a subset of which are of potential value for crop improvement. However, genetic variation between species is often directly or indirectly related to reproductive isolation, or to adaptation to different natural environments, and many introgressed genes prove to be difficult to use in crop improvement. In particular, problems such as segregation distortion (Jiang et al. 2000), suppression of recombination (Paterson et al. 1990), and linkage drag (Young and Tanksley 1989) often are encountered in interspecific crosses. As a consequence, plant breeders have traditionally had good reason to be reluctant to utilize interspecific crosses.

DNA markers provide a means of detecting and resolving complications such as segregation distortion or linkage drag encountered during interspecific gene introgression. In particular, the advanced backcross approach has been shown to facilitate the detection and

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s00122-005-2063-z

Communicated by F. Salamini

P. Chee · A. H. Paterson
Plant Genome Mapping Laboratory, University of Georgia, Athens, GA 30602, USA

P. Chee · A. H. Paterson
Department Crop and Soil Sciences, University of Georgia, Tifton, GA 31793, USA

P. Chee · X. Draye · C.-X. Jiang · L. Decanini · T. A. Delmonte
R. Bredhauer · C. W. Smith · A. H. Paterson (✉)
Department Soil and Crop Sciences, Texas A&M University, College Station, TX 77843, USA
E-mail: paterson@uga.edu
Tel.: +1-706-5830162
Fax: +1-706-5860160

Present address: X. Draye
Université catholique de Louvain,
Place Croix du Sud 2/11,
1348 Louvain-la-Neuve, Belgium

integration of beneficial quantitative trait loci (QTLs) from secondary gene pools into elite breeding lines (Tanksley and Nelson 1996). By using this approach, favorable alleles for agronomically important traits have been detected from interspecific backcrosses in tomato (Tanksley et al. 1996; Bernacchi et al. 1998), rice (Xiao et al. 1996; Thomson et al. 2003), and barley (Pillen et al. 2003). In tomato, *Lycopersicon esculentum*, the phenotypic improvement conferred by alleles from *L. hirsutum* and *L. pimpinellifolium* has since been confirmed for a number of QTLs by testing in near-isogenic introgression lines (Bernacchi et al. 1998).

Among the four cotton species that have been domesticated, an overwhelming majority of the US$20 billion annual world cotton fiber commerce is contributed by the two tetraploids, *Gossypium hirsutum* L. and *G. barbadense* L. Cultivated forms of *G. hirsutum* and *G. barbadense* have very different agronomic and fiber quality characteristics. The breeding of *G. hirsutum* (Upland cotton) has focused on maximum yield and broad adaptation, while breeding of *G. barbadense* (Sea Island, Pima, and Egyptian cotton) has emphasized fiber quality. The two tetraploid species are sexually compatible, although partial sterility, longer maturity, and hybrid breakdown are often observed in later generation hybrids (Stephens 1946). Nonetheless, the unique fiber properties of *G. barbadense* make it an ideal candidate for providing new genetic variation useful for improving fiber quality in *G. hirsutum*, the latter accounting for the vast majority of cotton grown in the USA and worldwide.

Early in the history of the textile industry, long and fine cotton fiber was sought because of its direct impact on the quality of the yarn and, ultimately, on the end products (Perkins et al. 1984). However, other fiber properties that contribute to textile processing performance, such as fiber elongation, which measures the degree of extensibility or elasticity of the fibers before a break occurs, are becoming increasingly important (May 2000). Modern textile mills are adopting more efficient spinning technologies that rely on high-speed and automation to achieve higher performance (Bradow and Davidonis 2000). Increases in elongation are associated with improved yarn strength (Riley 1997; May 2000). Therefore, fibers with good elongation generally cause less costly disruption in the spinning process, and the resulting yarn can endure more vigorous mechanical handling during fabric manufacturing.

The current study is the first installment of a long-term project to explore exotic crosses for valuable genes useful in improvement of cultivated *G. hirsutum*. In this study, cultivated *G. barbadense* served as a donor parent, and a modified backcross-self approach was used together with DNA markers to identify and characterize introgressed chromatin. This paper reports the results of QTL analysis for fiber elongation, with an analysis of fiber length and fineness presented in companion papers.

