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Genetic map and QTL controlling fiber quality traits in upland cotton (*Gossypium hirsutum* L.)

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Abstract Cotton is a leading natural fiber crop in the textile industry worldwide. The improvement of cotton fiber quality has become more important because of changes in spinning technology and ever-increasing demands. Mapping quantitative trait locus (QTL) for fiber quality traits will enable molecular marker-assisted selection (MAS) to improve fiber quality and provide an access to reveal the molecular mechanism of fiber development. A high-density intraspecific genetic map is constructed based on an upland cotton recombinant inbred line (RIL) population. A total of 25,313 SSR primer pairs were used and yielded 1,333 polymorphic markers, with a polymorphic ratio of 5.3 %, producing 1,382 polymorphic loci in the RIL population. The map comprised 1,274 loci and spanned 3,076.4 cM with an average distance of 2.41 cM between two adjacent markers. Based on the phenotypic data of fiber quality traits from five environments, a total of 59 QTL were detected. These QTL comprised 15 QTL for fiber upper half mean length, 10 QTL for fiber length uniformity, 9 QTL for fiber strength, 10 QTL for fiber elongation and 15 QTL for fiber micronaire, respectively. The genetic map constructed in this study is the most detailed upland cotton intraspecific map based on SSR markers to date, and could be used to construct consensus map or as reference genetic map for tetraploid cotton genome assembly. Stable QTL identified across multiple environments reflect some important and favorable alleles shaping fiber quality, and they are valuable candidate alleles for MAS breeding projects as well as for gene function research related to cotton fiber development and quality improvement.

Keywords Upland cotton (*G. hirsutum* L.) · Genetic map · Fiber quality traits · QTL

Zhaoyun Tan and Xiaomei Fang contributed equal work to this paper.

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Introduction

Cotton is grown in more than 80 countries, and contributes to the world economy as a leading natural fiber crop in the textile industry and a source of oil and protein from cottonseeds. The genus *Gossypium* consists of approximately 45 diploid (2n = 2x = 26) and 5 tetraploid (2n = 4x = 52) species (Percival et al. 1999), including four cultivated species, *G. arboreum* L., *G. herbaceum* L., *G. barbadense*

L. and *G. hirsutum* L.. Among the four cultivated species, *G. hirsutum* L., commonly known as upland cotton, is the most important species and provides about 95 % of the world's cotton fiber production.

Genetic improvement of fiber yield is the top priority goal in cotton breeding program. However, with the demands for higher quality cotton fiber to produce more competitive products and increase the manufacture efficiency, cotton breeders have also spent much effort to improve fiber quality. Due to the negative association between fiber yield and quality (Culp and Lewis 1973) and the narrow genetic base of modern cotton cultivars (Iqbal et al. 2001; Rungis et al. 2005; Lacape et al. 2007), the progress to continuously increase fiber productivity and simultaneously improve its fiber quality only using conventional breeding methods has been limited (Smith and Coyle 1997). Thus, the innovative breeding approaches have to be incorporated.

Great advances in molecular marker technologies make it possible for breeders to find a rapid and precise alternative approach to conventional breeding selection schemes (Tanksley and Hewitt 1988). Based on the detailed genetic maps, quantitative trait locus (QTL) controlling fiber quality traits could be precisely mapped on cotton genome and apply to marker-assisted selection (MAS) in breeding projects. Since the first genetic map was reported in cotton (Reinisch et al. 1994), numerous genetic maps have been developed and used to identify QTL. Up to now, 726 QTL related to fiber quality traits have been mapped on 42 molecular maps (Said et al. 2013). While most of these QTL were mapped based on interspecific populations (*G. barbadense* × *G. hirsutum*), issues with sterility, cytological abnormality, extremely late flowering, and distorted segregation limited their application, such as fine mapping the gene underlying these QTL and MAS (Lacape et al. 2010), which suggests that QTL mapping using the upland cotton intraspecific population is more practical. However, due to the narrow genetic background of modern upland cotton cultivars, QTL mapping based on intraspecific populations were of low resolution, far from being satisfactory for practical application. In addition, complicated gene expression in different development stages of cotton fiber (Lee et al. 2007; Taliercio and Boykin 2007; Hovav et al. 2008; Al-Ghazi et al. 2009; Paterson et al. 2012) and QTL meta-analysis (Lacape et al. 2010; Said et al. 2013) indicated that only a few QTL related to fiber development have been mapped. Predictably, much more new or elite QTL will be identified with new divergent mapping parents.

In the present study, we constructed a genetic map based on an upland cotton recombinant inbred line (RIL) population and used this map to detect QTL for fiber quality traits. The results were expected to be valuable for research on upland cotton genome structure and fiber development molecular mechanism and quality improvement through MAS.

Materials and methods

Mapping population and fiber quality traits evaluation

Two upland cotton cultivars, CCRI 35 and Yumian 1 were chosen to produce the segregating population. CCRI 35, a high yield and disease resistance cultivar, was widely planted in China in the last decade. Yumian 1, a high fiber quality cultivar, especially characterized with high fiber strength, was developed from multiple-cultivar intermating program (Zhang et al. 2009). The two parents were crossed in the summer of 2005 at Southwest University, Chongqing, China. F_1 individuals were self-pollinated to produce F_2 seeds in the winter of 2005 in Hainan, China. F_2 seeds were planted at Southwest University and a total of 180 F_2 individual plants were randomly selected in the summer of 2006. One hundred eighty F_2-derived lines were self-pollinated for four generations to produce $F_{2:6}$ seeds during 2006 and 2007. $F_{2:6}$ seeds were planted by lines in single-row plot (0.8 m wide and 5 m long, for 15 plants) in the summer of 2008 at Southwest University and one individual plant in each family line was randomly selected to form a population. From 2009 to 2012, 180 RIL lines were randomly planted by single-row plot (0.7 m wide and 5 m long, for 15 plants) during the summer season at Southwest University. All the naturally-opened bolls from the RIL population and parents were hand-harvested to gin fiber. Fiber samples were evaluated for fiber quality traits, using the high volume instrument (HVI) spectrum, at the Supervision Inspection and Testing Cotton Quality Center, Anyang, China. Data were collected on fiber elongation (FE, %), fiber upper half

mean length (FL, mm), fiber micronaire (FM), fiber strength (FS, cN/tex), and fiber length uniformity ratio (FU, %).

Assay of DNA markers

Total genomic DNA from fresh young leaves of the parents and the 180 lines were extracted according to the modified CTAB method (Zhang et al. 2005).

A total of 25,313 simple sequence repeat (SSR) primer pairs were employed in the present study and they were synthesized by Invitrogen Co. Ltd. (Shanghai, China). Among these SSR primers, 18,358 primer pairs were downloaded from Cotton Marker Database (http://www.cottonmarker.org/), including BNL, CIR, CM, DOW, Gh, HAU, JESPR, MGHES, MON, MUSB, MUCS/MUSS, NAU, NBRI (renamed by Tang et al. 2014), and TMB. The other 6,955 primer pairs were designed in our laboratory, including 5,000 PGML primer pairs, 1,592 SWU primer pairs, and 363 SWU06-/07-primer pairs (Tang et al. 2014).

All these primer pairs were first screened for polymorphism between the mapping parents and the primer pairs showing clear polymorphism were used to genotype the RIL population. PCR amplification and product test were performed according to the procedures by Zhang et al. (2005). Clear polymorphic DNA bands on the gels were used for scoring and genotyping. Loci detected were named with the primer name. For multiple polymorphic loci revealed by a same primer pair, an extra letter was added to the primer name, such as a/b/c, indicating the molecular size from the smallest to the largest.

Genetic map construction

JoinMap 4.0 (Van Ooijen and Voorrips 2006) was served to primarily group and order all the polymorphic loci with a LOD threshold from 4 to 8 according to shared markers from the previous maps (Guo et al. 2008; Xiao et al. 2009; Zhang et al. 2009; Yu et al. 2011; Blenda et al. 2012; Zhang et al. 2012). Linkage groups belonging to a given chromosome were then treated as separate data sets and reordered at a LOD values between 1 and 4. Map distances were calculated using Kosambi's mapping function.

QTL mapping

Multiple QTL mapping of MapQTL 6.0 (Van Ooijen 2009) was implemented to identify QTL and estimate their effects. The LOD threshold of significant QTL was calculated by 1,000 permutation tests, with a genome-wide significance level of $P < 0.05$. The QTL with the LOD value between 2.5 and the LOD value evaluated by permutation test were declared as putative QTL in the present study. Additive effects were defined with respect to the alleles of CCRI 35. Therefore, the positive genetic effect of each QTL indicated that the allele of CCRI 35 increased the phenotypic value, whereas the negative effect indicated that the allele of Yumian 1 increased the phenotypic value. QTL name was started with 'q', followed by a trait abbreviation (FL for fiber upper half mean length, FU for fiber length uniformity, FS for fiber strength, FE for fiber elongation and FM for fiber micronaire) and the chromosome number, and then followed by the number of QTL controlling the same trait on the chromosome. The graphic representation of genetic map and QTL bars representing 1-LOD drop intervals was carried out with Map Chart 2.2 (Voorrips 2006).

