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GENOME-WIDE IDENTIFICATION OF RECOMBINATION RATES OF MALE VERSUS FEMALE GAMETES IN INTERSPECIFIC POPULATION OF COTTON

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Abstract

Based on the established SSR-based BC_1 genetic linkage map, 2 genetic maps covered with 313 markers have been developed for 2 more backcross populations which was aimed to study the difference of recombination rates between male and female gametes. The total lengths of genetic maps for male and female were 4532.9cM and 4464.4cM respectively, and the average marker distances were 14.48cM and 14.26cM respectively. The results showed that there was no difference for the recombination rates between male and female gametes on the total map length and the average marker interval. There were 6 linkage groups showing significant differences between the 2 populations, which indicated that the gamete recombinant rates can only influence some chromosomes in cotton. Although a lot of marker intervals showed difference between maps, only 17 marker intervals were caused by the male and female gametes recombination rates. Further investigation showed that the male gamete mainly resulted in a longer genetic distance between markers, and increased the recombination rates; while the female gamete usually resulted in a shorter genetic distance of marker interval, and decreased the recombination rates. The present results will give us some useful instructions in cotton genetics and breeding.

Introduction

During the process of meiosis in plant cell, homologous chromosomes pair with each other and exchanges happen to matching part of the chromosome segments to generate recombinant gametes. Genetic recombination is due to the different DNA strand breaks and connections arising from the exchange of DNA fragments and re-combination to form new DNA molecules (Baker *et al*., 1976). The genetic recombination usually occurred during sexual reproduction in higher plants and animals. Many factors can affect the exchange of chromosomal segments during recombination, such as environment, genetic factors, sex, etc. In humans (Donis-Kveller *et al*., 1987), for example, the recombination of males was significantly less than that of females; however, some contrary results were reported in mouse (Reeves *et al*., 1990) and silkworm (Maeda, 1939). In maize and Arabidopsis, there have been reports about an increase of recombination rate in males (Robertson, 1984; Zhuchenko *et al*., 1989). In the previous reports, morphologic markers are usually used to study gamete recombination, which are limited to some particular chromosome and cannot determine the genetic laws on the whole genome. The adventure of molecular markers and genome-wide genetic maps make it possible to study the difference of recombination rate between the male and female gametes on the whole genome.

de Vicente & Tanksley (1991) reported that the recombination rate of the male and female gametes is different in tomato; by comparing the genetic distances of markers on corresponding chromosomes and the total length of the genome, it was found that the recombination rate of males was significantly reduced compared to females, but no differences in the region close to the centromeres. Busso *et al*., (1995) studied the recombination rate differences between male and female gametes in pearl millet with RFLP markers, 42 RFLP markers covered most of the genome, however, the genetic distance across the genome was not significantly different, differences only existed on some linkage groups and some marker intervals. Wang *et al*., (1995) compared the recombination rate differences of male and female gametes in barley, and established the linkage maps of homologous chromosomes 6 and 7 using doubled haploid populations. The genetic distances of male and female gametes on each homologous chromosome were significantly different; the map length of the male gamete was longer than that of the female gamete with obviously inconsistencies on some specific chromosome segments. The results also showed that environmental factor may be one of important factors leading to their differences.

Cotton, as an important cash crop, not only provides natural fibers, but also is an important source of oil in our life. The production requires cotton varieties with high quality and high yield, which requires us not only to make use of high-yield traits of upland cotton, but also the high quality traits and the resistance to verticillium wilt of sea-island cotton. Upland cotton and sea-island cotton are complementary to each other in traits, their hybrid is fertile (Stephens, 1946), interspecific hybridization between sea-island cotton and upland cotton is an important way to improve traits in upland cotton.

Molecular markers have been widely used in cotton genetics and breeding (Zhang *et al*., 2008; Ali *et al*., 2009; Azmat & Khan, 2010; Mumtaz *et al*., 2010). Recombination is an important genetic basis to generate admirable traits, and the study of differences in recombination rate between the male and female gametes in tetraploid cotton (upland and sea-island cotton) using SSR markers can be very helpful for parents selection, cross way in traditional breeding and marker-assisted selection in breeding.