Materials and methods

Population development and phenotyping

A backcross-self mating design was used in this study. About 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 successful pollination was then backcrossed three times to the maternal Tamcot 2111 to yield BC_3F_1s. A total of 24 lineages were 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. Although all progeny were grown to maturity and genotyped with restriction fragment length polymorphism (RFLP) markers, 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 (Table 1).

Seed of all BC_3F_2 families together with ten entries of each parent were planted in peat pellets and germinated in the greenhouse. Seedlings were hand-planted in the field (near College Station, Texas) during early April, a typical planting date for central Texas. Plants were spaced 30 cm (12 inches) apart within rows, and rows were 152 cm (60 inches) apart. All cultural practices were normal for cotton production in central Texas, including furrow irrigation and pre- and post-planting applications of herbicides for weed control and insecticides for the control of feeding and sucking insects. Seed cotton from all mature bolls of an individual BC_3F_2

Table 1 Summary of population size and the number of RFLP loci segregating in each BC_3F_2 family

Family	Number of:	
	F_2 individuals	Markers segregating[a]
94-02	92	24
94-03	152	23
94-04	54	13
94-05	134	5
94-06	89	14
94-07	121	25
94-09	129	9
94-10	122	11
94-11	167	12
94-14	164	2
94-15	169	19
94-18	148	1
94-21	57	18
94-22	125	10
94-24	184	16
94-25	46	13
94-26	141	22
94-27	140	7
94-28	164	17
94-29	172	29
94-30	22	7
94-31	86	10
94-33	160	6
94-34	138	15

plant were hand-harvested over a 2-week period in mid-October and ginned on a saw gin.

The fiber samples were sent to the Cotton Incorporated Textile Services Laboratory (Cotton Incorporated, Cary, N.C.) where fiber elongation measurements were made from a High-Volume Precision Instrument (HVI; Zellweger-Uster, Knoxville, Tenn.) comparable to those used in USA cotton classing. The basic mechanism for measuring elongation is discussed by Riley (1997). Fiber elongation is determined by gradually stretching a bundle of combed fiber clamped at a 3.2-mm (1/8 inch) length. The distance traveled between the two clamps during which the fibers break is recorded and expressed in percentage terms. For example, if a sample is stretched 0.0032 mm (0.00125 inch), elongation is 1%.

Genotyping and data analysis

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 RFLP markers selected for even representation of the cotton genome map (Reinisch et al. 1994; Jiang et al. 1998) and showing polymorphism between the two parents. The markers that detected introgression in the BC_3F_1 were used to evaluate the entire BC_3F_2 family for which they were segregating. Laboratory techniques were as described by Jiang et al. (2000). Because individual progenies segregated for only small portions of the genome, we did not construct a de novo genetic map from the backcross families. Instead, *G. barbadense* regions that were segregating in BC_3F_2 families were monitored as graphical genotypes (Young and Tanksley 1989) based on a detailed genetic map comprising over 2,500 loci (Rong et al. 2004).

Associations between fiber elongation phenotypes and marker genotypes were tested for statistical significance by one-way variance analyses for every marker locus segregating within each BC_3F_2 family. The analyses were performed with the GLM procedure of the SAS ver.8 software package (SAS Institute 1999), with a significance threshold set at the $P < 0.001$ level (F-test). The modes of gene action (a and d) were estimated for individual QTLs using the appropriate linear combination of the estimated model parameters, and their significance levels were assessed with corresponding contrasts as described by Paterson et al. (1990). QTLs were considered to be overdominant if the absolute value of the dominance/additive (d/a) ratio exceeded 3. The R^2 of each variance analysis provided an estimate of the proportion of phenotypic variance accounted for by a QTL at the corresponding marker locus.

For loci that were segregating in two or more families, two-way mixed model variance analyses were also performed, using the MIXED procedure of the SAS ver. 8 package. 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 G×F interaction (Self and Liang 1987). G effects and G×F effects were considered to be significant if $P < 0.001$.