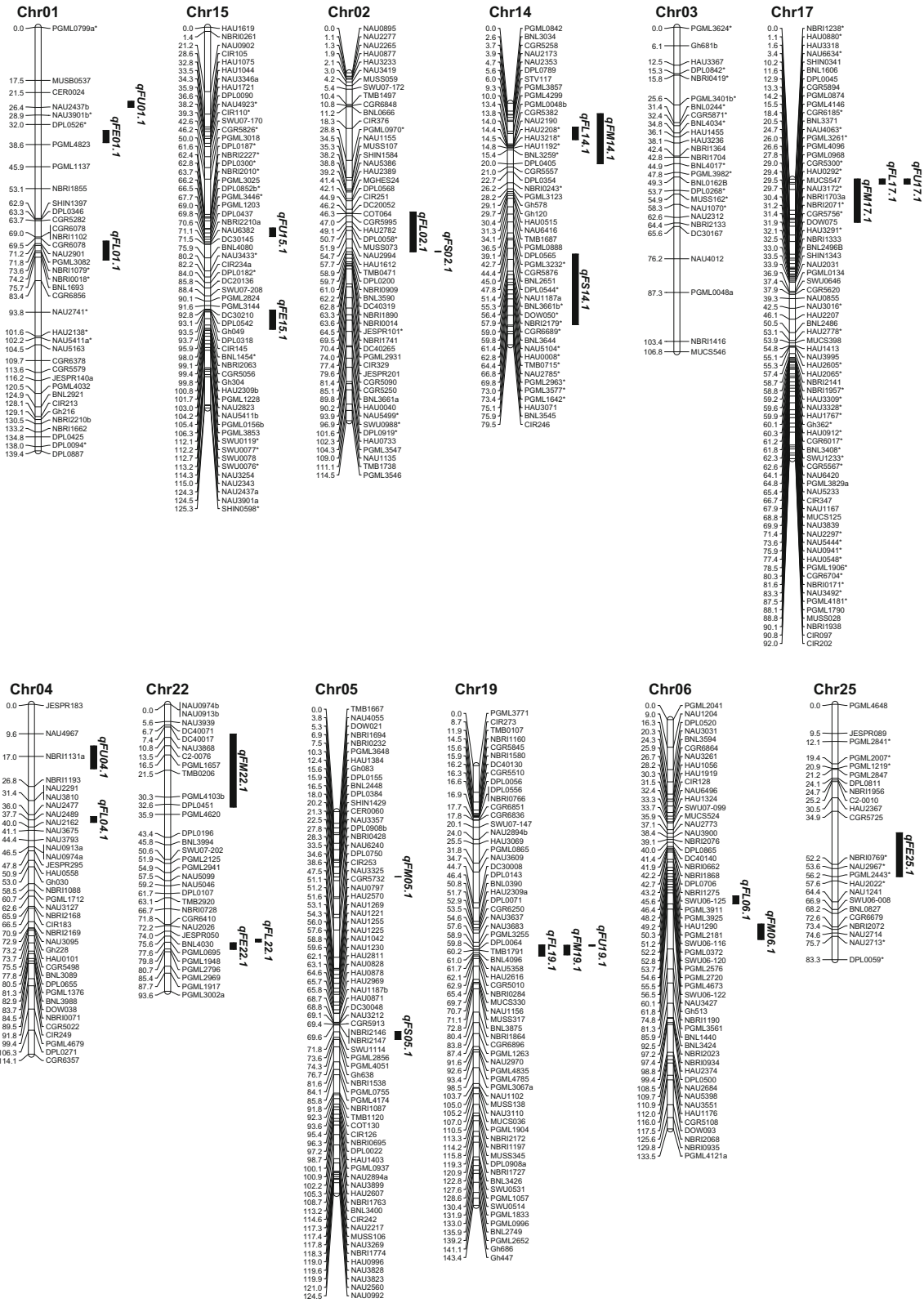
Results

Primer polymorphism and marker analysis

Among the 25,313 SSR primer pairs used to screen for polymorphism between the two parents, 1,333 polymorphic markers were yielded, accounting for 5.3 % of the total primer pairs. The polymorphic markers were used to genotype the RIL population, and produced 1,382 loci. For each locus, χ^2 test was performed to determine if the allele frequency was deviated from the expected Mendelian segregation ratio. Of the 1,382 loci, 518 loci showed significant segregation distortion ($P < 0.05$), accounting for 37.5 % of the total loci. Among the distorted loci, 452 loci were biased in favor of Yumian 1 alleles, whereas other 66 loci were biased in favor of CCRI 35 alleles.

Genetic map

Based on the linkage analysis of all the 1,382 loci, a genetic map with 1,274 loci was constructed