Materials and Methods

Plant materials and population development: *G. hirsutum* L. cv. 'Emian22' as female and *G. barbadense* L. acc. '3-79' as male were crossed to produce F_1. The population 1 (Pop 1) including 141 individuals was the BC_1 population [(Emian22 × 3-79) × Emian22] which had

been used to construct a 917-locus map (Zhang *et al*., 2008). 'Emian22' as female and '3-79' as male were crossed to F_1 respectively to generate population 2 (Pop 2) and population 3 (Pop 3). One hundred and fifteen individuals from Pop 2 and 116 individuals from Pop 3 were randomly selected. All materials were planted in the fields at Huazhong Agricultural University.

DNA isolation: Total genomic DNA was isolated from the young leaf tissue of the individual plants according to Paterson *et al*., (1993).

SSR genotyping: Based on the genetic map of Pop 1 (Zhang *et al*., 2008), co-dominant SSR markers with an interval of 10-20cM between adjacent markers were selected to analysis Pop 2 and Pop 3. Polymerase chain reactions (PCR), electrophoresis and silver staining were conducted based on the protocols of Lin *et al*., (2005). If a primer pair detected multiple loci, lowercase letters were assigned to these loci according to descending fragment size.

Data analysis: Linkage analysis was performed using Mapmaker Exp/3.0b (Lander *et al*., 1987) and map distances were calculated using the Kosambi mapping function (Kosambi 1944). The genetic maps were drawn by MapInspect (http://www.plantbreeding.wur.nl/UK/software_mapinspect.html). Total recombination per chromosome was compared by t-tests. Interval comparisons were made using chi-square 2 x 2 contingency tables.

Results

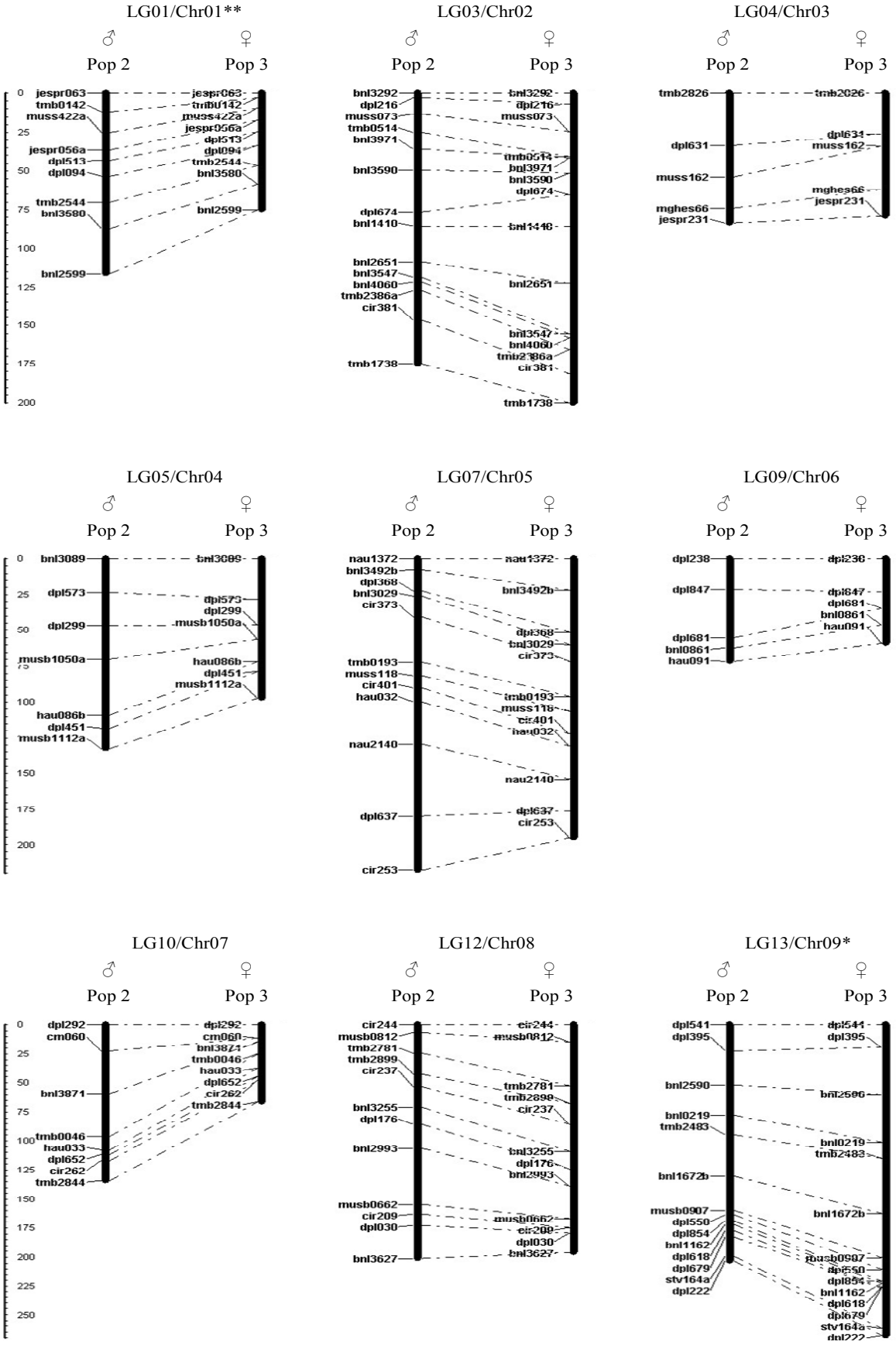
Characteristics of genetic maps for Pop 2 and Pop 3: A 917-locus interspecific genetic map based on SSRs has been developed in our laboratory (Zhang *et al*., 2008). Based on this map, co-dominant markers every 10-20cM were picked out, and a total of 347 markers were selected to analyze Pop 2 and Pop 3. A total of 30 linkage groups (LGs) with more than 3 loci were constructed for both populations, and each map comprised of 313 loci. The total map lengths of Pop 2 and Pop 3 were 4532.9cM and 4464.4cM, respectively, and covered 83.1% and 81.9% of the genetic map of Pop 1, respectively; the average marker distance were 14.48cM and 14.26cM, respectively.

