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QTL analysis of genotype × environment interactions affecting cotton fiber quality

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Abstract Cotton is unusual among major crops in that large acreages are grown under both irrigated and rainfed conditions, making genotype × environment interactions of even greater importance than usual in designing crop-improvement strategies. We describe the impact of well-watered versus water-limited growth conditions on the genetic control of fiber quality, a complex suite of traits that collectively determine the utility of cotton. Fiber length, length uniformity, elongation, strength, fineness, and color (yellowness) were influenced by 6, 7, 9, 21, 25 and 11 QTLs (respectively) that could be detected in one or more treatments. The genetic control of cotton fiber quality was markedly affected both by general differences between growing seasons ('years') and by specific differences in water management regimes. Seventeen QTLs were detected only in the water-limited treatment while only two were specific to the well-watered treatment, suggesting that improvement of fiber quality under water stress may be even more complicated than improvement of this already complex trait under well-watered conditions. In crops such as cotton with widespread use of both irrigated and rainfed production systems, the need to manipulate larger numbers of genes to confer adequate quality under both sets of conditions will reduce the expected rate of genetic gain. These difficulties may be partly ameliorated by efficiencies gained through identification and use of diagnostic DNA markers, including those identified herein.

Keywords DNA markers · Crop improvement · Plant water status · Polyploidy

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Introduction

Differential genotypic expression across environments, often referred to as genotype × environment interaction (G × E) is one of the unifying challenges facing plant and animal breeders. Many agriculturally important traits are end-point measurements, reflecting the aggregate effects of large numbers of genes acting independently and in concert, throughout the life cycle of an organism, and external factors at any time during the life cycle may change the 'developmental trajectory' of an organism in ways that may not be predictable. The extent to which G × E affects a trait is an important determinant of the degree of testing over years and locations that must be employed to satisfactorily quantify the performance of a crop genotype. Because testing is a major factor in the time and cost of developing new crop varieties, G × E interactions and their consequences have received much attention from crop scientists (see Romagosa and Fox 1993 for a review).

While many of the environmental parameters contributing to G × E are often unknown, water availability is a particularly important factor in determining the performance of different crop genotypes. About one-third of the world's arable land suffers from chronically inadequate supplies of water for agriculture, and in virtually all agricultural regions, crop yields are periodically reduced by drought (Kramer 1980; Boyer 1982). Global climatic trends may accentuate this problem in the future (Le Houerou 1996). Efficient irrigation technologies help to reduce the gap between potential and actual yield; however, diminishing water supplies in many regions impel intrinsic genetic improvement of crop pro-

ductivity under arid conditions (see Blum 1988) as a sustainable and economically viable solution to this problem. Even under irrigation, plants are often exposed to water deprivation due to diurnal fluctuations, intervals between irrigation, or limited supplies of irrigation water following dry winters. The development of drought-tolerant crops has been hindered by low heritability of key end-point measurements such as yield, and by lack of knowledge of more precise physiological parameters that reflect genetic potential for improved productivity under water deficit.

One major crop in which G × E associated with water availability may have an especially great impact is cotton, *Gossypium hirsutum* L. and *Gossypium barbadense* L. As an agronomic crop but one of relatively high value per unit land area, cotton growers are divided regarding the economics of irrigation usage. In the two largest cotton-producing states in the USA, Texas and Georgia, of 1999 planted acreage of 6,150,000 and 1,470,000 acres respectively (http://www.nass.usda.gov), about 2,000,000 (32.5%) and 570,000 (38.7% of) acres were irrigated. Few if any cotton breeding programs have the resources needed to breed cultivars specifically tailored to one of these two profoundly different production regimes (irrigated and rainfed), instead testing genotypes across a range of conditions and releasing the best average performers.

In this study, we have used genetic mapping to compare the sets of QTLs found to influence key parameters of cotton fiber quality under well-watered versus water-limited conditions. Published estimates, supported by our data below, show that heritability of cotton yield components and fiber properties is moderate to high (approximately 40–80%; Meredith and Bridge 1984; May 1999), indicating that these traits can be manipulated in early segregating generations. Indeed, this has motivated the development of instrumentation and service facilities that could provide reliable data on fiber samples of as little as 2 grams.

This manuscript describes one aspect of a larger study of the consequences of water-limited conditions for the genetic control of quality, productivity and physiological status, as well as interrelationships between these traits, in two generations of progeny from a cross between the predominant cultivated cotton species, *G. hirsutum* (hereafter *GH*) and *G. barbadense* (*GB*). The long-term goal of this work is to contribute to establishing a scientific framework for improving crop yield and quality under arid conditions, typefied by water deficit in conjunction with excessive heat. A fringe benefit of the choice of cotton as an experimental system is that it is polyploid, like many of the world's major crops; intensive study of duplicated genes and chromosomal regions may shed new light on the role of polyploidy in plant adaptation to environmental stress.

Materials and methods

Plant materials

Two field trials were conducted in 1996–97 in Nir-Am, located in the western Negev desert in Israel (31°N, 34°E) each with two irrigation regimes, well-watered and water-limited. The first experiment consisted of 900 interspecific F_2 cotton plants (self fertilized progenies of a F1 hybrid, *G. hirsutum* cv Siv'on × *G. barbadense* cv F-177), grown in ten main plots (five under each irrigation treatment). About 430 of these plants, which produced sufficient seed for the subsequent experiment, were completely phenotyped and genotyped (the remainder were not studied further). The second experiment consisted of 214 F_3 families (self fertilized progenies of the F_2, 107 from each treatment to eliminate any possible consequences of differential selection in the F_2) selected to represent the entire population with an emphasis on families for which parents exhibited extreme values of carbon isotope ratio ($d^{13}C$, an indicator of water-use efficiency). A split-plot design was used with irrigation in main plots, and three replicates of five plants per F_3 family as sub-plots. Average values of the 15 F3 plants (three replicates) were used for data analysis. In both experiments, plants were sown in 1.92-m spaced rows, at a density of 4 plants/m. Water was applied twice a week using a drip system, with the well-watered treatment receiving a total of about 300 mm over the season (consistent with commercial cotton production), and the water-limited treatment receiving about 40–50% of that quantity (starting later and ending earlier than the well-watered treatment). This degree of water limitation reduced dry matter yield and seed-cotton yield to 64% and 68% (respectively) of the control in year 1, and to 47% and 50% in year 2. Other management practices (fertilization, weed and pest control, defoliation, etc.) were consistent with commercial cotton production.

Harvest and lint quality assessment

In year 1 seedcotton of each individual F2 plant was harvested, whereas in year 2 seedcotton was harvested from one, randomly selected, plant per plot. In both experiments, however, seedcotton from all cotton bolls of a single plant was harvested as one bulk and ginned by a miniature saw gin. Fiber span length, length uniformity, fineness (Micronaire value), strength, elongation and color components (reflectance and yellowness) were determined with an HVI tester (Zellweger Uster Ag, Uster, Switzerland) at the official laboratory of the Israel Cotton Production and Marketing Board.

Genotyping and data analysis

A total of 253 RFLP loci spaced at average intervals of 23.1 cM were detected by published procedures using DNA probes sampled from a published map (Reinisch et al. 1994), supplemented with new probes to fill gaps. QTL analyses were performed using Mapmaker-QTL (Lander and Botstein 1989), for a total of ten data sets, including each of the four individual year × irrigation treatment combinations; two data sets combined across the respective irrigation treatments, two data sets combined across the respective years, one combined across both year and irrigation treatments, and one based on relative values (water-limited/well-watered) for the replicated year-2 study (relative values could not be calculated for the year-1 study, based on single plants).

Heritability was calculated based on F3-F2 regression (Smith and Kinman 1965) using original units (Table 1). Standard-unit regression (data not shown) was not significantly different from that based on original units, so original data were used.