Chr01
0.0 PGML0799a*
17.5 MUSB0537
21.5 CER0024
26.4 NAU2437b
28.9 NAU3901b*
32.0 DPL0526*
38.6 PGML4823
45.9 PGML1137
53.1 NBRI1855
62.9 SHIN1397
63.3 DPL0346
63.7 CGR5282
69.0 CGR6078
69.0 NBRI1102
69.5 CGR6078
71.2 NAU2901
71.8 PGML3082
73.6 NBRI1079*
74.2 NBRI0018*
75.7 BNL1693
83.4 CGR6856
93.8 NAU2741*
101.6 HAU2138*
102.2 NAU5411a*
104.5 NAU5163
109.7 CGR6378
113.6 CGR5579
116.2 JESPR140a
120.5 PGML4032
124.9 BNL2921
128.1 CIR213
129.1 Gh216
130.5 NBRI2210b
133.2 NBRI1662
134.8 DPL0425
138.0 DPL0094*
139.4 DPL0887
qFU01.1
qFE01.1
qFL01.1
Chr15
0.0 HAU1619
1.4 NBRI0261
21.2 NAU0902
28.6 CIR105
32.8 HAU1075
33.5 HAU1044
34.3 NAU3346a
35.9 HAU1721
36.6 DPL0090
38.2 NAU4923*
39.3 CIR110*
42.6 SWU07-170
46.2 CGR5826*
50.0 PGML3018
61.6 DPL0187*
62.4 NBRI2227*
62.8 DPL0300*
63.7 NBRI2010*
66.2 PGML3025
66.5 DPL0852b*
67.7 PGML3446*
69.0 PGML1203
69.8 DPL0437
70.6 NBRI2210a
71.1 NAU6382
71.5 DC30145
75.9 BNL4080
80.2 NAU3433*
82.2 CIR234a
84.0 DPL0182*
85.8 DC20136
88.4 SWU07-208
90.1 PGML2824
91.6 PGML3144
92.8 DC30210
93.1 DPL0542
93.5 GH049
93.7 DPL0318
95.9 CIR145
98.0 BNL1454*
99.1 NBRI2063
99.4 CGR5056
99.8 Gh304
100.8 HAU2309b
101.7 PGML1228
103.0 NAU2823
104.2 NAU5411b
105.4 PGML0156b
106.3 PGML3853
112.1 SWU0119*
112.2 SWU0077*
112.7 SWU0078
113.2 SWU0076*
114.3 NAU3254
115.0 NAU2343
124.3 NAU2437a
124.5 NAU3901a
125.3 SHIN0598*
qFU15.1
qFE15.1
Chr02
0.0 NAU0895
1.1 NAU2277
1.3 NAU2265
1.9 HAU0877
2.1 HAU3233
3.0 NAU3419
4.2 MUSS059
5.4 SWU07-172
10.4 TMB1497
10.8 CGR6848
11.2 BNL0666
18.3 CIR376
28.8 PGML0970*
34.5 NAU1155
35.3 MUSS107
38.2 SHIN1584
38.8 NAU5386
39.2 HAU2389
41.4 MGHES24
42.1 DPL0568
44.9 CIR251
46.2 DC20052
46.3 COT064
47.0 CGR5995
49.1 HAU2782
50.7 DPL0058*
51.9 MUSS073
54.7 NAU2994
57.7 HAU1612
58.9 TMB0471
59.7 DPL0200
61.0 NBRI0909
62.2 BNL3590
62.8 DC40319
63.3 NBRI1890
63.6 NBRI0014
64.5 JESPR101*
69.5 NBRI1741
70.4 DC40265
74.0 PGML2931
77.4 CIR329
79.6 JESPR201
81.4 CGR5090
85.1 CGR5250
89.8 BNL3661a
90.2 HAU0040
93.9 NAU5499*
96.9 SWU0988*
101.6 DPL0919*
102.3 HAU0733
104.3 PGML3547
109.0 NAU1135
111.1 TMB1738
114.5 PGML3546
qFU02.1
qFS02.1
Chr14
0.0 PGML0842
2.6 BNL3034
3.7 CGR5258
3.9 NAU2173
4.7 NAU2353
5.6 DPL0789
6.0 STV117
9.3 PGML3857
10.0 PGML4299
13.4 PGML0048b
13.8 CGR5382
14.0 NAU2190
14.4 HAU2208*
14.5 HAU3218*
14.8 HAU1192*
15.4 BNL3259*
20.0 DPL0405
21.0 CGR5557
22.7 DPL0354
26.2 NBRI0243*
28.2 PGML3123
29.1 Gh578
29.7 Gh120
30.4 HAU0515
31.3 NAU6416
34.1 TMB1687
36.5 PGML0888
39.1 DPL0565
42.1 PGML3232*
44.4 CGR5676
45.0 BNL2651
47.8 DPL0544*
51.4 NAU1187a
55.3 BNL3661b*
56.4 DOW050*
57.9 NBRI2179*
59.0 CGR6689*
59.8 BNL3644
61.4 NAU5104*
62.8 HAU0008*
64.4 TMB0715*
66.8 NAU2785*
69.8 PGML2963*
73.0 PGML3577*
73.4 PGML1642*
75.1 HAU3071
75.9 BNL3545
79.5 CIR246
qFL14.1
qFM14.1
qFS14.1
Chr03
0.0 PGML3624*
6.1 Gh681b
12.5 HAU3367
15.3 DPL0842*
15.8 NBRI0419*
25.6 PGML3401b*
31.4 BNL0244*
32.4 CGR5871*
34.8 BNL4034*
36.1 HAU1455
38.1 HAU3236
42.4 NBRI1364
42.8 NBRI1704
44.9 BNL4017*
47.8 PGML3982*
49.3 BNL0162B
53.7 DPL0268*
54.9 MUSS162*
58.3 NAU1070*
62.6 NAU2312
64.4 NBRI2133
65.6 DC30167
76.2 NAU4012
87.3 PGML0048a
103.4 NBRI1416
106.8 MUCS546
Chr17
0.0 NBRI1238*
1.1 HAU0880*
1.6 HAU3318
3.4 NAU8634*
10.2 SHIN0341
11.6 BNL1606
12.9 DPL0045
13.3 CGR5894
14.2 PGML0874
15.5 PGML4146
18.4 CGR6185*
20.5 BNL3371
24.7 NAU4063*
26.0 PGML3261*
26.6 PGML4096
27.8 PGML0968
29.0 CGR5300*
29.4 HAU0292*
29.5 MUCS547
29.7 NAU3172*
30.4 NBRI1703a
31.2 NBRI2071*
31.4 CGR5756*
31.9 DOW075
32.1 HAU3291*
32.5 NBRI1333
33.0 BNL2496B
33.5 SHIN1343
33.9 NAU2031
36.9 PGML0134
37.4 SWU0646
37.9 CGR5620
39.3 NAU0855
42.5 NAU3016*
46.1 HAU2207
50.5 BNL2486
53.1 HAU2778*
53.9 MUCS398
54.8 HAU1413
55.1 NAU3995
55.3 HAU2605*
57.4 HAU2065*
58.7 NBRI2141
58.8 NBRI1957*
59.2 HAU3309*
59.6 NAU3328*
59.9 HAU1767*
60.1 GH362*
60.3 HAU0912*
61.2 CGR6017*
61.8 BNL3408*
62.3 SWU1233*
62.6 CGR5567*
64.1 NAU6420
64.8 PGML3829a
65.4 NAU5233
66.7 CIR347
67.9 NAU1167
68.8 MUCS125
69.9 NAU3839
71.4 NAU2297*
73.6 NAU5444*
75.9 NAU0941*
77.4 NAU0548*
78.5 PGML1906*
80.3 CGR6704*
81.6 NBRI0171*
83.3 NAU3492*
87.5 PGML4181*
88.1 PGML1790
88.8 MUSS028
90.1 NBRI1938
90.8 CIR097
92.0 CIR202
qFU17.1
qFL17.1
qFM17.1
Chr04
0.0 JESPR183
9.6 NAU4967
17.0 NBRI1131a
26.8 NBRI1193
31.4 NAU2291
NAU3810
36.0 NAU2477
37.7 NAU2489
40.0 NAU2162
41.1 NAU3675
44.4 NAU3793
46.5 NAU0913a
NAU0974a
47.8 JESPR295
50.9 HAU0558
53.0 Gh030
58.5 NBRI1088
60.7 PGML1712
62.6 NAU3127
65.9 NBRI2168
66.3 CIR183
70.9 NBRI2169
72.9 NAU3095
73.2 Gh228
73.7 NAU0101
75.5 CGR5498
77.8 BNL3089
80.5 DPL0655
81.3 PGML1376
82.9 BNL3988
83.7 DOW038
84.5 NBRI0071
89.5 CGR5022
91.8 CIR249
99.4 PGML4679
106.3 DPL0271
114.1 CGR6357
qFU04.1
qFL04.1
Chr22
0.0 NAU0974b
NAU0913b
5.6 NAU3939
6.7 DC40071
7.4 DC40017
10.8 NAU3868
13.5 C2-0076
16.5 PGML1657
21.5 TMB0206
30.3 PGML4103b
32.6 DPL0451
35.9 PGML4620
43.4 DPL0196
45.8 BNL3994
50.6 SWU07-202
51.9 PGML2125
54.9 PGML2941
57.5 NAU5099
59.2 NAU5046
61.7 DPL0107
63.1 TMB2920
66.7 NBRI0728
71.8 CGR6410
72.2 NAU2026
74.0 JESPR050
75.6 BNL4030
77.6 PGML0695
79.8 PGML1948
80.7 PGML2796
85.4 PGML2969
87.7 PGML1917
93.6 PGML3002a
qFM22.1
qFL22.1
Chr05
0.0 TMB1667
3.8 NAU4055
5.3 DOW021
6.9 NBRI1694
7.5 NBRI0232
10.3 PGML3648
12.4 HAU1384
15.6 Gh083
15.9 DPL0155
16.5 BNL2448
18.0 DPL0384
20.2 SHIN1429
21.3 CER0060
22.5 NAU3357
27.8 DPL0908b
28.3 NBRI0428
33.5 NAU6240
34.6 DPL0750
38.6 CIR253
47.5 NAU3325
51.1 CGR5732
51.2 NAU0797
51.6 HAU2570
53.1 NAU1269
54.3 NAU1221
56.0 NAU1255
57.6 NAU1225
58.8 NAU1042
59.6 NAU1230
62.1 NAU2811
63.1 NAU0828
64.6 HAU0878
65.7 HAU2969
65.8 NAU1187b
68.7 HAU0871
68.8 DC30048
69.1 NAU3212
69.4 CGR5913
69.6 NBRI2146
NBRI2147
71.8 SWU1114
73.6 PGML2856
74.3 PGML4051
76.7 Gh638
81.6 NBRI1538
84.1 PGML0755
85.8 PGML4174
91.8 NBRI1087
92.3 TMB1120
93.6 COT130
95.4 CIR126
96.3 NBRI0695
97.2 DPL0022
98.7 HAU1403
100.1 PGML0937
100.9 NAU2894a
102.2 NAU3899
105.3 HAU2607
108.7 NBRI1763
113.2 BNL3400
114.6 CIR242
117.3 NAU2217
117.4 MUSS106
117.8 NAU3269
118.3 NBRI1774
119.0 HAU0996
119.6 NAU3828
119.9 NAU3823
121.0 NAU2560
124.5 NAU0992
qFM05.1
qFS05.1
Chr19
0.0 PGML3771
8.7 CIR273
11.9 TMB0107
14.5 NBRI1160
15.6 CGR5845
15.9 NBRI1580
16.2 DC40130
16.3 CGR5510
16.6 DPL0056
DPL0556
16.9 NBRI0766
17.7 CGR6851
17.8 CGR6836
20.1 SWU07-147
24.0 NAU2894b
25.5 HAU3069
31.8 PGML0865
34.7 NAU3609
44.7 DC30008
46.4 DPL0143
50.8 BNL0390
51.7 HAU2309a
52.9 DPL0071
53.5 CGR6250
54.6 NAU3637
57.6 NAU3683
58.9 PGML3255
59.8 DPL0064
60.2 TMB1791
61.0 NAU4096
61.7 NAU5358
62.1 HAU2616
62.9 CGR5010
65.4 NBRI0284
69.7 MUCS330
70.7 NAU1156
71.1 MUSS317
72.8 BNL3875
80.4 NBRI1864
83.8 CGR6896
87.4 PGML1263
91.6 NAU2970
92.6 PGML4835
93.4 PGML4785
98.5 PGML3067a
103.7 NAU1102
105.0 MUSS138
105.2 NAU3110
107.0 MUCS036
110.5 PGML1904
113.3 NBRI2172
114.2 NBRI1197
115.8 MUSS345
119.3 DPL0908a
120.9 NBRI1727
122.8 BNL3426
127.6 SWU0531
128.6 PGML1057
130.4 SWU0514
131.9 PGML1833
133.0 PGML0996
135.9 BNL2749
139.2 PGML2652
141.1 Gh686
143.4 Gh447
qFL19.1
qFU19.1
qFM19.1
Chr06
0.0 PGML2041
9.0 NAU1204
16.3 DPL0520
20.3 NAU3031
24.3 BNL3594
25.9 CGR6864
26.7 NAU3261
28.2 HAU1056
30.3 HAU1919
31.5 CIR128
32.4 NAU6496
33.3 HAU1324
33.7 SWU07-099
35.9 MUCS524
37.1 NAU2773
38.4 NAU3900
39.1 NBRI2076
40.0 DPL0865
41.4 DC40140
41.9 NBRI0662
42.2 NBRI1868
42.7 DPL0706
43.2 NBRI1275
45.6 SWU06-125
46.4 PGML3911
48.2 PGML3925
49.2 HAU1290
50.3 PGML2181
51.2 SWU06-116
52.2 PGML0372
52.8 SWU06-120
53.7 PGML2576
54.6 PGML2720
55.5 PGML4673
56.5 SWU06-122
60.1 NAU3427
61.8 Gh513
74.8 NBRI1190
81.3 PGML3561
85.9 BNL1440
92.5 BNL3424
97.2 NBRI2023
97.4 NBRI0934
98.8 HAU2374
99.4 DPL0500
108.5 NAU2684
109.7 NAU5398
110.9 NAU3551
112.0 HAU1176
116.0 CGR5108
117.5 DOW093
125.6 NBRI2068
129.8 NBRI0935
133.5 PGML4121a
qFL06.1
qFM06.1
Chr25
0.0 PGML4648
9.5 JESPR089
12.1 PGML2841*
19.4 PGML2007*
20.9 PGML1219*
21.2 PGML2847
24.1 DPL0811
24.7 NBRI1956
25.2 C2-0010
30.5 HAU2367
34.9 CGR5725
52.2 NBRI0769*
53.6 NAU2967*
56.2 PGML2443*
57.6 HAU2022*
64.4 NAU1241
66.9 SWU06-008
68.2 BNL0827
72.6 CGR6679
73.4 NBRI2072
74.6 NAU2714
75.7 NAU2713*
83.3 DPL0059*
qFE25.1