Results

Backcross-self population structure

With the donor genome reduced by half in every backcross generation, we expected to detect the *G. barbadense* allele at 12.5% of the RFLP loci after three sequential backcrosses to the recurrent parent. However, the frequency of RFLP loci that detected the *G. barbadense* allele in individual BC_3F_1 was only 7.3%. A number of chromosomal regions, including the entire length of chromosome 9, showed no *G. barbadense* introgression. Collectively, the 24 BC_3F_1 plants detected introgression for about 70% of the loci. Markers that detected no introgression, or were closely linked and therefore delineated the same introgressed segments, were not studied in the BC_3F_2 families. Consequently, a subset of 127 RFLP markers was used to monitor all of the introgressed regions segregating in the BC_3F_2 families. An average of 14 markers was needed to genotype the segregating chromosome segments in each BC_3F_2 family, with a range from 1 to 29 (Table 1). Of the markers that detected *G. barbadense* introgression, 46 markers (36%) segregated in only one family, 30 (23%) segregated in two families, 27 (21%) segregated in three families, and 26 (20%) segregated in four or more families.

Phenotypic distribution

The BC_3F_2 individuals showed a 1.3-fold range between the lowest and highest fiber elongation values, ranging from 4.5% to 10.6% (Fig. 1). The population as a whole was normally distributed for the trait, but the mean was shifted toward the *G. hirsutum* parent. This is consistent with the expectation that most lines carry only a small portion of the *G. barbadense* genome in an otherwise *G. hirsutum* background. Although the variation between the lowest and highest family mean was only about 20% (from 6.01% to 7.43% fiber elongation), the median falls near the *G. hirsutum* parent, while the *G. barbadense* parent falls near the low end of the distribution.

Number and location of QTLs

A total of 28 significant ($P < 0.001$) associations were detected from testing all 320 marker-trait combinations (Table 2). By assuming that blocks of linked markers within a family that showed significant marker-trait

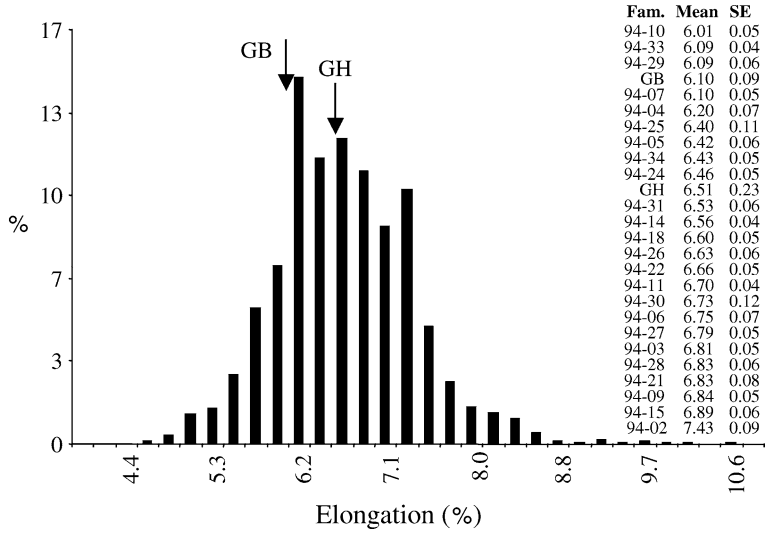

Fig. 1 Frequency distribution of the individual BC_3F_2 plants and the tabulated family means of the BC_3 families for fiber elongation

association represent a single QTL, a total of 22 non-overlapping QTLs were estimated to be segregating in the BC_3F_2 population. These QTLs mapped to 15 chromosomes or linkage groups; ten QTLs mapped onto seven chromosomes from the A-subgenome, and the remaining 12 QTLs mapped onto eight chromosomes from the D-subgenome. In only 12 of the 24 families could we detect one or more OTLs, with a maximum of

Table 2 Biometrical parameters of QTLs affecting fiber elongation. Each row corresponds to a one-way analysis for a single locus and a single family except those loci that are underlined, in which the RFLP locus or a nearby locus showed a significant among-family effect