Based on the length of the genetic map and the density of markers (above), a LOD = 3 threshold (a = 0.001 on a nominal basis, or 0.05 after accounting for multiple comparisons; Lander and Botstein 1989) was used to declare QTLs. Permutation tests (Churchill and Doerge 1994) were also done for all traits. LOD

Table 1 Estimates of heritability for cotton fiber quality traits using F3/F2 regression

Treatment[a]	Seed cotton yield	Dry matter yield	Fiber length	Fiber length uniformity	Fiber strength	Fiber elongation	Fiber fineness	Fiber color
Irr F3/Irr F2	–0.07	0.01	0.52	0.02	0.28	0.46	0.36	0.17
Irr F3/MinIrr F2	–0.15	0.13	0.49	–0.02	0.26	0.36	0.41	0.31
MinIrr F3/Irr F2	–0.02	0.01	0.78	0.06	0.46	0.62	0.51	0.56
MinIrr F3/MinIrr F2	0.08	0.07	0.67	0.11	0.61	0.4	0.54	0.55
Average (significance)	–0.04	0.06	0.61**	0.04	0.40**	0.46**	0.46**	0.40*

[a] 'Irr' = well-watered; 'MinIrr' = water-limited
* Significant at the 0.05 level
** Significant at the 0.01 level

thresholds suggested by the permutation tests for the various subsets (by year, by irrigation and relative values) were generally similar to those suggested for the complete data set and, therefore, the latter thresholds were used. The thresholds suggested for most traits (length, elongation, strength, fineness and yellowness) fell between 3.74 and 3.92, and indicated that LOD = 3 corresponded to about 0.25 (after accounting for multiple comparisons). Higher thresholds were suggested for length uniformity (LOD threshold = 4.84, a = 0.38 for LOD = 3). The threshold suggested for lint reflectance was extremely high (LOD threshold = 7.88, a = 0.78 for LOD = 3) and was not met by any QTL. This was assumed to reflect the high "noise" caused by the interference of trash (plant parts that are more frequent in lint samples processed by small gins), and therefore lint reflectance was not considered further. Although our primary threshold for declaring a QTL was the LOD > 3.0 criterion, we have also noted which QTLs were further confirmed by the more stringent thresholds based on permutation testing.

Modes of gene action for individual QTLs were calculated and expressed (Table 3) as described (Paterson et al. 1991). QTLs were considered to be heterotic if the absolute value of the d/a ratio exceeded 3.

Interactions of QTLs with environment were evaluated based on two criteria. Single-point analysis of variance using SAS (Joyner 1985) is a straightforward method to evaluate statistical interactions, which we employed using the multiple-environment data (including both treatments in each of the 2 years), but single-marker analysis usually has a lower power to detect QTLs than pairs of flanking markers (Lander and Botstein 1989). MapMaker-QTL uses flanking marker information but is not well-suited to formal analysis of G × E, one can easily identify QTLs that are significant in one treatment and not in another, but to simply apply this standard would be to make a distinction between QTLs that barely met significance (LOD 3.01) and those that barely missed significance (LOD 2.99). To compensate for this, we added the additional criterion that a QTL must not only reach significance in one environment and fail to do so in another, but must also show a LOD difference >2 (100-fold) between the environments to be considered to show genotype × environment interaction. Many significant interactions showing a LOD difference >2 could be corroborated by single-point analysis of variance using SAS (Joyner 1985), based on genotype at the nearest single marker(s). Single-point analysis of variance missed some interactions that could be detected using interval analysis; this is as expected, in view of the much lower power of single markers than pairs of flanking markers to detect QTLs (Lander and Botstein 1989). Crop performance under stress (water-limited treatment) relative to a control (well-watered treatment) is a widely accepted measure of stress adaptation, therefore QTLs derived from the relative data set were also considered to represent genotype × environment interactions.

Results

Histograms of phenotypes, effects of macroenvironmental factors, and parent-progeny regressions

Phenotypic distributions for each trait, in each year and environment, are shown in Fig. 1 together with the parental and F1 values. Fiber length, length uniformity and strength showed normal distribution, whereas fiber elongation, fineness and yellowness each did not show a normal distribution in three of the four year × irrigation combinations; therefore, their log values were used for further analyses. Although some traits (length uniformity) showed substantial differences between years, the overall distributions of quality related phenotypes for populations grown under different water regimes in a single year were very similar. Heterosis for fiber length, strength and fineness (micronaire) were evident, in that the F1 was substantially higher (length, strength) or lower (micronaire) than the superior parent.

The analysis of a complex trait in early generations is especially appropriate in the case where the trait shows relatively high heritability. While others have shown that fiber quality traits are generally of high heritability (Meredith and Bridge 1984; May 1999); we also evaluated this for our own data by performing F3/F2 regressions (Smith and Kinman 1965). Our experimental design permitted us to estimate the dispersion in these estimates, as well. In the F2 generation, equal numbers of plants were assigned at random to 'well-watered' versus 'water-limited' conditions (as defined above). A subset of equal numbers of plants from each F2 regime were chosen for F3 analysis, and were grown in both regimes. Therefore, we were able to conduct four independent estimates of heritability for each trait, by regressing (for example), the 'well-watered' F3 phenotype on the 'well-watered' F2 phenotype (and the other three possible combinations), for the subset of plants (families) that had complete data. Virtually all measures of fiber quality showed high and highly significant heritability (ranging from 0.40 to 0.61, generally consistent with the literature), with one exception. "Fiber length uniformity," measuring the dispersion in lengths of the population of mature fibers from a cotton plant, was low (in fact non-significant heritability), and was similar to that of param-