◀**Fig. 1** The genetic map and QTL controlling fiber quality traits from upland cotton (CCRI 35 × Yumian 1) RIL population. The marker with *asterisk* was distorted locus. The QTL controlling fiber quality traits and the bars representing 1-LOD likelihood intervals are beside the linkage group. QTL are shown as FL for fiber upper half mean length, FU for fiber length uniformity, FS for fiber strength, FE for fiber elongation, and FM for fiber micronaire

(Fig. 1; Table 1), and the map spanned 3,076.4 cM with an average distance of 2.41 cM between two adjacent markers. At-subgenome comprised of 500 loci and spanned 1,462.6 cM with an average distance of 2.93 cM between two adjacent markers. Dt-subgenome contained 774 loci and spanned 1,613.8 cM with an average distance of 2.09 cM between two adjacent markers.

On the whole, all mapped loci were well-proportioned distributed across the entire genome, but still some chromosomes had more loci or fewer loci than other chromosomes. For example, Chr. 20 was mapped with 112 loci, whereas Chr. 12 was mapped with only 12 loci. Chromosome with the longest recombination length was Chr. 16 which spanned 216.4 cM, and the shortest one was Chr.12 which spanned only 65.0 cM. There were four large gaps (adjacent marker interval >20 cM), including two, one and one distributed on Chr. 11, Chr. 13 and Chr. 21, respectively.

The phenotypic analysis of fiber quality traits

The phenotypic data of the five fiber quality traits were summarized in Table 2. The two parents were only significantly different at fiber strength. All the five fiber quality traits of the RIL population showed a wide range of variation. Skewness and kurtosis test