QTL	Chromosome/ linkage group	Locus	Family	R^{2a}	a^a	d^a	d/aratio[a]	Mode of action[b]	Homeolog[c]
EL01.1	Chr01	G1097	94-11	9	0.52	−0.15	−0.29	A	Chr15: PAR077a PGH468b
EL01.1	Chr01	pGH468a	94-11	8	0.56	−0.13	−0.23	A	Chr15: PAR077a PGH468b
EL01.1[d]	Chr01	A1204	–	–	0.30	−0.02	−0.07	A	
EL01.1	Chr01	pGH377	94-11	9	0.53	−0.18	−0.34	A	
EL01.2	Chr01	A1686a	94-26	2	0.56	0.17	0.30	A	
EL02.1	Chr02	pGH399a	94-07	12	−0.59	0.02	−0.04	A	Chr17: PGH399b*
EL02.1	Chr02	pAR390	94-07	14	−0.63	0.08	−0.13	A	
EL05.1	Chr05	pAR206b	94-04	28	0.87	0.11	0.13	–	Chr22: A1535a PAR206a
EL06.1	Chr06	PXP4-69	94-29	11	0.55	−0.34	−0.61	A	
EL06.2	Chr06	A1152	94-26	11	0.57	0.14	0.24	A	
EL12.1	Chr12	A1210a	94-10	12	−0.47	−0.17	0.37	–	
ELA01.1	LGA01	G1125b	94-28	9	−0.64	−0.04	0.06	A	
ELA03.1	LGA03	pGH243	94-24	20	1.21	0.02	0.02	A	LGD02: PAR566
ELA03.1	LGA03	pAR864	94-24	11	0.6	0.26	0.44	A	
ELA03.1	LGA03	A1672	94-26	9	0.45			–	LGD02: A1174* PGH505
ELA03.2	LGA03	pAR570a	94-06	18	0.68	−0.31	−0.46	A	LGD02: PAR570b*
EL17.1	Chr17	pAR172a	94-10	15	0.77	−0.03	−0.03	A	Chr03: PAR172b
EL17.1	Chr17	pGH399b	94-10	12	0.74	−0.16	−0.22	A	Chr02: PGH399a*
EL18.1	Chr18	P9-53B	94-02	20	0.94			–	
EL20.1	Chr20	A1158b	94-29	15	0.72	0.27	0.38	A	Chr10: A1158a
EL22.1	Chr22	pAR138b	94-29	10	−0.62	−0.18	0.29	A	Chr04: PAR138a
EL23.1	Chr23	pAR209	94-11	13	−0.46	−0.15	0.32	A	
EL26.1	Chr26	A1310b	94-29	8	0.77	−0.14	−0.18	A	Chr12: A1252
ELD02.1	LGD02	A1174	94-21	21	−0.54			–	LGA03: A1672*
ELD02.2	LGD02	pAR570b	94-10	11	0.59	0.15	0.25	A	LGA03: PAR570a*
ELD08.1	LGD08	pAR482	94-15	17	0.12	0.81	6.80	H	
ELD08.2	LGD08	P2-9	94-24	11	−0.19	0.57	−2.97	D	Chr05: A1318b G1112a
ELD08.3	LGD08	pAR137a	94-28	12	−0.62	0.14	−0.22	A	
ELD08.4	LGD08	pAR137a	94-29	16	0.51	−0.72	−1.42	A, D	

[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, with missing value corresponding to dominant or severely distorted DNA marker loci

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

[d] Two-way analysis for multiple families

five QTLs detected per family (family 94-29), and only one QTL was detected in two families. The chromosomal location and subgenomic distributions of QTLs are shown for chromosome 1 and linkage group (LG) D08 in Fig. 2 (as example), with plots for the remaining chromosomes available online as supplementary (ESM) Fig. S1. The biometrical parameters of all significant marker-trait associations are listed in Table 2. The percentage of variance explained (PVE) by individual loci was quite small for most QTLs, averaging about 13%. However, four QTLs were found to explain more than 20% PVE (*EL05.1*, *ELA03.1*, *EL18.1*, *ELD02.1*).

Consistency of QTLs across families and homoeologous regions

A total of 83 DNA marker loci were segregating in two or more families; therefore, we performed two-way ANOVA to test for marker-trait associations and assess their consistency among families. Although less than one association is expected to be significant by chance alone at the 1% level among 83 loci studied, two loci were significant ($P < 0.001$) for the among-family G effect (Table 2). Of these two loci, the locus pAR138b on chromosome 22 also detected a QTL in the within-family analysis. Family 94-29 showed significant association at this locus, and while two other segregating families did not reach the threshold for declaring a QTL ($P < 0.001$), they both were significant at the $P < 0.005$ level. The second locus, A1204 on chromosome 1, failed to reach the significance threshold ($P < 0.001$) in all segregating families, however the markers flanking it detected a QTL in family 11 (Fig. 2). Thus, the significant G effect corroborates the within-family analysis in indicating the presence of a QTL in these regions.