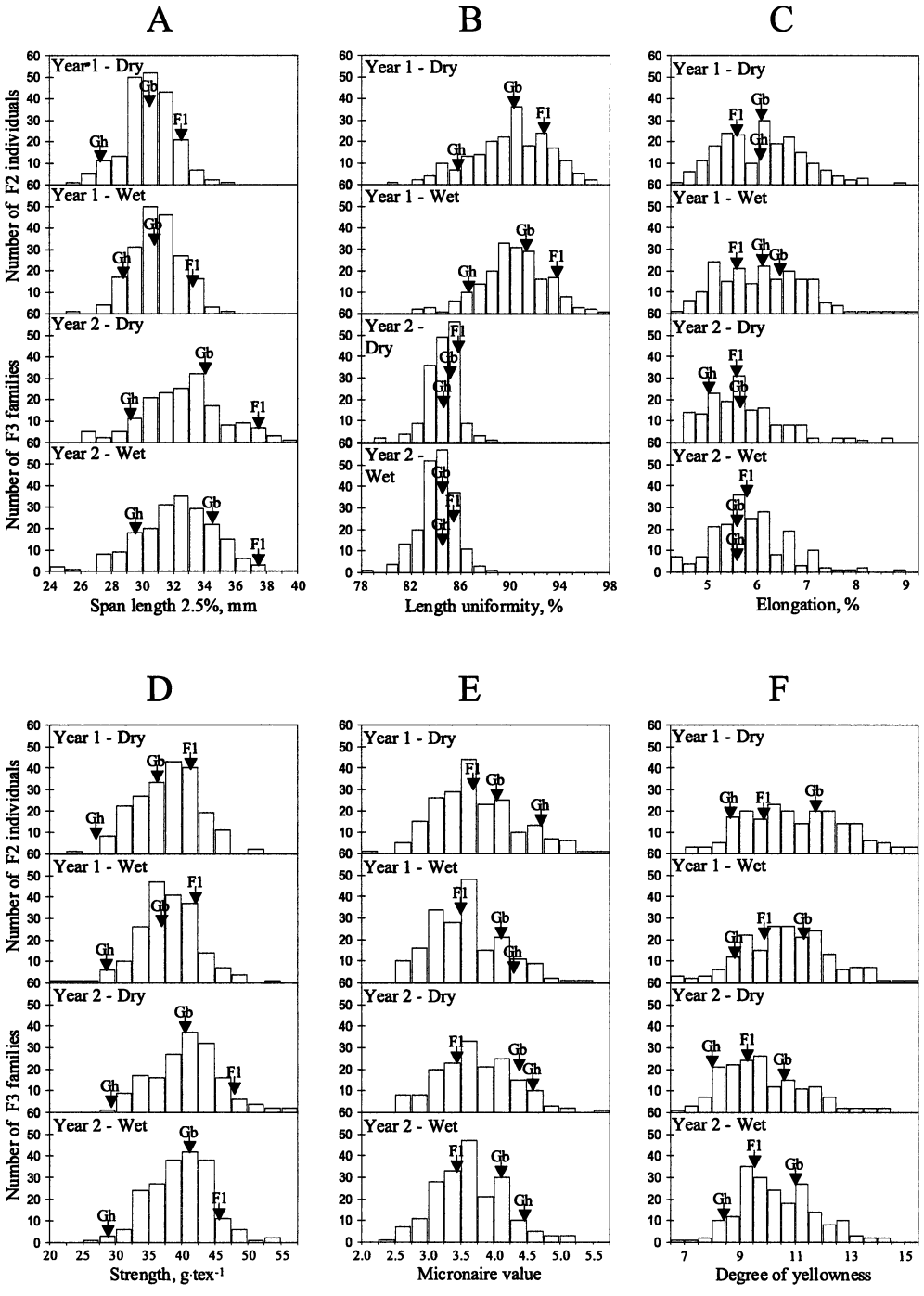


Fig. 1 Histograms for fiber quality phenotypes in 2 years and under two irrigation treatments. The average values of the *G. hirsutum* parent (*Gh*), *G. barbadense* parent (*Gb*), and F1 hybrid (*F1*) are indicated. The water-limited treatment is abbreviated as 'dry' and the well-watered treatment is referred to as 'wet.' All phenotypes are shown in original units in these graphs, although several phenotypes were transformed prior to further analysis (as described in text)

eters such as seed cotton yield and dry matter yield. While we have presented QTLs for fiber uniformity, we acknowledge that they must be interpreted with caution. However, the high heritabilities of most fiber traits support the validity of an early generation study.

QTLs controlling fiber quality, and their interactions with irrigation regime

The details of the genetic map produced herein have been described elsewhere (Saranga et al. 2002). A total of 79 QTLs were detected for six fiber quality traits (Table 2, Fig. 2). Detailed biometrical parameters for each QTL detected, in each year, under each irrigation treatment, pooled across all data sets, and based on relative values, are provided in Table 3.

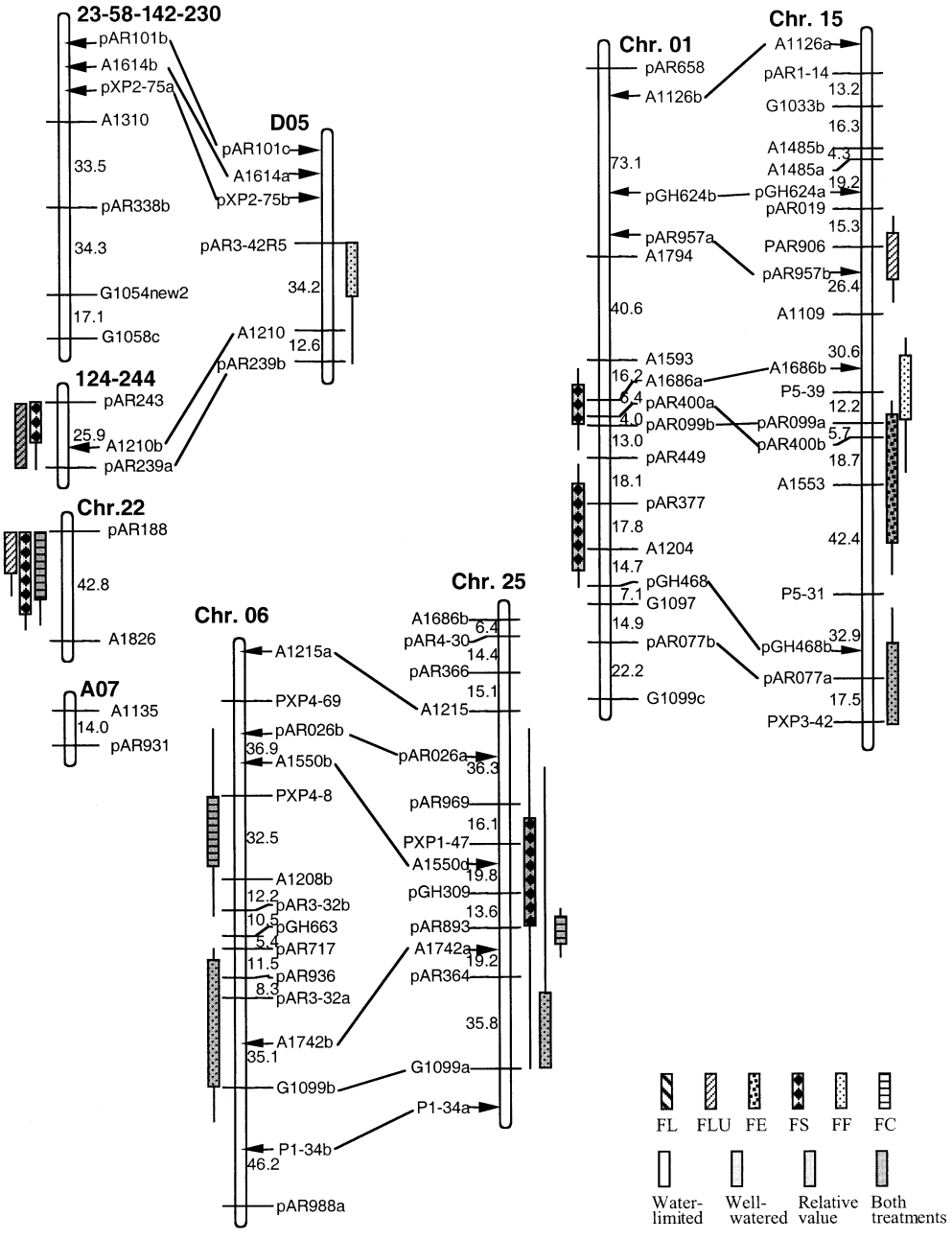


Fig. 2 Likelihood intervals for QTLs associated with lint quality traits in the interspecific cotton (*G. hirsutum* × *G. barbadense*) population. *Bars and whiskers* indicate 1 LOD (10-fold) and 2 LOD (100-fold) likelihood intervals. The *solid line* connecting different probes indicate homoeologous chromosomal segments. *Arrows* indicate the inferred location of markers used to align the homoeologous linkage groups, based on the published map. *FL*, fiber length; *FLU*, fiber length uniformity; *FS*, fiber strength; *FE*, fiber elongation; *FF*, fiber fineness; *FC*, fiber color