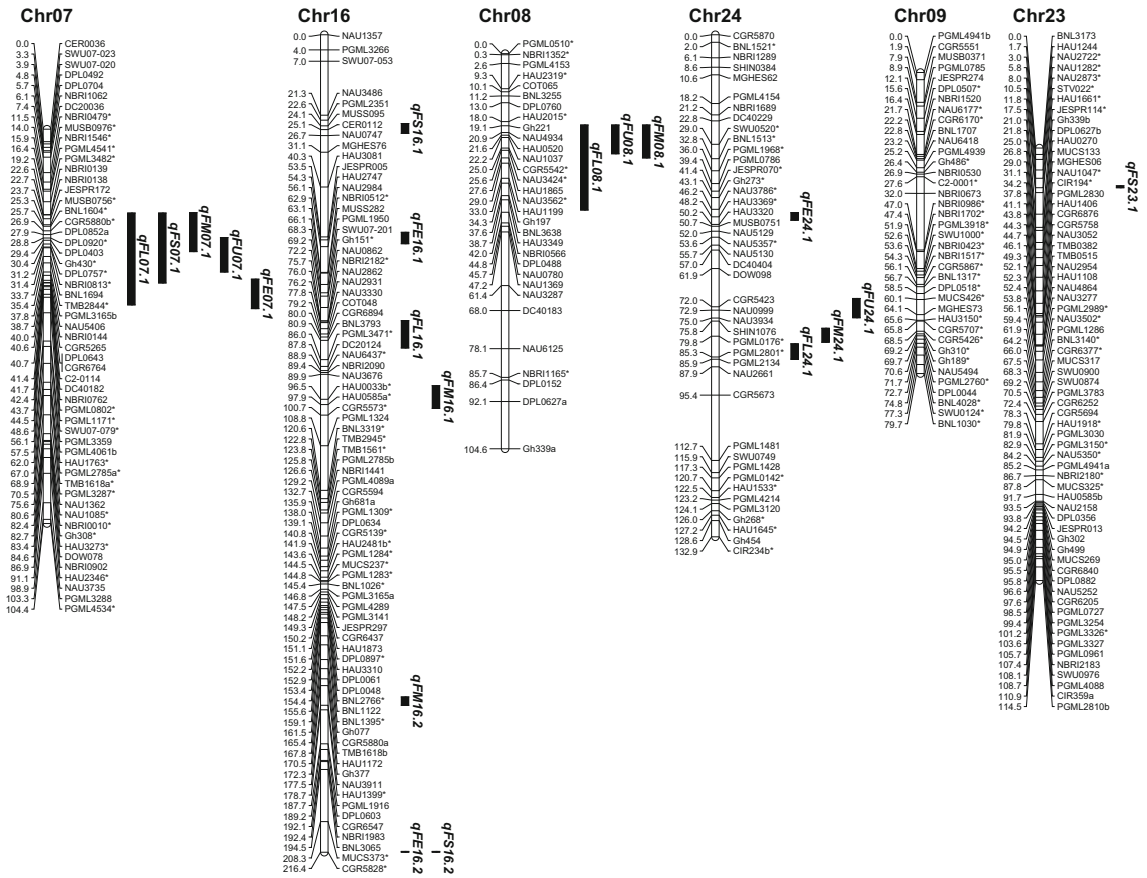


Fig. 1 continued

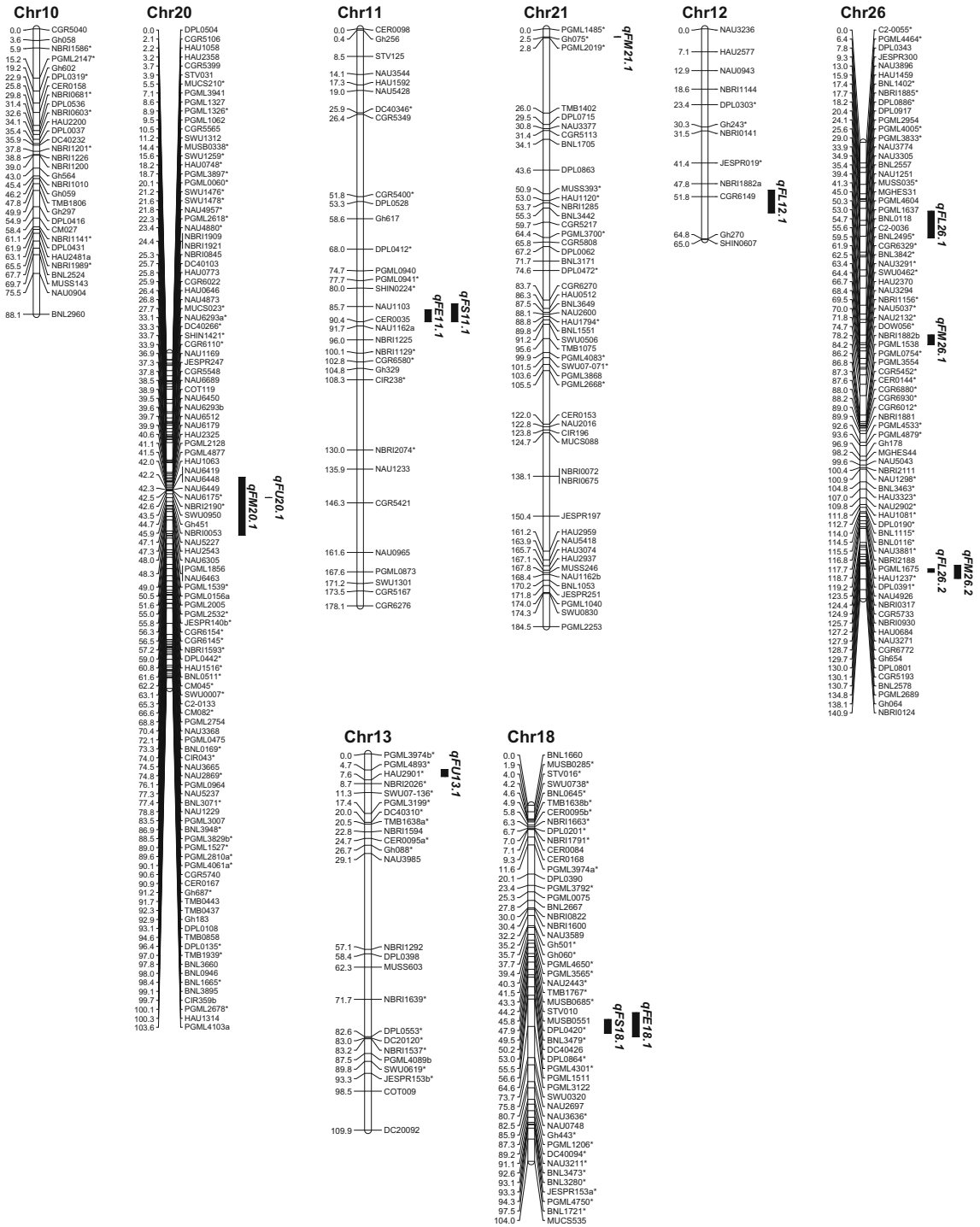


Fig. 1 continued

Table 1 Distribution of loci and distortion loci on the genetic map from the RIL population

Chromosome	Loci	Length (cM)	Average interval (cM)	Distortion loci	Distortion ratio (%)
01	37	139.4	3.77	9	24.3
02	54	114.5	2.12	6	11.1
03	26	106.8	4.11	12	46.2
04	37	114.1	3.08	17	45.9
05	70	124.5	1.78	11	15.7
06	54	133.5	2.47	22	40.7
07	55	104.4	1.90	26	47.3
08	31	104.6	3.38	8	25.8
09	38	79.7	2.10	24	63.2
10	31	88.1	2.84	8	25.8
11	31	178.1	5.75	9	29.0
12	12	65.0	5.42	3	25.0
13	24	109.9	4.58	16	66.7
At	500	1,462.6	2.93	171	34.2
14	48	79.5	1.66	18	37.5
15	58	125.3	2.16	16	27.6
16	78	216.4	2.77	24	30.8
17	74	92.0	1.24	35	47.3
18	50	104.0	2.08	32	64.0
19	65	143.4	2.21	20	30.8
20	112	103.6	0.92	45	40.2
21	49	184.5	3.76	11	22.4
22	32	93.6	2.92	17	53.1
23	65	114.5	1.76	18	27.7
24	43	132.9	3.09	16	37.2
25	23	83.3	3.62	9	39.1
26	77	140.9	1.83	36	46.8
Dt	774	1,613.8	2.09	297	38.4
Total	1,274	3,076.4	2.41	468	36.7

showed that these traits were approximately in normal distribution. The variance analysis result showed that fiber quality traits possessed of significant environmental and genetic efforts except for fiber elongation ($P < 0.05$) in the RIL population (Table 3). Correlation analysis showed that complex significant correlation exists among fiber quality traits (Table 4). Fiber strength was significantly positive-correlated with fiber length and uniformity. Fiber micronaire was significantly positive-correlated with fiber length and strength. Fiber micronaire was significantly negative-correlated with fiber uniformity. Fiber elongation was significantly negative-correlated with fiber length and strength.

QTL identified for fiber quality traits

With the multiple QTL mapping method, a total of 59 QTL were detected for five fiber quality traits based on the phenotype data from 5 environments, including 28 significant QTL and 31 putative QTL (Table 5). These QTL were mapped on 23 chromosomes (Fig. 1; Table 5), with 23 QTL distributed on At-subgenome chromosomes and 36 QTL distributed on Dt-subgenome chromosomes. Parent CCRI 35 conferred 22 favorable alleles, whereas Yumian 1 conferred 37 favorable alleles.

For fiber upper half mean length, 15 QTL (5 significant QTL and 10 putative QTL) were identified

Table 2 Phenotypic data analysis of five fiber quality traits for the parents and the RIL population

Trait	Environment	Parent		Population				
		CCRI 35	Yumian 1	Mean	Max	Mini	Skewness	Kurtosis
Length (mm)	2008	30.3	30.2	30.5	34.0	25.8	0.02	0.53
	2009	29.6	30.7	30.4	33.3	27.0	0.01	−0.03
	2010	27.2	28.7	29.6	32.6	26.4	−0.13	−0.21
	2011	30.8	30.7	29.9	33.0	26.4	−0.07	0.48
	2012	29.9	28.4	29.0	31.8	27.0	0.36	−0.12
Uniformity (%)	2008	83.9	82.5	85.8	88.1	81.7	−0.67	0.97
	2009	86.0	86.1	85.4	87.5	82.0	−0.48	0.39
	2010	83.7	84.0	83.3	86.2	79.2	−0.47	0.33
	2011	84.9	84.4	84.3	86.7	79.9	−0.61	0.50
	2012	85.5	84.5	86.5	89.3	83.4	−0.32	−0.04
Strength (cN/tex)	2008	27.1	30.7	31.8	39.4	25.3	0.44	0.90
	2009	30.8	37.5	33.9	40.8	26.9	0.36	0.36
	2010	28.3	35.4	29.7	35.6	24.2	0.04	0.55
	2011	33.5	38.2	32.9	40.0	26.2	−0.14	0.69
	2012	31.2	35.6	30.8	35.4	27.5	0.39	0.35
Elongation (%)	2008	6.2	6.3	6.5	6.7	6.2	0.00	−0.35
	2009	6.4	6.7	6.5	6.8	6.2	−0.16	−0.46
	2010	6.8	6.1	6.5	7.1	5.7	−0.22	0.08
	2011	6.3	6.1	6.4	7.1	5.8	0.33	0.47
	2012	6.8	7.1	6.7	7.2	6.2	0.13	−0.10
Micronaire	2008	4.2	4.4	4.6	6.2	2.8	−0.34	1.38
	2009	4.4	4.3	4.4	5.3	2.9	−0.38	0.22
	2010	5.4	4.8	4.2	5.1	3.1	−0.26	0.28
	2011	4.2	3.9	4.1	5.4	2.8	−0.17	−0.31
	2012	4.9	4.3	4.6	5.7	3.3	−0.09	0.42

and mapped on 14 chromosomes (Fig. 1; Table 5), explaining 6.1–13.4 % of the phenotypic variation. qFL07.1 and qFL19.1 were identified in three environments, qFL08.1 and qFL17.1 were identified in two environments, and all other QTL could be detected only for one environment. Among these QTL, 5 favorable alleles were contributed by CCRI 35 and all other favorable alleles were contributed by Yumian 1.

For fiber length uniformity, 10 QTL (6 significant QTL and 4 putative QTL) were identified and mapped on 10 chromosomes (Fig. 1; Table 5), explaining 6.3–11.4 % of the phenotypic variation. Only qFU08.1 was identified in two environments and all other QTL were identified in only one environment. Among these QTL, 4 favorable alleles were contributed by CCRI 35, whereas other favorable alleles were contributed by Yumian 1.

For fiber strength, 9 QTL (5 significant QTL and 4 putative QTL), were identified and mapped on 8 chromosomes (Fig. 1; Table 5), explaining 6.1–26.5 % of the phenotypic variation. qFS07.1 and qFS14.1 were identified in five and three environments, respectively, showing that they were very stable QTL. Besides qFS05.1 identified in two environments, all other QTL could be detected only in one environment. Six favorable alleles including all the stable QTL were contributed by Yunmian1 and 3 favorable alleles were contributed by CCRI 35.

For fiber elongation, 10 QTL (5 significant and 5 putative QTL) were identified and mapped on nine chromosomes (Fig. 1; Table 5), explaining about 4.8–11.1 % of the phenotypic variation. All the 10 QTL were identified in only one environment.

Table 3 Variance analysis of fiber quality traits in the RIL population

Trait	Source of variation	Degree freedom	Variance	F
Length	Environment	4	68.44	90.64**
	Genotype	179	3.79	5.01**
	Error	710	0.76	
Uniformity	Environment	4	262.38	202.07**
	Genotype	179	1.59	1.23*
	Error	710	1.30	
Strength	Environment	4	443.20	162.86**
	Genotype	179	10.55	3.88**
	Error	710	2.72	
Elongation	Environment	4	1.84	50.25**
	Genotype	179	0.03	0.73
	Error	710	0.04	
Micronaire	Environment	4	6.99	61.42**
	Genotype	179	0.50	4.42**
	Error	710	0.11	

*, ** Significances with the probability levels of 0.05 and 0.01, respectively

For fiber micronaire, 15 QTL (7 significant QTL and 8 putative QTL) were identified and mapped on 13 chromosomes (Fig. 1; Table 5), explaining between 6.3 and 15.4 % of the phenotypic variation. qFM07.1 and qFM08.1 were identified in four and three environments, respectively, indicating that they were stable QTL. qFM22.1 was identified in two environments, and all other QTL were detected only in one environment. Among these QTL, 5 favorable alleles decreasing the trait value were conferred by CCRI 35, whereas other favorable alleles were conferred by Yumian 1.