Eight loci, all of which also detected a QTL in the within-family analysis, were significant ($P < 0.001$) for G×F interactions (ESM Table S1) . The presence of G×F interaction was due to the introgressed allele showing different effects among the segregating families. The most extreme case of G×F interaction was observed at locus *pAR137a* in LG D08 (Fig. 2). In family 94-28, the *G. barbadense* allele at this locus conferred a 0.62% additive decrease in fiber elongation that accounted for 12% of PVE. Interestingly, in family 94-29, this same locus conferred a 0.51% additive increase in fiber elongation that accounted for 16% of PVE. This locus also segregated in family 94-05, which showed no association with fiber elongation. The opposing effects of the same introgressed allele in two different families resulted in a highly significant G×F interaction.

A total of 22 genomic regions were identified in which both homoeologous loci were segregating and, thus, could be tested for phenotypic associations (Table 2). Fourteen regions harbored QTLs for fiber elongation and three (21%) showed QTLs for both homeologous loci (*EL02.1* = *EL17.1*; *ELA03.1* = *ELD02.1*; *ELA03.2* = *ELD02.2*). All three homoeologous regions were detected by duplicated RFLP loci.

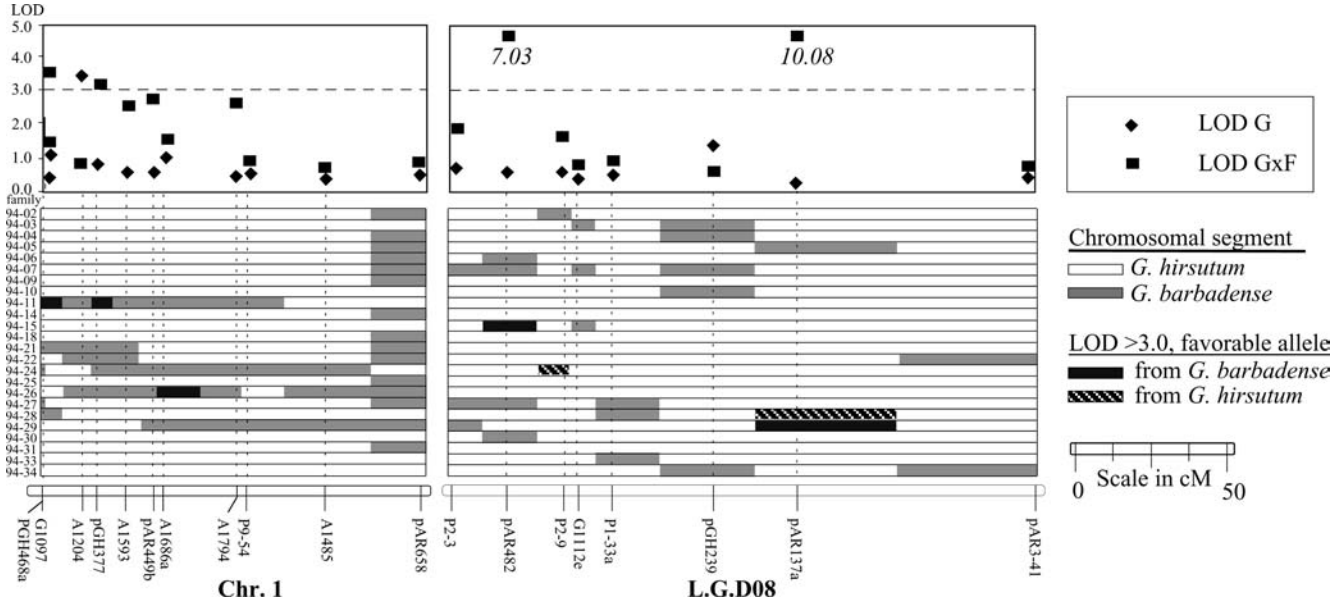

Fig. 2 Graphical genotype (*bottom section*) and significance plot of marker-trait associations (*top section*) for chromosome 1 and linkage group (LG) D08 (with the remaining chromosomes across the cotton genome available on-line as ESM Fig. S1). For the graphical genotype, each *horizontal bar* represents the indicated chromosome for each of the 24 BC_3F_2 families, with *shaded areas* depicting regions containing *Gossypium 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. For the significance plot, *box* symbols represent the genotype × family (*G*×F) interaction, and *diamond* symbols represent the genotype (*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