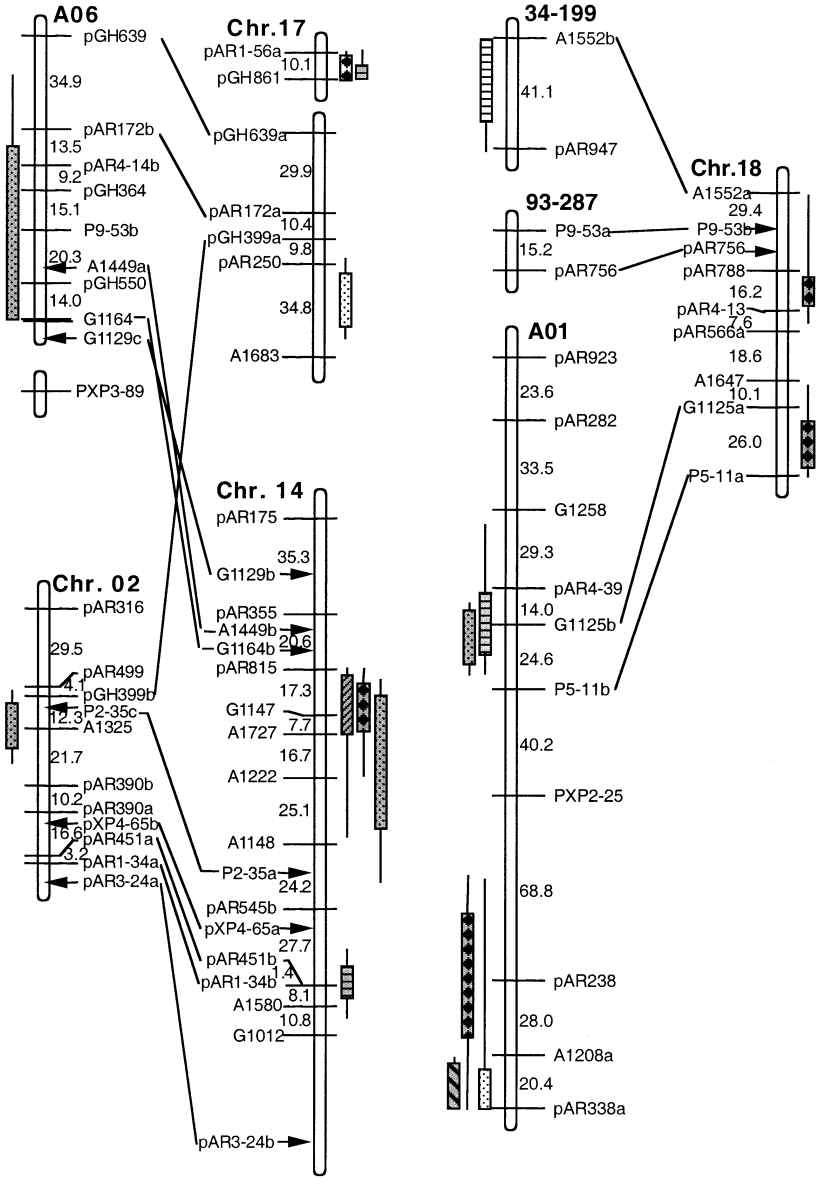
Table 2 Summary of QTLs in an interspecific cotton (*G. hirsutum* × *G. barbadense*) population associated with fiber length (FL), length uniformity (FLU), strength (FS), elongation (FE), fineness (FF) and color (FC)

Trait	# QTLs LOD>3 (A/D genome)	Range of % variation explained	Favorable genotype[a]				Environment sensitivity[b]				
			GH	H+	H–	*GB*	Year 1 (single plants)	Year 2 (family rows)	Water-limited	Well-watered	Relative value
FL	6 (5/1)	2.9–13.7	3	0	1	2	1	1	1	1	0
FLU	7 (3/4)	2.1–13.3	3	0	2	2	3	1	2	1	0
FE	9 (4/5)	2.5–7.3	4	0	1	4	2	3	0	0	0
FS	21 (7/14)	2.4–17.4	2	0	3	16	4	2	7	0	6
FF	25 (10/15)	2.2–30.3	4	0	7	14	4	7	5	0	2
FC	11 (5/6)	2.5–14.9	6	1	2	2	2	1	2	0	1

[a] Number of QTLs at which *G. hirsutum* (*GH*) or *G. barbadense* (*GB*) are favorable, or the heterozygote superior (H+) or inferior (H–) to either homozygote (overdominance or underdominance, respectively)

[b] Number of QTLs specifically effective under well-watered or water-limited irrigation regime, or specifically affected relative values (water-limited/well-watered)

Fig. 2 (continued)



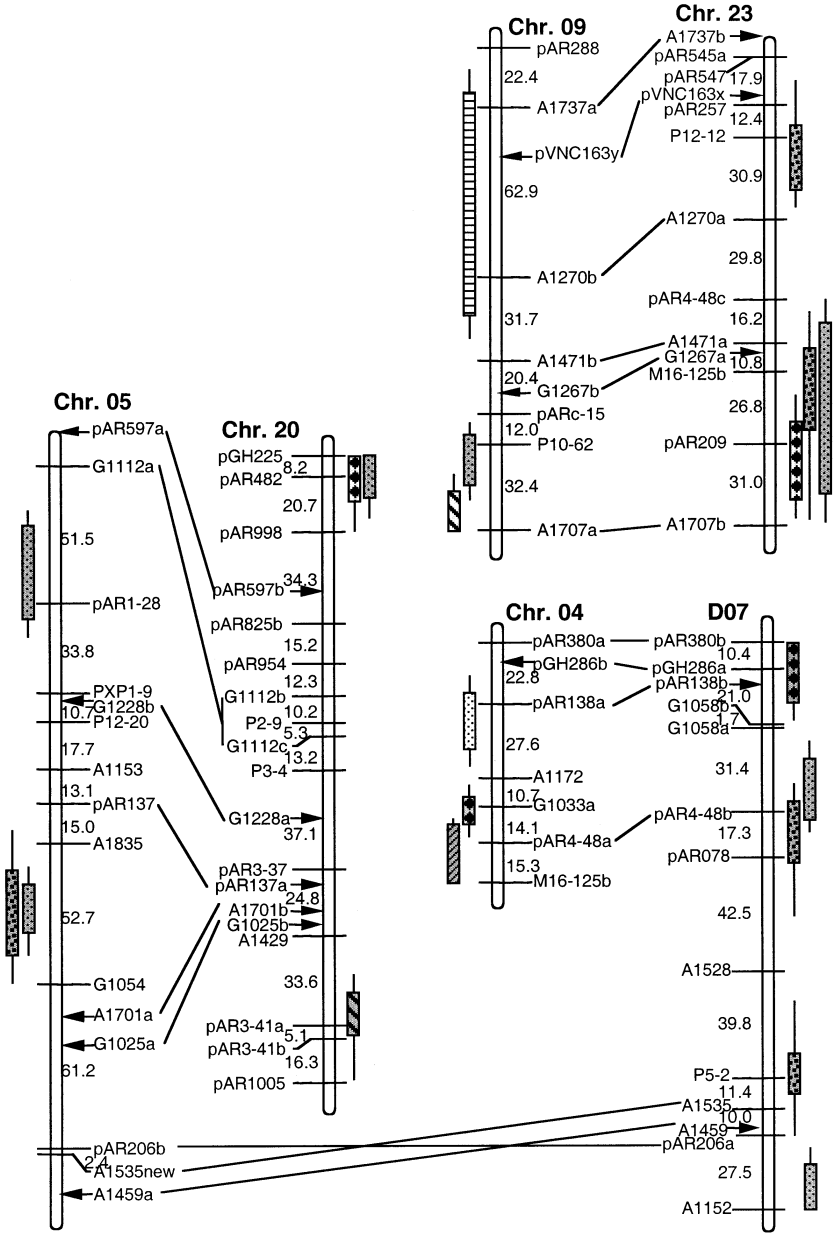
This genetic population exhibited greater-than-expected recombination in some chromosomal intervals leading to several larger-than-expected gaps in the map. However, in only one case was a QTL discovered in the middle of a large gap that could not be verified by one or both flanking markers. This case was a QTL affecting fiber fineness on chromosome 5 (between markers A1835 and G1054), found in both well-watered and water-limited environments. Also mapping to this region, but verifiable by flanking markers, is a QTL affecting fiber elongation in both treatments. We opted to include the fiber fineness QTL in our presentation and discussion, but some may prefer to discount it as a possible artifact. Since it was found in both well-watered and water-limited environments, it has no particular impact on the fundamental thesis of this paper.