The most loci were on LG34/Chr19 with 29 loci, and the least on LG24/Chr02 and LG36/Chr04 with 4 loci; there were 10.4 loci on each LGs on average. There were 141 and 172 loci located on At sub-genome and Dt sub-genome, respectively. There were 21 and 27 intervals with 30-40cM, 9 and 10 intervals with >40cM in Pop 2 and Pop 3, respectively (Fig. 1, Table 1).

Table 1. The characteristics of the linkage maps and comparisons between the corresponding linkage groups in the Pop 2 and Pop 3

LG/Chr	Total length		Average marker interval		Male/Female	P value [a]
	Pop 2	Pop 3	Pop 2	Pop 3		
1/Chr01	116.5	75.1	12.94	8.34	1.55	0.009**
3/Chr02	175	199.8	12.50	14.27	0.88	0.510
4/Chr03	83.8	79.8	16.76	15.96	1.05	0.866
5/Chr04	132.8	97.4	18.97	13.91	1.36	0.241
7/Chr05	217.6	195	18.13	16.25	1.12	0.612
9/Chr06	71.5	58.9	14.30	11.78	1.21	0.658
10/Chr07	134.2	66.7	16.78	8.34	2.01	0.136
12/Chr08	201.6	196.1	16.80	16.34	1.03	0.881
13/Chr09	203.3	267.7	14.52	19.12	0.76	0.038*
14/Chr10	121.2	94.5	20.20	15.75	1.28	0.198
15/Chr11	146.1	121.4	13.28	11.04	1.20	0.276
16/Chr11	159.1	144.6	14.46	13.15	1.10	0.549
17/Chr12	161.2	150	13.43	12.50	1.07	0.404
18/Chr12	173.5	99.1	19.28	11.01	1.75	0.193
20/Chr13	123.9	111.9	20.65	18.65	1.11	0.744
24/Chr14	123.1	94.6	30.78	23.65	1.30	0.212
25/Chr15	56.4	39.4	9.40	6.57	1.43	0.249
28/Chr16	153.1	306.5	8.06	16.13	0.50	0.011*
31/Chr17	39.6	78.2	7.92	15.64	0.51	0.365
32/Chr18	181.7	146.4	13.98	11.26	1.24	0.431
34/Chr19	312.6	501.7	10.78	17.30	0.62	0.001**
35/Chr20	230.7	187	19.23	15.58	1.23	0.215
36/Chr21	55.5	87.9	13.88	21.98	0.63	0.212
37/Chr21	173.4	122.8	19.27	13.64	1.41	0.122
38/Chr22	103.4	114.9	10.34	11.49	0.90	0.381
39/Chr23	177.8	176.5	17.78	17.65	1.01	0.929
41/Chr24	279.9	215.6	16.46	12.68	1.30	0.039*
42/Chr25	264	193.9	12.57	9.23	1.36	0.033*
43/Chr26	63	91.7	12.60	18.34	0.69	0.345
44/Chr26	97.4	149.3	12.18	18.66	0.65	0.254
All	4532.9	4464.4	14.48	14.26	1.02	0.823