Discussion

The features that make advanced generations particularly suited for QTL analysis with interspecific crosses have been shown at the theoretical (Tanksley and Nelson 1996) and empirical levels (Tanksley et al. 1996). The backcross-self mating design used in the present study differs from the advanced backcross-QTL analysis proposed by Tanksley and Nelson (1996) in two ways. First, we developed a series of 24 independently derived BC_3 plants by backcrossing a randomly selected individual from each lineage to its original recurrent parent. Second, we imposed a generation of selfing prior to QTL mapping. In principle, the selfing process would ensure an equal frequency of the *G. barbadense* and *G. hirsutum* allele for any markers segregating in each BC_3F_2 family. Further, because cotton is bred as a self-pollinating crop in the USA, it was essential to be able to see the phenotypic consequences of all possible allele dosages at a locus in order to prioritize QTLs for further study.

The main advantage of using an advanced-generation progeny for QTL analysis with interspecific crosses is that the action of individual genetic loci is more clearly resolved than in earlier generations because recombination and segregation have broken the donor genome into smaller components (Tanksley and Nelson 1996). Therefore, it is not surprising that a substantially larger number of QTLs was discovered in the advanced-generation population as compared to prior QTL analyses of cotton fiber based upon F_2 populations. For example, 22 QTLs for fiber elongation were detected in this study as compared to only one, two, and nine QTLs reported by Mei et al. (2004), Jiang et al. (1998), and Paterson et al. (2003), respectively. Although other factors such as the significance threshold, parental selection, population size, and marker density may affect the outcome of a QTL analysis, the generally larger QTL number found in the BC_3F_2 population suggests that many QTLs of small effect may have escaped detection in prior studies. Since the backcrossing had reduced the genetic variation in individual BC_3F_2 families (Fig. 1), small effects previously not significant were inferred with confidence to indicate QTLs.

In addition, it may offer refinements in the localization of QTLs identified because QTL analysis is conducted along small non-overlapping segments of introgressed chromosomes, as opposed to the entire length of a chromosome in the F_2 generation. One possible strategy would be to develop segregating populations using isogenic lines extracted from a family differing only in the region containing a QTL. Since most of the genetic variance in such a population will be from the effect of this QTL, it becomes possible to dissect the remaining interval more accurately by examining various recombinants for flanking markers.

Another advantage of the population design used in this study is that more than one family may be segregating for the same chromosomal segment, thereby allowing us to investigate the effects of genetic background on introgressed *G. barbadense* chromatin. For example, 11 of the 22 overlapping regions detected QTLs for fiber elongation segregating in more than one family, and two (18%) were significant ($P < 0.001$) for the among-family G effect. For these two regions, the *G. barbadense* allele has the same phenotypic effect across all families (increased elongation in *EL01.1* but decreased elongation in *EL22.1*), but the within-family analysis failed to reach the significance threshold in some families due to factors such as insufficient population size to detect the QTL, segregation distortion of the diagnostic marker, or perhaps higher genetic variance from other QTLs. One QTL region showed a non-significant among-family G effect, suggesting that some families may not contain the QTL allele because of recombination between the RFLP marker and the QTL. Alternatively, this could indicate spurious QTL detection (Bernardo 2004).

Interestingly, a substantial number of the QTL regions (8 or 73%) present in multiple families showed G×F interactions, indicating that the introgressed region may have a strong positive effect on fiber elongation in one family but a lesser or even opposite effect in other families. Similar interactions between QTLs and genetic backgrounds were observed in backcross populations of other species (Bernacchi et al. 1998; Lecomte et al. 2004). A possible explanation for this observation is that these chromosomal regions may harbor QTLs with opposite effects and the linkages were broken in some of the BC_3F_2 families, resulting in either positive or negative effects depending on which QTL is present (Bernacchi et al. 1998). Alternatively, the effects of these QTLs may depend on the presence of genetic loci from other donor chromosome segments.