A summary of the inheritance of each trait follows.

Fiber length

A total of six QTLs were detected with statistical significance in one or more data sets. Two of these (Chr. 20, LG A05) also met the permutation-based LOD threshold of 3.75. Increased fiber length was conferred by the allele from the long-fibered parent (GB) at two loci (on LGs A01, A03); the allele from the short-fibered parent (GH) at three loci (on Chrs. 20, A02, A05). One locus (on Chr. 9) showed a heterotic effect (d/a ratio > 3), with reduced fiber length conferred by the heterozygote. A total of four (66%) of the QTLs showed significant interaction with environmental factors. Two QTLs showed significant interaction with irrigation treatments, one (Chr. 9) significant in the water-limited treatment but not the well-watered treatment, and one (LG A03) in the well-watered but not the water-limited treatment. Two

Fig. 2 (continued)

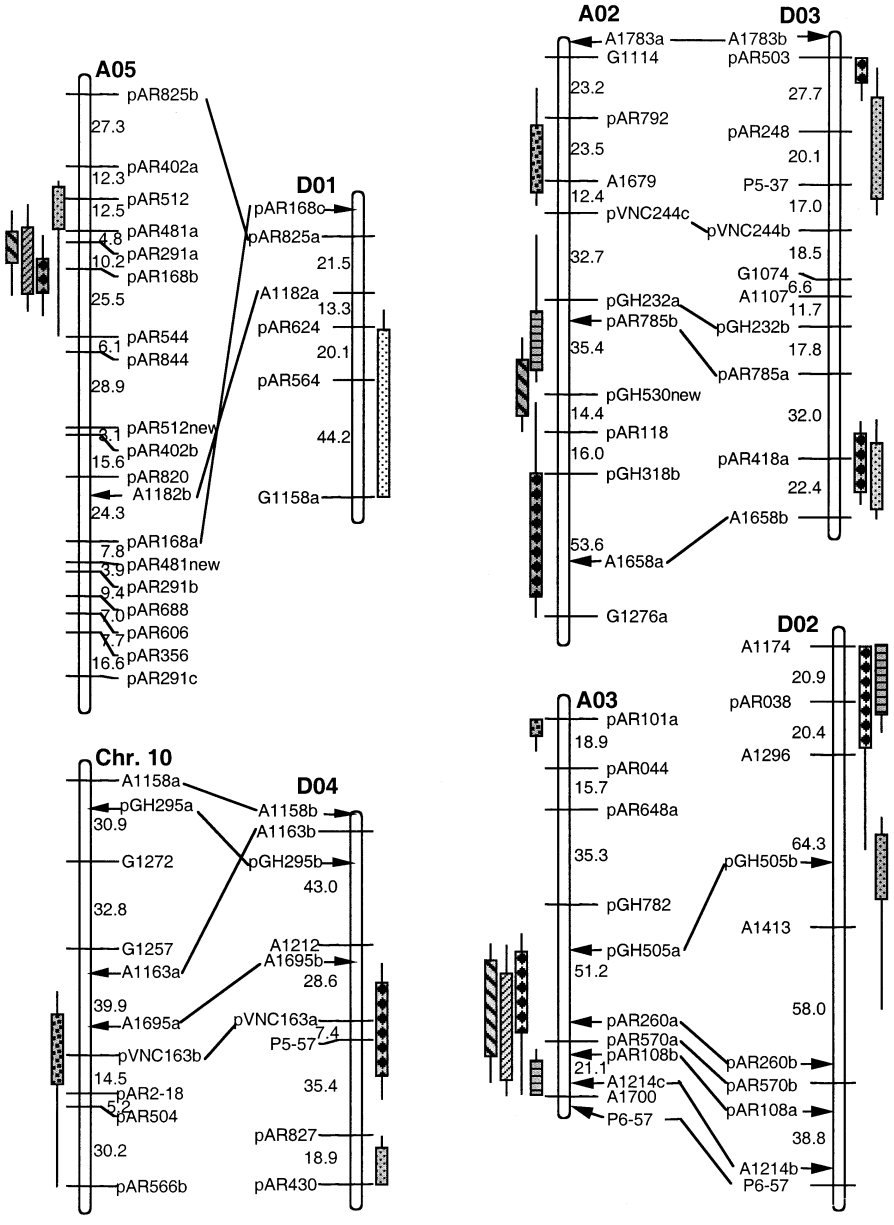


QTLs showed significant interaction with years; LG A01 reached significance in year 1 but not year 2, and A05 reached significance in year 2 but not year 1 (corroborated by analysis of variance).

Fiber length uniformity

A total of seven QTLs were detected with statistical significance in one or more data sets. Two of these (Chr. 4, LG A03) also met the permutation-based threshold of 4.84. Increased fiber length uniformity was conferred by the GB allele at two loci (on Chr. 22, LG A03); and the GH allele at three loci (on Chrs. 4, 15, and LG A05). The heterozygote showed lower fiber length uniformity at two loci (on Chrs. 14, 22). Five (62%) of the QTLs showed significant interactions with environmental factors. Three QTLs (Chr. 14, Chr. 22, LG A03) showed significant effects in year 1 but not year 2 (two based only on analysis of variance, narrowly missing significant LOD scores), while one QTL (Chr. 4) could be discerned in year 2 but not year 1. Another QTL on LGA05 was significant only in year 1, but it did not meet any criteria for significant interaction. Two QTLs (Chr. 15, Chr. 22) were detected only in the water-limited treatment, while one (LGA03) was only detected in the well-watered treatment.

Fig. 2 (continued)



Fiber elongation

A total of nine QTLs were detected with statistical significance in one or more data sets. Five of these (Chr. 5, Chr. 15, Chr. 23, LGA03, LGD07) also met the permutation-based threshold of 3.92. Increased fiber elongation was conferred by the GH allele at four loci [Chrs. 5, 15, 23 (M16-125a) and LG D07]; and the GB allele at four loci (Chr. 10, LG A02, A03, D07). The heterozygote showed lower fiber elongation at one locus (Chr. 23). Five (56%) of the QTLs showed significant interactions with environmental factors. Two QTLs [Chr. 23 (M16-125a), LG A03] could only be discerned in year 1 (Chr. 23 was corroborated by analysis of variance), while three QTLs [Chrs. 10, 23 (P12-12) and LG D07] only showed significant effects in year 2. None of the QTLs showed interaction with irrigation treatment.

Fiber strength

A total of 21 QTLs were detected with statistical significance in one or more data sets. Eleven of these [Chr. 1 (2), Chr. 14, Chr. 18 (2), Chr. 22 (2), LGA03, LGA05, LGD02, LGD03] also met the permutation-based threshold of 3.74. Increased fiber strength was conferred by the allele from the higher fiber-strength GB parent at 16 loci [on chromosomes 4, (A-subgenome), 14, 17, 18 (2), 20, 22, 23 (D subgenome) and linkage groups A01, A02, A03, D02, D03 (2), D04, and D07]; and the GH allele at two loci (Chr. 1, and LG A05). The heterozygote showed