Discussion

High-density genetic map

The genetic map constructed in the present study represents the most saturated upland cotton intraspecific genetic maps to date. It spanned about 70.0 % of the entire recombination length of tetraploid cotton genome estimated to be 4,400–4,660 cM (Lacape et al. 2003; Rong et al. 2004; Yu et al. 2011). The marker polymorphic ratio was much lower than that in the previous reports (Lin et al. 2009; Zhang et al. 2009). The advance of this genetic map was mainly attributed to the large amount of SSR primer pairs and the approximately even distribution of loci across the entire genome. The chromosomes with fewer loci and the gaps identified in our study might suggest that there was low marker diversity in these chromosomes or regions between the two parents. The recombination length of some chromosomes was much shorter than other chromosomes and the similar result was also reported in the other studies (Zhang et al. 2009; Yu et al. 2011; Zhao et al. 2012; Zhang et al. 2012). Regarding to the physical length of their homologous chromosomes in D genome (Paterson et al. 2012), it seems that lower recombination rate in these chromosomes/regions played a major role leading to the result. In addition, more loci were distributed on Dt-subgenome than At-subgenome, which was consistent with the reports in the other studies (Yu et al. 2011; Zhang et al. 2012; Zhao et al. 2012), and the possible reason was that D/Dt genome was more divergent than A/At genome among cotton species (Guo et al. 2008).

Segregation distortion

Segregation distortion is widespread in plant populations, and is regarded as the source and force of plant

Table 4 Correlation coefficients among fiber quality traits in 180 recombinant inbred lines

	Length	Uniformity	Strength	Elongation
Uniformity	0.093			
Strength	0.610**	0.341**		
Elongation	−0.281**	−0.072	−0.261**	
Micronaire	−0.497**	0.185*	−0.297**	−0.133

*, ** Correlation is significant at the probability levels of 0.05 and 0.01, respectively

Table 5 QTL controlling fiber quality traits identified from the RIL population

Trait	QTL	Chromosome	Environment	Nearest marker	LOD	Additive	PVE (%)
Length	qFL01.1	01	2011	PGML03082	2.6	+0.30	6.5
	qFL02.1	02	2008	DC20052	2.7	−0.33	6.7
	qFL04.1	04	2011	NAU2489	2.5	+0.28	6.1
	qFL06.1	06	2009	NAU3427	2.6	−0.34	6.5
	qFL07.1	07	2008	PGML03165b	3.2*	−0.36	7.8
			2010	NBRI0138	2.9	−0.36	7.2
			2012	NBRI0138	5.5*	−0.38	13.4
	qFL08.1	08	2008	NAU4934	3.3*	+0.37	8.0
			2012	NAU3287	2.8	+0.33	7.0
	qFL12.1	12	2008	CGR6149	2.6	−0.33	6.3
	qFL14.1	14	2011	PGML04299	3.2*	−0.31	8.0
	qFL16.1	16	2011	BNL3793	4.4*	−0.36	10.6
	qFL17.1	17	2008	NBRI1238	3.8*	−0.40	9.2
			2012	NBRI1238	2.9*	−0.27	7.3
	qFL19.1	19	2008	PGML03255	2.8	−0.35	6.8
			2009	PGML03255	2.6	−0.34	6.5
			2010	PGML03255	2.5	−0.34	6.2
	qFL22.1	22	2009	PGML00695	2.8	−0.37	7.0
	qFL24.1	24	2009	PGML02801	2.7	−0.39	6.8
	qFL26.1	26	2011	PGML03833	2.5	+0.31	6.2
	qFL26.2	26	2012	BNL2578	2.7	+0.31	6.8
Uniformity	qFU01.1	01	2011	NAU2437b	2.6	+0.38	6.5
	qFU04.1	04	2012	NBRI1131a	3.4*	−0.38	8.5
	qFU07.1	07	2010	PGML03165b	2.6	−0.34	6.6
	qFU08.1	08	2009	Gh221	3.4*	−0.29	8.5
			2010	NAU3424	2.5	−0.35	6.3
	qFU13.1	13	2010	PGML04893	2.8	−0.38	6.9
	qFU15.1	15	2009	PGML03446	4.7*	−0.36	11.4
	qFU17.1	17	2010	HAU3318	3.6*	−0.39	8.9
	qFU19.1	19	2011	PGML03255	3.0*	+0.39	7.4
	qFU20.1	20	2012	Gh451	2.5	+0.27	6.3
	qFU24.1	24	2008	NAU0999	3.2*	+0.32	7.9
Strength	qFS02.1	02	2008	TMB0471	2.5	−0.52	6.1
	qFS05.1	05	2008	PGML04051	3.2*	−0.60	8.0
			2012	PGML04051	2.5	−0.37	6.2
	qFS07.1	07	2008	NBRI0144	7.1*	−0.91	16.6
			2009	DPL0643	11.9*	−1.24	26.5
			2010	NAU5406	7.7*	−0.74	17.9
			2011	NBRI0144	3.6*	−0.67	8.7
			2012	NBRI0762	5.2*	−0.58	12.6
	qFS11.1	11	2011	NAU1103	3.3*	+0.70	8.1
	qFS14.1	14	2009	PGML03577	2.8	−0.67	6.9
			2010	NAU1187a	3.6*	−0.59	8.9
			2011	NAU1187a	3.7*	−0.64	9.1
	qFS16.1	16	2008	MUSS095	3.8*	−0.64	9.2
	qFS16.2	16	2011	CGR5828	2.8	−0.72	6.9
	qFS18.1	18	2012	PGML03122	2.7	+0.44	6.7
	qFS23.1	23	2012	STV022	2.7	+0.41	6.7

Table 5 continued

Trait	QTL	Chromosome	Environment	Nearest marker	LOD	Additive	PVE (%)
Elongation	qFE01.1	01	2011	DPL0526	2.9	−0.07	7.1
	qFE07.1	07	2012	NBRI0762	4.5*	−0.07	11.1
	qFE11.1	11	2011	CER0035	3.2*	−0.07	7.8
	qFE15.1	15	2010	BNL1454	3.4*	+0.08	8.5
	qFE16.1	16	2012	JESPR005	3.2*	−0.06	7.9
	qFE16.2	16	2011	CGR5828	2.7	+0.07	6.7
	qFE18.1	18	2012	PGML03122	3.5*	+0.06	8.6
	qFE22.1	22	2011	PGML03002a	2.6	+0.06	6.5
	qFE24.1	24	2010	HAU3369	2.6	+0.07	6.4
	qFE25.1	25	2008	NBRI0769	2.7	−0.04	4.8
Micronaire	qFM05.1	05	2011	CER0060	2.6	+0.16	6.4
	qFM06.1	06	2010	Gh513	2.6	+0.13	6.4
	qFM07.1	07	2008	DPL0403	4.8*	+0.15	11.6
			2009	DPL0643	6.5*	+0.17	15.4
			2011	DPL0920	3.2*	+0.16	7.7
			2012	NBRI0139	3.8*	+0.13	9.4
	qFM08.1	08	2008	HAU1865	3.4*	−0.13	8.4
			2009	HAU1865	3.3*	−0.13	8.1
			2012	HAU1865	2.9	−0.10	7.4
	qFM14.1	14	2011	DPL0405	3.3*	+0.19	8.2
	qFM16.1	16	2012	HAU0585a	3.0	−0.11	7.4
	qFM16.2	16	2008	NAU3911	2.9	−0.14	7.1
	qFM17.1	17	2012	NBRI1238	3.8*	+0.12	9.4
	qFM19.1	19	2012	PGML03255	3.0	+0.11	7.5
	qFM20.1	20	2008	NAU6689	3.9*	+0.15	9.6
	qFM21.1	21	2012	Gh075	2.5	+0.10	6.3
	qFM22.1	22	2008	PGML01657	2.8	+0.14	7.0
			2011	NAU3868	2.6	+0.14	6.4
	qFM24.1	24	2010	PGML00176	3.3*	+0.11	8.2
	qFM26.1	26	2011	BNL2495	3.2*	−0.18	7.8
	qFM26.2	26	2009	BNL2578	2.9	−0.14	7.3

+ indicates that CCRI 35 allele increases the trait value, and − indicates that Yumian 1 allele increases the trait value

PVE phenotypic variance explained

* LOD was larger than the significant LOD threshold calculated by 1,000 permutation tests ($P < 0.05$)

evolution (Taylor and Ingvarsson 2003). The percentage, degree, origin and genetic effects of segregation distortion vary significantly with species, population types, crosses and marker types in plants (Xu et al. 1997). Previous studies considered that higher segregation distortion in RIL population may mainly result from genetic drift (Zhang et al. 2009), genetic incompatibility and genome instability (Zhang et al. 2009) and the divergence between species (Paterson et al. 1988). The segregation distortion ratio in this study is high and most distorted loci skewed to Yumian 1 alleles, the same phenomenon was found in the other studies with Yumian 1 as one parent (Hu et al. 2008; Zhang et al. 2009), and the results suggested that Yumian 1 alleles probably played a critical role in segregation distortion. Considering the mapping parent Yumian 1 with complicated parentage (Zhang et al. 2009), we deduce that both the parentage of parent Yumian 1 and the population type contributed to the high segregation distortion in the present study. Similarly, most segregation distortion loci occurred in clusters, and it is consistent with the result

found in the interspecific populations (Reinisch et al. 1994; Lacape et al. 2003; Guo et al. 2007; Zhang et al. 2008; Yu et al. 2011), and the intraspecific populations (Shen et al. 2005, 2007; Lin et al. 2009; Zhang et al. 2009). These results indicated that genetic hitchhiking effects commonly occurred in cotton. Furthermore, many segregation distortion regions were close to or even overlapping with the QTL intervals and this phenomenon implies that some relationship exists between the alleles underlying these QTL and the alleles causing segregation distortion.