The observation that 15 BC_3 families had a mean fiber elongation higher than the superior parent and the fact that the *G. barbadense* parent contributed favorable alleles in 64% (14/22) of the QTLs detected in this study suggests that although the *G. barbadense* parent has lower fiber elongation than the *G. hirsutum* parent, some of the introgressed *G. barbadense* alleles can enhance the performance of the *G. hirsutum* parent. While these results generally support the notion that superior QTLs may be recovered from an inferior parent (Tanksley and Nelson 1996; Xiao et al. 1996), this needs to be interpreted with caution because each of the parents used in our population development has excellent fiber elongation within their respective species. It is possible that each of the two species contained different loci conferring fiber elongation and that the improved performance observed in the BC_3F_2 families is due to a chance accumulation of favorable alleles from each of the two parents. Interestingly, the vast majority of QTLs do not show homoeologous associations (Table 2), suggesting that transgression is not due to corresponding loci in the A- and D-subgenomes.

Because fiber elongation and strength are usually reported together in the HVI (Bradow and Davidonis 2000), the genetic relationships between these traits have

been extensively studied. Several studies have reported a low but discernible phenotypic correlation between fiber elongation and fiber strength (Riley 1997; May 2000), however this correlation was not always detected (Kloth 1998). In this study, fiber elongation and strength was not correlated despite the large sample size tested ($r = -0.01$; $P > 0.7491$; $n = 2{,}992$). The lack of correlation is also reflected in the fivefold difference in the number of QTLs detected for the two traits: 22 for fiber elongation and only four for fiber strength. However, the correlation between fiber elongation and strength could be present at the genotypic level, even though it was non-existent at the phenotypic level (Kloth 1998). Interestingly, two of the four (50%) fiber strength QTLs did correspond to QTLs for fiber elongation, suggesting the possibility that some common genetic loci may affect both traits.

Current trends in cotton breeding methods (Bowman 2000), predominantly involving crossing closely related parents followed by backcrossing or direct reselection from existing cultivars, seem likely to result in a plateau with respect to the amounts and rates of genetic gain. Some argue (Helms 2000; Meredith 2000) that cotton has reached such a plateau for productivity and many important fiber quality traits. Results from this study and those reported from other QTL analyses (Jiang et al. 1998; Paterson et al. 2003) indicate that many unexplored avenues exist to improve Upland cotton through new interspecific gene combinations; yet less than 1% of the parental material used in private cotton breeding programs and 3% in public programs are from exotic sources (Bowman 2000), including *G. barbadense*. The availability of DNA markers linked to *G. barbadense* QTLs could assist breeders in transferring and maintaining these QTL regions during cultivar development.

Acknowledgements We acknowledge the financial support from the Texas and Georgia Agricultural Experiment Stations, Texas Higher Education Coordinating Board, Cotton Incorporated, and USDA-IFAFS. XD was a postdoctoral research associate of the Fonds National Belge de la Recherche Scientifique.

References

Bernacchi D, Beck-Bunn T, Emmatty D, Eshed Y, Inai S, Lopez J, Petiard V, Sayama H, Uhlig J, Zamir D, Tanksley S (1998) Advanced backcross QTL analysis of tomato. II. Evaluation of near-isogenic lines carrying single-donor introgressions for desirable wild QTL-alleles derived from *Lycopersicon hirsutum* and *L. pimpinellifolium*. Theor Appl Genet 97:170–180

Bernardo R (2004) What proportion of declared QTL in plants are false? Theor Appl Genet 109:419–424

Bowman DT (2000) Attributes of public and private cotton breeding programs. J Cotton Sci 4:130–136

Bradow JM, Davidonis GH (2000) Quantitation of fiber quality and the cotton production-processing interface: a physiologist's perspective. J Cotton Sci 4:34–64

Helms AB (2000) Yield study report. In: Dugger P, Richter D (eds) Proc Beltwide Cotton Production Conf. National Cotton Council of America, San Antonio, Tex., pp