[a]: * and ** represent significant at the 0.05 and 0.01 probability level, respectively


LG01/Chr01**
♂
♀
Pop 2
Pop 3
0
25
50
75
100
125
150
175
200
jespr063
tmb0142
muss422a
jespr056a
dpl513
dpl094
tmb2544
bnl3580
bnl2599
LG03/Chr02
bnl3292
dpl216
muss073
tmb0514
bnl3971
bnl3590
dpl674
bnl1410
bnl2651
bnl3547
bnl4060
tmb2386a
cir381
tmb1738
LG04/Chr03
tmb2826
dpl631
muss162
mghes66
jespr231
LG05/Chr04
bnl3089
dpl573
dpl299
musb1050a
hau086b
dpl451
musb1112a
LG07/Chr05
nau1372
bnl3492b
dpl368
bnl3029
cir373
tmb0193
muss118
cir401
hau032
nau2140
dpl637
cir253
LG09/Chr06
dpl238
dpl847
dpl681
bnl0861
hau091
LG10/Chr07
dpl292
cm060
bnl3871
tmb0046
hau033
dpl652
cir262
tmb2844
LG12/Chr08
cir244
musb0812
tmb2781
tmb2899
cir237
bnl3255
dpl176
bnl2993
musb0662
cir209
dpl030
bnl3627
LG13/Chr09*
dpl541
dpl395
bnl2590
bnl0219
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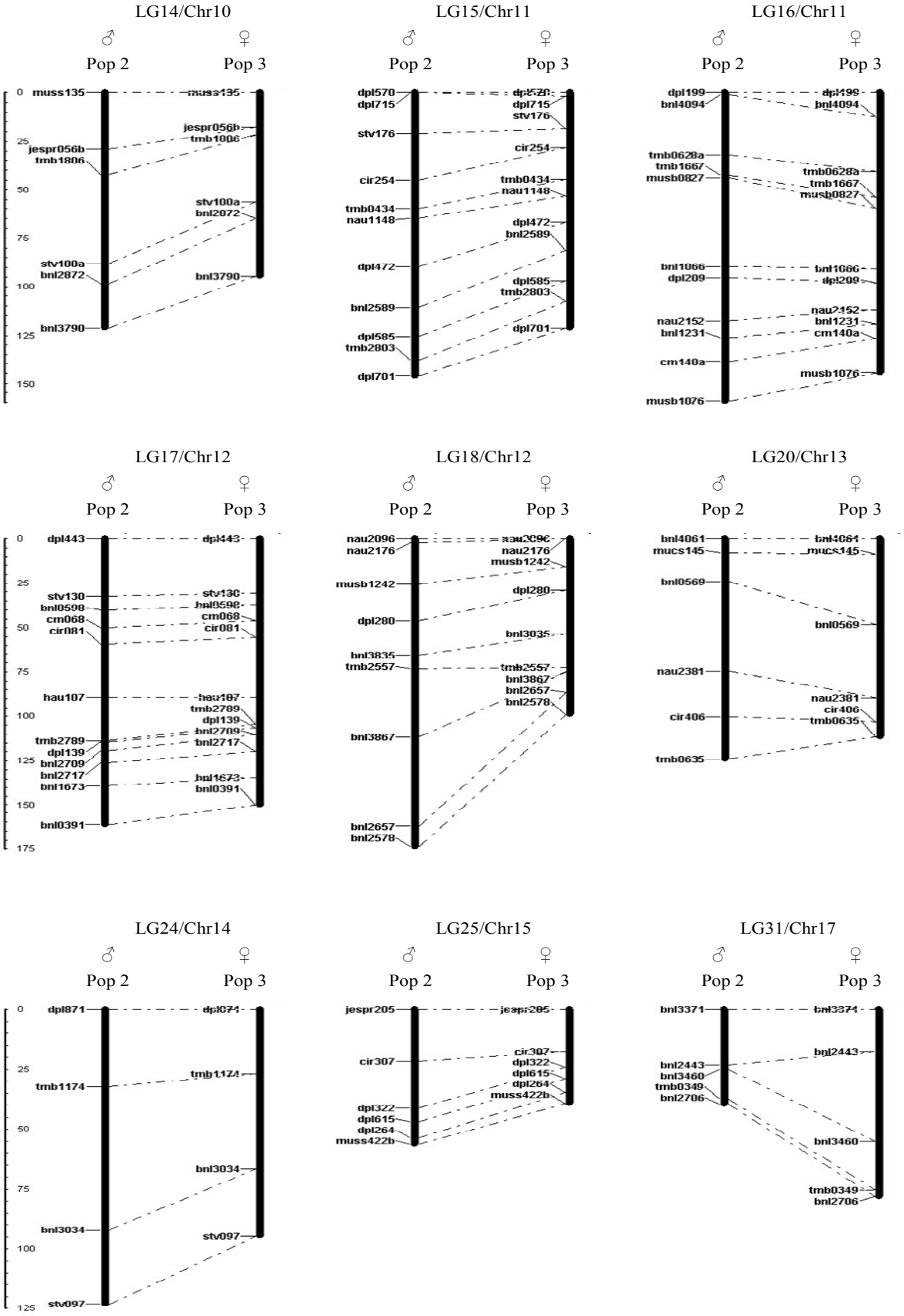
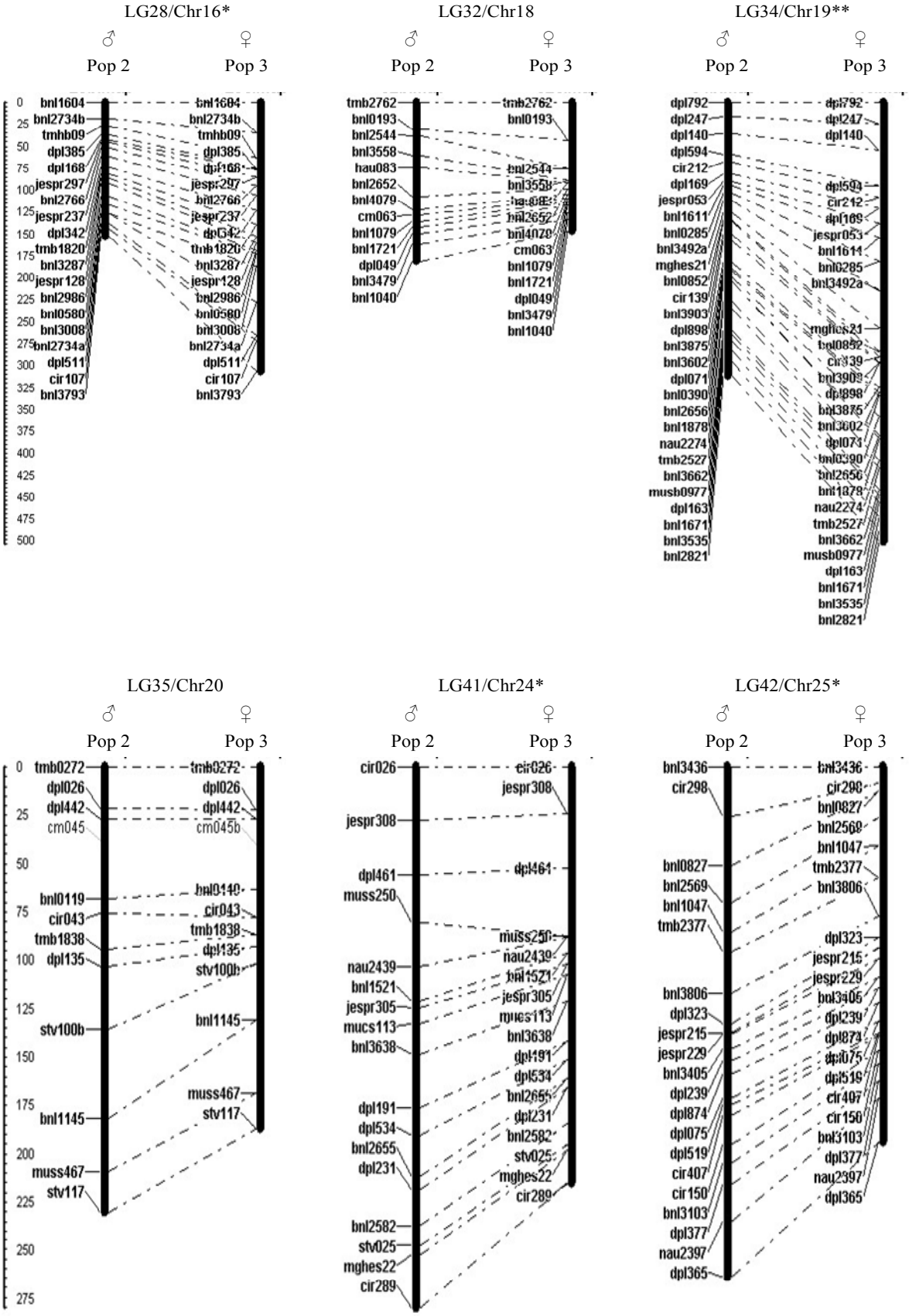
musb0907
dpl550
dpl854
bnl1162
dpl618
dpl679
stv164a
dpl222