Table 3 Biometrical parameters of QTLs affecting quality traits of cotton lint

Chromosome or linkage group	Nearest marker	*P*(f) at nearest marker[a]			LOD Scores[b]						Relevant data set	QTL effects in relevant data set				Mode of action[c]
		M	Y*M	I*M	All	Year 1	Year 2	Dry	Wet	Dry/Wet		Var %	a	d	d/a	
A. Fiber length; permutation threshold 3.75																
Chr09	A1707a	*		*+	2.07	0.68	1.71	3.24	0.78	0.97	Dry	4.1	0.066	–0.877	–13.38	–
Chr20	pAR3-41a	***			**4.96**	1.57	3.56	2.74	2.34	0.05	All	2.9	–0.553	0.025	–0.05	A
LGA01	pAR338a	**	+		2.17	3.19	0.64	1.45	0.83	0.27	Year 1	4.2	0.408	–0.272	–0.67	RA
LGA02	pGH530new	***			3.6	1.91	2.12	2.39	1.5	0.84	All	3.5	–0.296	0.796	–2.69	–
LGA03	pAR570a	**	+	+	2.63	3.7	0.51	0.37	3.65	0.42	Wet	13.7	1.090	0.853	0.78	DA
LGA05	pAR291a	***	*		**5.4**	2.43	**3.79**	3.51	3.25	1.28	Year 2	4.8	–0.452	0.928	–2.06	R
B. Fiber length uniformity; permutation threshold 4.84																
Chr04	M16-125b		+		1.65	0.81	**4.84**	1.11	1.42	1.93	Year 2	13.3	–0.736	0.610	–0.83	R
Chr14	G1147	**	**		3.00	2.92	0.88	1.24	2.08	1.03	All	2.9	0.075	–0.787	–10.56	–
Chr15	pAR906	**		*+	1.84	1.8	0.29	3.25	0.49	1.7	Dry	3.9	–0.907	–0.111	0.12	AD
Chr22	pAR188	***	*	*+	2.78	2.87	1.05	4.11	0.04	0.07	Dry	5.7	0.086	–1.19	–13.8	–
Chr22 (124–244)	pAR243	***			3.04	1.69	2.46	1.81	1.59	0.73	All	2.1	0.415	–0.282	–0.68	RA
LGA03	pAR570a	***	*+	+	3.79	3.94	0.96	0.89	**4.92**	1	Wet	7.4	0.945	0.145	0.15	A
LGA05	pAR168b	***			3.53	3.01	1.07	1.71	2.39	0.41	All	2.3	–0.496	0.178	–0.36	AR
C. Fiber elongation (log transformed); permutation threshold 3.92																
Chr05	A1835	**			**5.00**	2.55	2.82	1.68	3.54	0.48	All	7.3	–0.024	–0.007	0.31	AD
Chr10	pVNC163b	*	+		2.32	0.58	3.1	1.03	1.96	0.79	Year 2	5.5	0.021	–0.017	–0.81	R
Chr15	pAR400b	**			**4.64**	2.29	3.44	1.94	3.89	1.58	All	4.3	–0.019	0.010	–0.51	RA
Chr23	P12-12	***	+		**4.59**	1.77	**3.95**	3.48	2.46	0.85	Year 2	8.9	–0.006	–0.033	5.71	–
Chr23	M16-125a	*	*+		3.14	3.64	1.4	1.41	2.1	0.45	Year 1	5.7	–0.021	–0.005	0.22	AD
LGA02	A1679	**			3.45	2.2	2.01	2.98	3.1	1.28	All	3.4	0.012	–0.018	–1.42	R
LGA03	pAR101a	***	+		**5.77**	**4.23**	1.86	3.67	2.23	0.54	Year 1	5.1	0.023	0.002	0.09	A
LGD07	P5-2	**	+		3.77	1.04	3.12	1.91	2.09	1.18	Year 2	4.4	0.021	0.003	0.14	AD
LGD07	pAR078	***			**4.49**	2.06	2.73	2.34	2.34	0.55	All	3.5	–0.011	–0.015	1.39	D
D. Fiber strength; permutation threshold 3.74																
Chr01	A1204	***			0.73	2.07	0.17	2.95	2.30	**4.10**	Dry/Wet	13.4	–0.016	–0.038	2.35	D
Chr01	A1686a	***			0.91	1.24	0.1	2.34	1.57	**3.93**	Dry/Wet	12.4	–0.004	–0.043	10.92	–
Chr04	G1033a	***			1.19	0.94	0.07	1.51	0.58	3.14	Dry/Wet	8.7	0.032	–0.057	–1.78	–
Chr14	G1147	***			**6.22**	**4.02**	3.03	3.16	3.31	0.84	All	4.4	1.090	–1.104	–1.01	R
Chr17 (106–277)	pGH861	**		**+	1.68	0.53	1.45	3.13	1.07	2.03	Dry	4.1	1.096	–1.756	–1.60	R
Chr18	P5-11a	**	+		**3.82**	0.99	3.57	3.43	1.74	0.52	All	9	1.374	–3.265	–2.38	–
Chr18	pAR788	**	+		**3.99**	1.46	3.67	2.38	2.97	0.73	All	4.5	0.797	–2.278	–2.86	–
Chr20	pGH225	****		+	2.55	1.44	1.09	3.05	0.56	0.9	Dry	3.5	1.784	0.332	0.19	AD
Chr22	pAR188	**	+	*+	3.21	3.81	0.45	**4.40**	0.24	1.49	Dry	17.4	1.231	–3.830	–3.11	–
Chr22 (124–244)	pAR243	***		+	**6.11**	**3.97**	2.57	**4.84**	2.5	2.71	Dry	6.5	1.562	–0.951	–0.61	RA
Chr23	pAR209	***	+	+	3.71	3.4	0.85	3.56	0.89	1.38	Dry	7.2	1.769	–1.475	–0.83	RA
Chr25	pGH309	**			3.43	2.5	1.64	2.7	1.69	1.19	All	3.9	0.191	–1.923	–10.07	R
LGA01	pAR238	***			3.04	2.91	0.82	2.49	0.72	1.7	All	3.1	1.036	–1.249	–1.21	R
LGA02	pGH318b	**			3.33	1.66	1.82	2.22	1.21	1.07	All	5	1.543	0.383	0.25	AD
LGA03	pAR570a	***	+	+	**5.99**	**4.1**	2.07	**5.99**	2	**3.91**	Dry	9.6	1.471	–2.488	–1.69	R
LGA05	pAR168b	***	+		**4.03**	**4.64**	0.93	2.47	2.51	1.84	Year 1	6	–1.644	–0.224	–0.14	A
LGD02	pAR038	***		**+	**3.79**	**3.88**	2.3	**5.68**	1.03	3.58	Dry	12.3	2.615	–1.186	–0.45	AR

Table 3 (continued)