Jiang C, Wright R, El-Zik K, Paterson A (1998) Polyploid formation created unique avenues for response to selection in *Gossypium* (Cotton). Proc Natl Acad Sci USA 95:4419–4424

Jiang C, Chee P, Draye X, Morrell P, Smith C, Paterson A (2000) Multi-locus interactions restrict gene flow in advanced-generation interspecific populations of polyploid *Gossypium* (Cotton). Evolution 54:798–814

Kloth RH (1998) Analysis of commonality for traits of cotton fiber. J Cotton Sci 2:17–22

Lecomte L, Duffe P, Buret M, Servin B, Hospital F, Causse M (2004) Marker-assisted introgression of five QTLs controlling fruit quality traits into three tomato lines revealed interactions between QTLs and genetic backgrounds. Theor Appl Genet 109:658–668

May OL (2000) Genetic variation for fiber quality. In: Basra AS (ed) Cotton fibers–developmental biology, quality improvement, and textile processing. Food Products Press, New York, pp 183–229

Mei M, Syed NH, Gao W, Thaxton PM, Smith CW, Stelly DM, Chen ZJ (2004) Genetic mapping and QTL analysis of fiber-related traits in cotton (*Gossypium*). Theor Appl Genet 108:280–291

Meredith MR (2000) Cotton yield progress–why has it reached a plateau. Better Crops 84:6–9

Paterson AH, DeVerna J, Lanini B, Tanksley SD (1990) Fine mapping of quantitative trait loci using selected overlapping recombinant chromosomes, from an interspecies cross of tomato. Genetics 124:735–742

Paterson AH, Saranga Y, Menz M, Jiang C, Wright RJ (2003) QTL analysis of genotype×environmental interactions affecting cotton fiber quality. Theor Appl Genet 106:384–396

Perkins HH, Ethridge DE, Bragg CK (1984) Fiber. In: Kohel RJ, Lewis CF (eds) Cotton. American Society of Agronomy, Madison, pp 438–508

Pillen K, Zacharias A, Leon J (2003) Advanced backcross QTL analysis in barley (*Hordeum vulgare* L.). Theor Appl Genet 107:340–352

Reinisch AJ, Dong JM, Brubaker C, Stelly D, Wendel JF, Paterson AP (1994) A detailed RFLP map of cotton (*Gossypium hirsutum* × *Gossypium barbadense*): chromosome organization and evolution in a disomic polyploid genome. Genetics 138:829–847

Riley CR (1997) Improved high volume instrument elongation measurements. J Cotton Sci 1:61–71

Rong J, Abbey C, Bowers JE, Brubaker CL, Chang C, Chee PW, Delmonte TA, Ding X, Garza JJ, Marler BS, Park CH, Pierce GJ, Rainey KM, Rastogi VK, Schultze SR, Trolinder NL, Wendel JF, Wilkins TA, Williams-Coplin D, Wing RA, Wright RJ, Zhao X, Zhu L, Paterson AH (2004) A 3,347-locus genetic recombination map of sequence-tagged sites reveals features of genome organization, transmission and evolution of cotton (*Gossypium*). Genetics 166:389–417

SAS Institute (1999) SAS/STAT User's guide, ver. 8. SAS Institute, Cary, N.C.

Self SG, Liang KL (1987) Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. J Am Stat Assoc 82:605–610

Stephens SG (1946) The genetics of "Corky". The New World alleles and their possible role as an interspecific isolating mechanism. J Genet 47:150–161

Tanksley SD, Nelson CJ (1996) Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. Theor Appl Genet 92:191–203

Thomson MJ, Tai TH, McClung AM, Lai X-H, Hinga EM, Lobos KB, Xu Y, Martinez CP, McCouch SR (2003) Mapping quantitative trait loci for yield, yield components and morphological traits in an advanced backcross population between *Oryza rufipogon* and the *Oryza sativa* cultivar Jefferson. Theor Appl Genet 107:479–493

Xiao J, Grandillo S, Ahn S, Yuan L, Tanksley SD, McCouch SR (1996) Genes from wild rice improve yield. Nature 384:223–224

Young ND, Tanksley SD (1989) RFLP analysis of the size of chromosomal segments retained around the *Tm-2* locus of tomato during backcross breeding. Theor Appl Genet 77:353–359