LG14/Chr10
♂ Pop 2
♀ Pop 3
0 muss135 muss135
jespr056b
25 tmb1806
jespr056b
tmb1806
50
stv100a
bnl2872
75
stv100a
bnl2872
bnl3790
100
125 bnl3790
150
LG15/Chr11
♂ Pop 2
♀ Pop 3
dpl570
dpl715
stv176
stv176
cir254
cir254
tmb0434
nau1148
tmb0434
nau1148
dpl472
bnl2589
dpl472
dpl585
tmb2803
bnl2589
dpl585
tmb2803
dpl701
dpl701
LG16/Chr11
♂ Pop 2
♀ Pop 3
dpl199
bnl4094
tmb0628a
tmb1667
musb0827
tmb0628a
tmb1667
musb0827
bnl1066
dpl209
bnl1066
dpl209
nau2152
bnl1231
cm140a
nau2152
bnl1231
cm140a
musb1076
musb1076
LG17/Chr12
♂ Pop 2
♀ Pop 3
0 dpl443 dpl443
25
stv130
bnl0598
cm068
50 cir081
stv130
bnl0598
cm068
cir081
75
hau107
tmb2789
dpl139
bnl2709
tmb2789
dpl139
bnl2709
bnl2717
bnl2717
bnl1673
bnl0391
125
bnl1673
150 bnl0391
175
LG18/Chr12
♂ Pop 2
♀ Pop 3
nau2096
nau2176
musb1242
musb1242
dpl280
dpl280
bnl3035
bnl3835
tmb2557
tmb2557
bnl3867
bnl2657
bnl2578
bnl3867
bnl2657
bnl2578
LG20/Chr13
♂ Pop 2
♀ Pop 3
bnl4061
mucs145
bnl0569
bnl0569
nau2381
nau2381
cir406
tmb0635
cir406
tmb0635
LG24/Chr14
♂ Pop 2
♀ Pop 3
0 dpl871 dpl871
25
tmb1174
tmb1174
50
bnl3034
75
bnl3034
stv097
100
125 stv097
LG25/Chr15
♂ Pop 2
♀ Pop 3
jespr205
jespr205
cir307
cir307
dpl322
dpl615
dpl264
muss422b
dpl322
dpl615
dpl264
muss422b
LG31/Chr17
♂ Pop 2
♀ Pop 3
bnl3371
bnl3371
bnl2443
bnl2443
bnl3460
tmb0349
bnl2706
bnl3460
tmb0349
bnl2706