Chromosome or linkage group	Nearest marker	*P*(f) at nearest marker[a]			LOD Scores[b]						Relevant data set	QTL effects in relevant data set				Mode of action[c]
		M	Y*M	I*M	All	Year 1	Year 2	Dry	Wet	Dry/Wet		Var %	a	d	d/a	
LGD03	pAR418a	***			3.51	1.16	2.55	3.34	1.55	**4.48**	Dry/Wet	15	0.029	–0.035	–1.21	R
LGD03	pAR503	***			0.21	0.61	0	0.71	0.29	3.73	Dry/Wet	11.7	0.023	–0.040	–1.78	R
LGD04	pVNC163a	***			2.05	1.46	1.22	2.02	0.8	3.43	Dry/Wet	11	0.031	–0.013	–0.43	AR
LGD07	pGH286	**			3.11	1.39	2.09	1.93	2.14	0.49	All	2.5	0.715	–1.246	–1.74	R
E. Fiber fineness (log transformed); permutation threshold 3.84																
Chr02	A1325	***	+		**4.2**	**4.15**	0.79	2.32	2.34	0.92	Year 1	5.2	0.024	0.004	0.16	AD
Chr04	pAR138	**		+	2.92	1.72	1.49	3.55	0.41	1.25	Dry	8	–0.005	0.040	–8.89	–
Chr05	pAR1-28	***	+		**4.43**	2.06	**5.43**	1.92	2.91	0.19	Year 2	22.6	0.009	0.064	7.48	–
Chr05	G1054	***	+		**5.9**	2.26	**4.57**	**3.93**	3.22	1.18	Year 2	30.2	–0.016	0.071	–4.59	–
Chr06	pAR936	**			**4.99**	2.84	2.42	3.12	2.22	1.76	All	3.5	–0.019	0.016	–0.83	R
Chr09	P10-62	***	+		**6.12**	2.07	**4.76**	**4.01**	2.63	2.48	Year 2	8.3	–0.01	0.037	–3.71	–
Chr14	A1222	**	+		**3.95**	1.21	3.39	2.18	2.31	1.39	Year 2	5.5	–0.016	0.018	–1.10	R
Chr15	P5-39	**		+	3.17	1.02	2.56	3.43	0.67	0.78	Dry	5.5	–0.014	0.030	–2.10	R
Chr15	pAR077a	**			3.45	1.54	2.19	1.96	1.92	0.43	All	3.9	0.001	0.026	26.00	–
Chr17	pAR250	***		+	**9.78**	**5.00**	**5.32**	**8.08**	2.9	0.32	Dry	17.1	–0.030	0.037	–1.24	R
Chr20	pGH225	***			3.17	1.22	1.93	1.31	1.79	0.17	All	2.6	–0.015	0.007	–0.47	RA
Chr23	pAR209	***	+		**4.71**	3.83	1.72	3.25	2	1.23	Year 1	5.8	–0.020	–0.020	1.01	D
Chr25	G1099a	**			3.72	2.71	2.28	2.57	1.69	1.47	All	4.2	–0.020	0.006	–0.31	AR
LGA01	pAR238	**		+	3.71	1.96	2.39	3.33	0.97	2.04	Dry	6.9	–0.014	0.033	–2.47	R
LGA01	G1125b	***			3.49	1.06	2.67	2.79	1.17	0.35	All	2.7	–0.010	0.018	–1.92	R
LGA05	pAR512	***	*+		3.28	3.77	1.62	2.86	2.24	1.69	Year 1	5.7	0.017	0.027	1.60	D
LGA06	pGH364	***			3.31	1.18	2.76	3.29	1.64	1.97	All	2.2	–0.014	0.002	–0.16	AR
LGD01	G1158a	*	*	*+	2.71	2.07	2.09	3.21	0.44	0.93	Dry	12.4	0.011	0.048	4.49	–
LGD02	A1413	**	+		3.69	1.63	**4.15**	3.54	1.82	2.14	Year 2	30.3	–0.023	0.066	–2.88	R
LGD03	A1658b	***	+		3.26	0.51	3.78	2.78	1.31	3.34	Dry/Wet	16.5	–0.042	0.118	–2.81	R
LGD03	pAR248		*		2.47	3.47	1.97	2.95	2.24	0.99	Year 1	5.3	0.025	0.007	0.28	AD
LGD04	pAR430	***	+		2.84	0.41	**4.02**	2.27	1.29	1.69	Year 2	7.6	–0.015	0.034	–2.29	R
LGD05	pAR3-42R5	***			2.21	1.32	1.8	1.71	0.76	3.41	Dry/Wet	14	–0.089	0.040	–0.45	AR
LGD07	A1152	**			4.02	2.6	1.53	2.81	1.52	2.54	All	4.6	0.019	0.018	0.98	DA
LGD07	pAR4-48b	**	+		2.68	0.35	3.63	1.29	1.4	0.59	Year 2	8.8	–0.005	0.038	–7.19	–
F. Fiber yellowness (log transformed); permutation threshold 3.84																
Chr06	A1208b	*	+		**3.93**	3.24	1.11	**3.85**	1.87	1.06	Year 1	11.1	0.012	0.043	3.65	D
Chr09	A1270b	**		*+	2.66	1.32	2.33	3.01	0.9	0.75	Dry	4.2	0.018	0.004	0.24	AD
Chr14	pAR1-34b	***	+		**5.43**	**4.72**	1.23	3.04	2.58	1.08	Year 1	5.3	–0.029	0.012	–0.42	AR
Chr17(106–277)	pGH861	**	+		2.84	0.53	3.02	1.47	1.41	0.67	Year 2	4.1	0.003	–0.025	–8.33	–
Chr18(34–199)	A1552b	**		+	3.01	1.35	2.89	3.12	0.56	1.12	Dry	13	–0.031	–0.027	0.88	DA
Chr22	pAR188	**			3.00	1.04	2.85	2.09	1.23	0.34	All	3	0.015	–0.010	–0.68	RA
Chr25	pGH309	***			**9.19**	**5.14**	**4.17**	**4.19**	**6.48**	0.85	All	9.7	0.035	–0.004	–0.11	A
LGA01	G1125b	**			1.84	1.47	1.16	2.49	0.5	3.11	Dry/Wet	10.3	–0.009	0.045	–5.04	–
LGA02	pGH232a	***			**11.67**	**9.44**	**5.45**	**6.59**	**6.2**	1.09	All	14.9	0.037	–0.004	–0.11	A
LGA03	A1700	***			3.18	1.66	2.58	1.45	1.79	1.21	All	2.5	0.015	0.001	0.07	AD
LGD02	A1174	***			**4.98**	2.68	2.52	2.73	3.38	0.8	All	3.9	0.017	0.013	0.75	DA

Footnotes see page 394

◀ **Table 3** (continued)

[a] *, ** and *** indicate significant effect at the 0.05, 0.01 and 0.001 levels; the column of Y*M*I interaction was omitted and cases of significance are indicated as footnotes; + indicate a significant interaction based on a LOD difference >2 between the 2 years or between the two irrigation regimes

[b] LOD score of the relevant data set is underlined, the LOD > permutation threshold is written in bold numbers. 'Relevant data set' indicates treatment for which quantitative parameters [% variance explained, additive (a), dominance (d), d/a ratio, and mode of gene action] are shown. In cases for which the marker locus showed significant interaction (as defined in text) with treatments (years or irrigation regimes), the treatment with the highest LOD score was considered the relevant data set, excluding the pooled data set, 'All', since it is rendered invalid by the interaction. In cases for which the marker locus showed no interaction with treatments, the treatment (including the pooled data set, 'All') with the highest LOD score was considered the relevant data set. In cases where both Y*M and I*M interactions were significant the effect of the specific irrigation regime is presented as a relevant data set

[c] The mode of gene action was calculated following the method described by Paterson et al. (1991). All modes of gene action (A = additive, D = dominant, R = recessive) with likelihoods within one LOD unit of the unrestricted model (considering all possible modes of gene action) are listed, in decreasing order of likelihood. In cases of overdominance (where the absolute value of the dominance effect substantially exceeds the additive effect), MapMaker-QTL generally finds no mode of gene action to be within 1 LOD unit of the unrestricted model. Such cases are indicated by "–". In the text, we considered a locus to exhibit overdominance if the absolute value of the d/a ratio exceeded 3

lower fiber strength at two loci (Chr. 22, 25) and lower relative fiber strength at one locus (Chr. 01). Thirteen (67%) of the QTLs were significantly affected by environmental factors, with some of the QTLs affected by more than one factor. Six QTLs reached significance only in one year, four in year 1 (Chr. 22, 23, LG A03, A05) and two in year 2 (both on Chr. 18). Seven QTLs [Chr 17, 20, 22 (2), 23, LGs A03, D02] reached significance only under water-limited conditions. Six QTLs [Chr 1 (2), Chr 4, LGD03 (2), LGD04] could only be detected as 'relative effects,' or changes in the ratio of the phenotype in the non-irrigated/irrigated environment.