Common or stable QTL across multiple populations and environments

Due to the most detailed intraspecific genetic map constructed in the present study, 59 QTL controlling fiber quality traits were detected. Among these QTL detected, only 11 QTL were detected in two or more environments and some QTL with large effects were detected in merely one environment. The same results were also found in the other studies (Shen et al. 2007; Zhang et al. 2009; Zhang et al. 2012), and these results further proved that environmental factor played an important role in QTL expression. However, according to the common shared markers in the QTL-regions, 16 QTL detected in the present study were identified in the other populations and these QTL included qFE07.1 (Sun et al. 2012; Wang et al. 2013), qFE15.1 (Sun et al. 2012), qFE24.1 (Shen et al. 2007), qFL07.1 (Sun et al. 2012; Wang et al. 2013), qFL14.1 (Sun et al. 2012), qFL17.1 (Wang et al. 2013), qFM05.1 (Sun et al. 2012), qFM07.1 (Sun et al. 2012), qFM14.1 (Sun et al. 2012), qFM16.1 (Sun et al. 2012), qFM16.2 (Wang et al. 2013), qFS02.1 (Wang et al. 2013), qFS07.1 (Sun et al. 2012; Wang et al. 2013), qFS23.1 (Shen et al. 2007), qFS24.1 (Shen et al. 2007) and qFU07.1 (Sun et al. 2012). Furthermore, 21 QTL detected in the present study were also identified in the populations with the same mapping parents in our previous studies and these QTL included qFE07.1 (Ni et al. 2011; Zhang et al. 2012), qFE11.1 (Ni et al. 2011), qFE15.1 (Zhang et al. 2012), qFE24.1 (Zhang et al. 2012), qFE16.1 (Zhang et al. 2012), qFL01.1 (Ni et al. 2011), qFL07.1 (Chen et al. 2008; Ni et al. 2011), qFL08.1 (Zhang et al. 2012), qFL12.1 (Zhang et al. 2012), qFL17.1 (Zhang et al. 2012), qFL19.1 (Zhang et al. 2012), qFL24.1 (Zhang et al. 2012), qFM07.1 (Ni et al. 2011; Zhang et al. 2012), qFM08.1 (Ni et al. 2011), qFM17.1 (Zhang et al. 2012), qFM24.1 (Zhang et al. 2012), qFS07.1 (Chen et al. 2008; Ni et al. 2011; Zhang et al. 2012), qFS14.1 (Ni et al. 2011), qFS23.1 (Zhang et al. 2012), qFU07.1 (Zhang et al. 2012) and qFU24.1 (Zhang et al. 2012). The QTL identified across multiple environments and populations revealed that they were important for fiber quality traits, even though some of them were largely affected by environmental factors.

Favorable QTL allele origin

In the present study, although the two parents only had significant difference in fiber strength, there are 22 favorable alleles originated from CCRI 35 and 37 favorable alleles originated from Yumian 1. Meanwhile, cultivar Yumian 1 with high fiber strength had more favorable fiber strength alleles than cultivar CCRI 35 with low fiber strength. The same results were also found in the previous studies (Zhang et al. 2009; Sun et al. 2012; Zhang et al. 2012; Wang et al. 2013). Additionally, favorable alleles for fiber elongation and micronaire were also detected in the populations developed from the parents that didn't have significant difference in these traits (Shen et al. 2005; Sun et al. 2012). These results confirmed that different cultivars comprised of different favorable alleles for the same traits at different position on the genome.

QTL-rich regions

The phenomenon of QTL-rich regions for at least three fiber traits was observed on Chr07, Chr08, Chr17, Chr19 and Chr24, and the similar result was also reported in the previous studies (Paterson et al. 2003; Zhang et al. 2009; Sun et al. 2012; Zhang et al. 2012; Yu et al. 2013). These regions were also near or within the QTL hotspots (Rong et al. 2007; Said et al. 2013).The recent study found that large numbers of coordinately regulated genes existed near 'hotspots' for cotton fiber QTL (Paterson et al. 2012), and this discovery seems to imply that the QTL-rich regions maybe result from the closely-linked alleles. However, we couldn't exclude the possibility that these QTL-rich regions are contributed by pleiotropic alleles, especially for those QTL with overlapping intervals to date.

In conclusion, the genetic map constructed in the present study is the most detailed upland cotton

intraspecific map based on SSR markers to date. It generally reveals the upland cotton genome structure and could be used to construct detailed consensus map or as reference genetic map for tetraploid cotton genome assembly. The large number of QTL detected and their distribution on entire genome indicated that regulation of cotton fiber quality traits were complicated with genetic and environmental factors. Stable QTL, especially the qFS07.1 and qFS14.1, reflect some important and favorable alleles shaping fiber strength, and they could be the candidate alleles for MAS breeding projects as well as for gene function research to reveal the molecular regulation mechanism of fiber strength.

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References

Al-Ghazi Y, Bourot S, Arioli T, Dennis ES, Llewellyn DJ (2009) Transcript profiling during fiber development identifies pathways in secondary metabolism and cell wall structure that may contribute to cotton fiber quality. Plant Cell Physiol 50:1364–1381

Blenda A, Fang DD, Rami JF, Garsmeur O, Luo F, Lacape JM (2012) A high density consensus genetic map of tetraploid cotton that integrates multiple component maps through molecular marker redundancy check. PLoS One 7:e45739

Chen L, Zhang ZS, Hu MC, Wang W, Zhang J, Liu DJ, Zheng J, Zheng FM, Ma J (2008) Genetic linkage map construction and QTL mapping for yield and fiber quality in upland cotton. Acta Agron Sin 34:1199–1205 (in Chinese with English abstract)

Culp TW, Lewis CF (1973) Breeding methods for improving yield and fiber quality of upland cotton (*Gossypium hirsutum*). Crop Sci 13:686–689

Guo WZ, Cai CP, Wang CB, Han ZG, Song XL, Wang K, Niu XW, Wang C, Lu KY, Shi B, Zhang TZ (2007) A microsatellite-based, gene-rich linkage map reveals genome structure, function, and evolution in *Gossypium*. Genetics 176:527–541

Guo WZ, Cai CP, Wang CB, Zhao L, Wang L, Zhang TZ (2008) A preliminary analysis of genome structure and composition in *Gossypium hirsutum*. BMC Genomics 9:314

Hovav R, Udall JA, Hovav E, Rapp R, Flagel LE, Wendel JF (2008) A majority of cotton genes are expressed in single-celled fiber. Planta 227:319–329

Hu WJ, Zhang XY, Zhang TZ, Guo WZ (2008) Molecular tagging and source analysis of QTL for elite fiber quality in upland cotton. Acta Agron Sin 34:578–586 (in Chinese with English abstract)

Iqbal J, Reddy OUK, El-Zik KM, Pepper AE (2001) A genetic bottleneck in the 'evolution under domestication' of Upland cotton *Gossypium hirsutum* L. examined using DNA fingerprinting. Theor Appl Genet 103:547–554

Lacape JM, Nguyen TB, Thibivilliers S, Bojinov B, Courtois B, Cantrell RG, Burr B, Hau B (2003) A combined RFLP–SSR–AFLP map of tetraploid cotton based on a *Gossypium hirsutum* × *Gossypium barbadense* backcross population. Genome 46:612–626

Lacape JM, Dessauw D, Rajab M, Noyer JL, Hau B (2007) Microsatellite diversity in tetraploid *Gossypium* germplasm: assembling a highly informative genotyping set of cotton SSRs. Mol Breed 19:45–58

Lacape JM, Llewellyn D, Jacobs J, Arioli T, Becker D, Calhoun S, Al-Ghazi Y, Liu SM, Palaï O, Georges S, Giband M, de Assunção H, Barroso V, Claverie M, Gawryziak G, Jean J, Vialle M, Viot C (2010) Meta-analysis of cotton fiber quality QTLs across diverse environments in a *Gossypium hirsutum* × *G. barbadense* RIL population. BMC Plant Biol 10:132