LG28/Chr16*
♂
♀
Pop 2
Pop 3
0 bnl1604 bnl1604
25 bnl2734b bnl2734b
tmhb09 tmhb09
50 dpl385 dpl385
75 dpl168 dpl168
100 jespr297 jespr297
bnl2766 bnl2766
125 jespr237 jespr237
150 dpl342 dpl342
175 tmb1820 tmb1820
bnl3287 bnl3287
200 jespr128 jespr128
225 bnl2986 bnl2986
250 bnl0580 bnl0580
bnl3008 bnl3008
275 bnl2734a bnl2734a
300 dpl511 dpl511
cir107 cir107
325 bnl3793 bnl3793
350
375
400
425
450
475
500
LG32/Chr18
♂
♀
Pop 2
Pop 3
tmb2762 tmb2762
bnl0193 bnl0193
bnl2544 bnl2544
bnl3558 bnl3558
hau083 hau083
bnl2652 bnl2652
bnl4079 bnl4079
cm063 cm063
bnl1079 bnl1079
bnl1721 bnl1721
dpl049 dpl049
bnl3479 bnl3479
bnl1040 bnl1040
LG34/Chr19**
♂
♀
Pop 2
Pop 3
dpl792 dpl792
dpl247 dpl247
dpl140 dpl140
dpl594 dpl594
cir212 cir212
dpl169 dpl169
jespr053 jespr053
bnl1611 bnl1611
bnl0285 bnl0285
bnl3492a bnl3492a
mghes21 mghes21
bnl0852 bnl0852
cir139 cir139
bnl3903 bnl3903
dpl898 dpl898
bnl3875 bnl3875
bnl3602 bnl3602
dpl071 dpl071
bnl0390 bnl0390
bnl2656 bnl2656
bnl1878 bnl1878
nau2274 nau2274
tmb2527 tmb2527
bnl3662 bnl3662
musb0977 musb0977
dpl163 dpl163
bnl1671 bnl1671
bnl3535 bnl3535
bnl2821 bnl2821
LG35/Chr20
♂
♀
Pop 2
Pop 3
0 tmb0272 tmb0272
dpl026 dpl026
25 dpl442 dpl442
cm045 cm045b
50
bnl0119 bnl0119
75 cir043 cir043
tmb1838 tmb1838
100 dpl135 dpl135
stv100b stv100b
125
stv100b bnl1145
150
muss467
175 bnl1145 stv117
200
muss467
stv117
225
250
275
LG41/Chr24*
♂
♀
Pop 2
Pop 3
cir026 cir026
jespr308 jespr308
dpl461 dpl461
muss250 muss250
nau2439 nau2439
bnl1521 bnl1521
jespr305 jespr305
mucs113 mucs113
bnl3638 bnl3638
dpl191 dpl191
dpl534 dpl534
bnl2655 bnl2655
dpl231 dpl231
bnl2582 bnl2582
stv025 stv025
mghes22 mghes22
cir289 cir289
LG42/Chr25*
♂
♀
Pop 2
Pop 3
bnl3436 bnl3436
cir298 cir298
bnl0827 bnl0827
bnl2569 bnl2569
bnl1047 bnl1047
tmb2377 tmb2377
bnl3806 bnl3806
dpl323 dpl323
jespr215 jespr215
jespr229 jespr229
bnl3405 bnl3405
dpl239 dpl239
dpl874 dpl874
dpl075 dpl075
dpl519 dpl519
cir407 cir407
cir150 cir150
bnl3103 bnl3103
dpl377 dpl377
nau2397 nau2397
dpl365 dpl365