Fiber fineness

A total of 25 QTLs were detected with statistical significance in one or more data sets. Eleven of these [Chr. 2, Chr. 5 (2), Chr. 6, Chr. 9, Chr. 14, Chr. 17, Chr. 23, LGD02, LGD04, LGD07] also met the permutation-based threshold of 3.84. Increased fiber fineness (lower Micronaire value) was conferred by the GH allele at four loci (Chr. 2, LGs A05, D03, D07); and the GB allele at 14 loci [Chr. 6, 14, 15, 17, 20, 23, 25, LGs A01 (2), A06, D02, D03, D04, D05]. The heterozygote showed lower fiber fineness at seven loci [Chr. 4, 5 (2), 9, 15, LGs D01, D07]. Eighteen (72%) of the QTLs showed significant interactions with environmental factors. Four QTLs (Chr. 2, 23, LGs A05 and D03) could be discerned in year 1 but not year 2 (two were corroborated by analysis of variance), while eight QTLs [Chrs. 5 (2), 9, 14, LGs D02, D03, D04, D07] showed significant effects in year 2 but not year 1. Five of the QTLs (Chr. 4, 15, 17, LGs A01, D01) showed interaction with irrigation treatment, being detected in the water-limited treatment but not the well-watered treatment. Two of the QTLs (LGs D05 and D05) could only be detected as a 'relative effect,' or a change in the ratio of the phenotype in the non-irrigated/irrigated environment.

Fiber color yellowness

A total of 11 QTLs were detected with statistical significance in one or more environments. Five of these (Chr. 6, Chr. 14, Chr. 25, LGs A02, D02) also met the permutation-based threshold of 3.84. Reduced fiber yellowness (better quality) was conferred by the GH allele at six loci (Chr. 9, 22, 25, LGs A02, A03, D02); and the GB allele at two loci (Chr. 14, 18). The heterozygote showed higher fiber yellowness at two loci (Chr. 6, LG A01) and lower fiber yellowness at one locus (Chr. 17). Six (55%) of the QTLs showed significant interactions with environmental factors. Two QTLs (Chrs. 6, 14) could only be discerned in year 1, while one QTL (Chr. 17) only showed significant effects in year 2. Two of the QTLs (Chrs. 9, 18) showed interaction with irrigation treatment, being detected only in the water-limited environment. One of the QTLs (LG A01) could only be detected as a 'relative effect,' or a change in the ratio of the phenotype in the non-irrigated/irrigated environment.

Discussion

The genetic control of cotton fiber quality, as reflected by QTLs detected by genome-wide mapping, is markedly affected both by general differences between growing seasons ('years') and by specific differences in water regimes. There appears to exist a basal set of QTLs that are relatively unaffected by environmental parameters and may account for progress from selection in a wide range of environments, such as the diverse sets of environments that are often employed in mainstream cotton breeding programs. Differences between years were reflected in similar numbers of QTLs that were specific to each of the 2 years in the study (16 in year 1, and 15 in year 2).

An especially important finding was that 17 QTLs were detected only in the water-limited treatment while only two were specific to the well-watered treatment. This suggests that improvement of fiber quality under water stress may be even more complicated than improvement of this already-complex trait under well-watered conditions.

Most of the QTLs detected for 'relative values,' calculated as the family breeding value (average phenotype) in the stressed environment divided by the breeding value of the same family in the non-stressed environment,

were associated with chromosomal locations for which we found no main-effect QTLs. This is not especially surprising as a ratio; this measure may pick up non-linear interactions between genotype and environment that are too small to reach significance individually. It also warrants further investigation whether this trait requires a more-stringent significance threshold, although several of the QTLS we found had LOD > 4, ten-fold above our minimum threshold. Among the nine QTLs for relative values, only two (for fiber strength near pAR418a on LGD03, and fiber fineness near A1658b on LGD03) were associated with main-effect QTLs. The phenotypic effects and LOD scores for these two associations were correlated across the various treatments (see Table 3; for example the LOD scores for the 2 QTLs in the five treatments were 3.51, 1.16, 2.55, 3.44, 1.55; and 3.26, 0.51, 3.78, 2.78, 1.31). This particular genomic region appears to contain a QTL involved with fiber architecture (so affecting both strength and fineness, either as pleiotropic effects of one gene or correlated effects of multiple closely-linked genes) that is particularly sensitive to water status.

Regarding fiber quality, we found no evidence for the sort of inverse relationship that has been suggested for productivity, i.e. that selection for stress tolerance will generally result in reduced trait values under favorable environments and a decrease in average overall production (Finley and Wilkinson 1963; Rosielle and Hamblin 1981; Acevedo and Fereres 1993). Our findings might be reconciled with this long-held expectation in that simultaneous improvement of quality for both well-watered and water-limited conditions will require the manipulation of a larger number of genes than for either of the treatments alone, reducing the expected rate of genetic gain (Falconer and Mackay 1996). This may be an especially important factor in the improvement of cotton, a crop for which growers are divided regarding the economics of irrigation usage. Identification and use of diagnostic DNA markers may be especially important in ameliorating the reduced genetic gain associated with breeding cotton for a wide range of water regimes.

The use of an interspecific cross in this work enabled us to further investigate the extent to which superior QTLs might be found in an apparently inferior parent (Tanksley and Nelson 1995). The cotton species *G. hirsutum* and *G. barbadense* are thought to be derived from a common polyploid ancestor that formed naturally perhaps 1 million years ago (Wendel 1989), and has diverged into five modern polyploid species. Cultivated forms of the two species differ in that *G. hirsutum* tends to have a higher yield and earlier maturity, but *G. barbadense* has markedly superior fiber length, strength and fineness. While most favorable QTLs for these traits were indeed derived from the expected parent, an appreciable number of exceptions (Table 2) support the notion that new interspecific gene combinations may be created that are superior for human purposes than either of the naturally occurring species. Although mainstream cotton breeders only occasionally use such crosses, introgression from *G. hirsutum* (GH) has played a major role in the breeding of *G. barbadense* (Wang et al. 1995), and many of the problems associated with use of such crosses can be mitigated by DNA markers (Jiang et al. 2000).

These results generally support previous studies of fiber quality (Jiang et al. 1998) and other traits (Wright et al. 1998; Wright et al. 1999; Jiang et al. 2000a, 2000b) in suggesting that the D-subgenome, from an ancestor that does not produce spinnable fiber, plays an important role in the genetic determination of fiber quality in tetraploid (AADD) cotton. Among the total of 79 marker-trait associations reported here, 45 (57%) are located on D-subgenome chromosomes. This modest excess of D-subgenome QTLs (chi-squares = 1.76, $p = 0.2$) falls short of statistical significance, but reinforces the finding (Jiang et al. 1998) that the D-subgenome of cotton contributes to the improvement of fiber quality – and continues to hint that the D-subgenome may even contribute a higher level of phenotypically relevant variability to AADD tetraploids than does the A-subgenome, derived from an ancestor that does produce spinnable fiber.

Only six pairs of fiber quality QTLs appear to map to homoeologous locations (Fig. 2) (Fiber fineness QTLS on Chr. 2–Chr. 14, Chr. 9–Chr. 23, and Chrs. 6–25; Fiber strength QTLs on LGs A02–D03 and A03–D02, and fiber yellowness QTLs on Chr. 6–Chr. 25), so few that such associations are readily explained by chance (using the methods described in Lin et al. 1995). The paucity of homoeologous associations supports the previously suggested notion that the A-subgenome (for which diploid forms do produce spinnable fiber) may already have contained favorable alleles at some major loci affecting fiber traits when polyploids evolved, as a result of prior natural selection. By contrast, the D-subgenome (for which diploid forms do not produce spinnable fiber), may have come under selection at these primary fiber-determining loci only after polyploid formation, and therefore harbor greater allelic diversity among tetraploid forms.

Genotype × environment interactions affecting key quality attributes such as fiber quality present special challenges in the improvement of crops such as cotton, in which similarly large acreages are grown under irrigated and rainfed conditions, respectively. While it is anecdotally accepted that some genotypes are better-suited to irrigation and others to rainfed production, the study and manipulation of specific genes that confer adaptation to these very different environments has previously focused largely on simply inherited variants useful in disease or insect management. These new findings suggest that complex traits such as fiber quality may also be fine-tuned to arid conditions, presumably in conjunction with the development of genotypes that also contain genes conferring adaptations such as osmotic adjustment that help to maintain productivity under arid conditions (Saranga et al. 2001).

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