Lee JJ, Woodward AW, Chen ZJ (2007) Gene expression changes and early events in cotton fibre development. Ann Bot 100:1391–1401

Lin ZX, Zhang YX, Zhang XL, Guo XP (2009) A high-density integrative linkage map for *Gossypium hirsutum*. Euphytica 166:35–45

Ni HJ, Wang W, Teng ZH, Zhang J, Liu DH, Zhang ZS (2011) QTL mapping of yield and fiber quality traits in upland cotton. J Southwest Univ (Nat Sci Ed) 33:7–14 (in Chinese with English abstract)

Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksely SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721–726

Paterson AH, Saranga Y, Menz M, Jiang CX, Wright RJ (2003) QTL analysis of genotype by environment interaction affecting cotton fiber quality. Theor Appl Genet 106:384–396

Paterson AH, Wendel JF, Gundlach H, Guo H, Jenkins J, Jin D, Llewellyn D, Showmaker KC, Shu S, Udall J, Yoo MJ, Byers R, Chen W, Doron-Faigenboim A, Duke MV, Gong L, Grimwood J, Grover C, Grupp K, Hu G, Lee TH, Li J, Lin L, Liu T, Marler BS, Page JT, Roberts AW, Romanel E, Sanders WS, Szadkowski E, Tan X, Tang H, Xu C, Wang J, Wang Z, Zhang D, Zhang L, Ashrafi H, Bedon F, Bowers JE, Brubaker CL, Chee PW, Das S, Gingle AR, Haigler CH, Harker D, Hoffmann LV, Hovav R, Jones DC, Lemke C, Mansoor S, ur Rahman M, Rainville LN, Rambani A, Reddy UK, Rong JK, Saranga Y, Scheffler BE, Scheffler JA, Stelly DM, Triplett BA, Van Deynze A, Vaslin MF, Waghmare VN, Walford SA, Wright RJ, Zaki EA, Zhang T, Dennis ES, Mayer KF, Peterson DG, Rokhsar DS, Wang X, Schmutz J (2012) Repeated polyploidization of *Gossypium* genomes and the evolution of spinnable cotton fibres. Nature 492:423–427

Percival AE, Wendel JF, Stemart JM (1999) Taxonomy and germplasm resourses. In: Smith CW, Cothren JT (eds) Cotton: origin, history, technology, and production. Wiley, New York, pp 33–63

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

Rong JK, Abbey C, Bowers JE, Brubaker CL, Chang C, Chee PW, Delmonte TA, Ding X, Garza JJ, Marler BS, Park C, Pierce GJ, Rainey KM, Rastogi VK, Schulze SR, Tronlinde NL, Wendel JF, Wilkins TA, Wing RA, Wright RJ, Zhao X, Zhu L, Paterson AH (2004) A 3347-locus genetic recombination map of sequence-tagged sites reveals features of genome organization, transmission and evolution of cotton (*Gossypium*). Genetics 166:389–417

Rong JK, Feltus FA, Waghmare VN, Pierce GJ, Chee P, Draye X, Saranga Y, Wright RJ, Wilkins TA, May LO, Smith CW, Gannaway JR, Wendel JF, Paterson AH (2007) Meta-analysis of polyploid cotton QTL shows unequal contributions of subgenomes to a complex network of genes and gene clusters implicated in lint fiber development. Genetics 176:2577–2588

Rungis D, Llewellyn D, Dennis ES, Lyon BR (2005) Simple sequence repeat (SSR) markers reveal low levels of polymorphism between cotton (*Gossypium hirsutum* L.) cultivars. J Agric Res 56:301–307

Said JI, Lin ZX, Zhang XL, Song MZ, Zhang JF (2013) A comprehensive meta QTL analysis for fiber quality, yield, yield related and morphological traits, drought tolerance, and disease resistance in tetraploid cotton. BMC Genomics 14:776

Shen XL, Guo WZ, Zhu XF, Yuan YL, Yu JZ, Kohel RJ, Zhang TZ (2005) Molecular mapping of QTLs for fiber qualities in three diverse lines in upland cotton using SSR markers. Mol Breed 15:169–181

Shen XL, Guo WZ, Lu QX, Zhu XF, Yuan YL, Zhang TZ (2007) Genetic mapping of quantitative trait loci for fiber quality and yield trait by RIL approach in upland cotton. Euphytica 155:371–380

Smith CW, Coyle GG (1997) Association of fiber quality parameters and within-boll yield components in upland cotton. Crop Sci 37:1775–1779

Sun FD, Zhang JH, Wang SF, Gong WK, Shi YZ, Liu AY, Li JW, Gong JW, Shang HH, Yuan YL (2012) QTL mapping for fiber quality traits across multiple generations and environments in upland cotton. Mol Breed 188:441–451

Taliercio EW, Boykin D (2007) Analysis of gene expression in cotton fiber initials. BMC Plant Biol 7:22

Tang SY, Teng ZH, Zhai TF, Fang XM, Liu F, Liu DJ, Zhang J, Liu DX, Wang SF, Zhang K, Shao QS, Tan ZY, Paterson AH, Zhang ZS (2014) Construction of genetic map and QTL analysis of fiber quality traits for Upland cotton (*Gossypium hirsutum* L.). Euphytica (Online). doi:10.1007/s10681-014-1189-y

Tanksley SD, Hewitt J (1988) Use of molecular markers in breeding for soluble solids content in tomato—a re-examination. Theor Appl Genet 75:811–823

Taylor DR, Ingvarsson PK (2003) Common features of segregation distortion in plants and animals. Genetica 117:27–35

Van Ooijen JW (2009) MapQTL 6.0. Software for the mapping of quantitative trait loci in experimental populations. Plant Research International, Wageningen

Van Ooijen JW, Voorrips RE (2006) JoinMap 4.0, software for the calculation of genetic linkage maps. Plant Research International, Wageningen

Voorrips RE (2006) MapChart 2.2: Software for the graphical presentation of linkage maps and QTLs. Plant Research International, Wageningen

Wang FR, Xu ZZ, Sun R, Gong YC, Liu GD, Zhang JX, Wang LM, Zhang CY, Fan SJ, Zhang J (2013) Genetic dissection of the introgressive genomic components from *Gossypium barbadense* L. that contribute to improved fiber quality in *Gossypium hirsutum* L. Mol Breed 32:547–562

Xiao J, Wu K, Fang DD, Stelly DM, Yu J, Cantrell RG (2009) New SSR markers for use in cotton (*Gossypium* spp.) improvement. J Cotton Sci 13:75–157

Xu YB, Zhu LH, Huang N, McCouch SR (1997) Chromosomal regions associated with segregation distortion of molecular markers in F_2, backcross, doubled haploid, and recombinant inbred populations in rice (*Oryza sativa* L.). Mol Gen Genomics 253:535–545

Yu Y, Yuan DJ, Liang SG, Li XM, Wang XQ, Lin ZX, Zhang XL (2011) Genome structure of cotton revealed by a genome-wide SSR genetic map constructed from a BC_1 population between *Gossypium hirsutum* and *G. barbadense*. BMC Genomics 12:15

Yu JW, Zhang K, Li SY, Yu SX, Zhai HH, Wu M, Li XL, Fan SL, Song MZ, Yang DG, Li YH, Zhang JF (2013) Mapping quantitative trait loci for lint yield and fiber quality across environments in a *Gossypium hirsutum* × *Gossypium barbadense* backcross inbred line population. Theor Appl Genet 126:275–287

Zhang ZS, Xiao YH, Luo M, Li XB, Luo XY, Hou L, Li DM, Pei Y (2005) Construction of a genetic linkage map and QTL analysis of fiber-related traits in upland cotton (*Gossypium hirsutum* L.). Euphytica 144:91–99

Zhang YX, Lin ZX, Xia QZ, Zhang MJ, Zhang XL (2008) Characteristics and analysis of simple sequence repeats in the cotton genome based on a linkage map constructed from a BC_1 population between *Gossypium hirsutum* and *G. barbadense*. Genome 51:534–546

Zhang ZS, Hu MC, Zhang J, Liu DJ, Zheng J, Zhang K, Wang W, Wan Q (2009) Construction of a comprehensive PCR-based marker linkage map and QTL mapping for fiber quality traits in upland cotton (*Gossypium hirsutum* L.). Mol Breed 24:49–61

Zhang K, Zhang J, Ma J, Tang SY, Liu DJ, Teng ZH, Liu DX, Zhang ZS (2012) Genetic mapping and quantitative trait locus analysis of fiber quality traits using a three-parent composite population in upland cotton (*Gossypium hirsutum* L.). Mol Breed 29:335–348

Zhao L, Lv YD, Cai CP, Tong XC, Chen XD, Zhang W, Du H, Guo XH, Guo WZ (2012) Toward allotetraploid cotton genome assembly: integration of a high-density molecular genetic linkage map with DNA sequence information. BMC Genomics 13:539