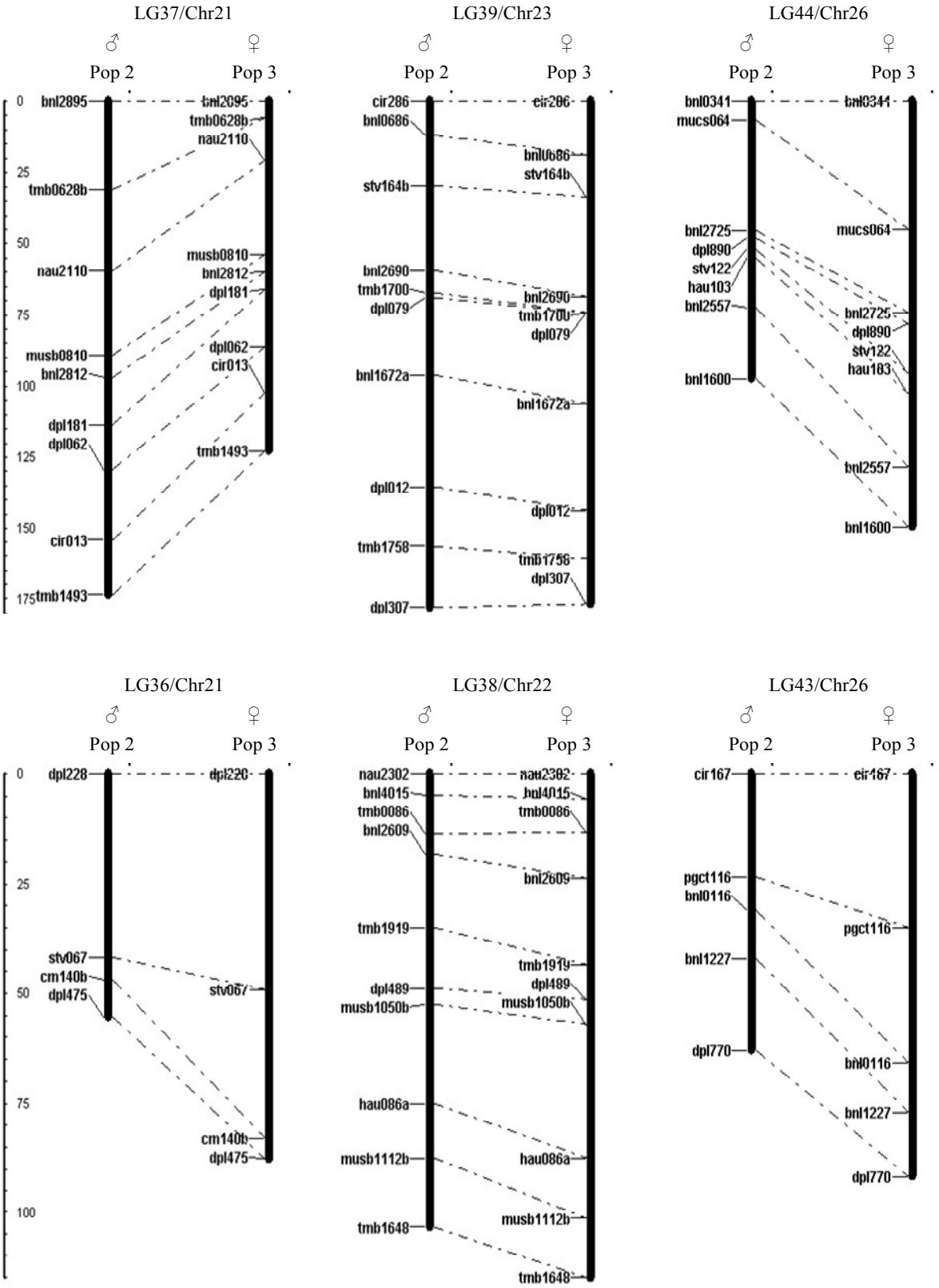


Fig. 1. The genetic linkage maps of 313 markers for Pop 2 and Pop 3 which reflect the recombinant rates of female and male gametes, respectively.
(♀and ♂represent the genetic maps of Pop 2 and Pop 3, respectively. LGs with * and ** showed significant difference between Pop 2 and Pop 3 at the 0.05 and 0.01 probability level, respectively.)

Influences of male versus female gametes on recombinant rate of chromosomes: Since both recurrent parents were homozygous, recombination measured in each population reflects crossing-over rates leading to male and female gametes (de Vicente & Tanksley 1991). Chromosome length differences between Pop 2 and Pop 3 were very small on LG04/Chr03, LG09/Chr06, LG12/Chr08 and LG39/Chr23. However, there were some greatly different marker intervals (MLs) on these LGs/Chrs, the complementation of MLs made the smaller differences of the entire LGs/Chrs (Fig. 1). The other LGs/Chrs showed obvious difference between these two populations, which were derived from the big different MLs or the accumulation of small different MLs. However, the overall length of the two maps was not significant different, and the average distance between two markers of the entire map was also not significant different (Table 1).

Among the 30 LGs, the map lengths of 21 LGs were longer in Pop 2 than those in Pop 3, and 9 LGs shorter. Six LGs were significantly different between the two populations by t-test, among which LG01/Chr01 and LG34/Chr19 were different at P <0.01 (Table 1). The map lengths of three LGs, LG01/Chr01, LG41/Chr24 and LG42/Chr25 were longer in Pop 2; LG13/Chr09, LG28/Chr16 and LG34/Chr19 were longer in Pop 3, which were caused by male and female gametes, respectively.

There was respective one different LG caused by male and female gametes in the At sub-genome of cotton and respective two LGs in the Dt sub-genome, which indicated that the influence of male and female gametes on the At and Dt sub-genomes was not specific (Table 1). However, it seemed that chromosomes on the Dt sub-genome were more sensitive to the recombination rate of gametes.

Influences of male and female gametes on recombinant rate of MLs: Fig. 1 showed that there were many MLs with large difference between Pop 2 and Pop 3, 2×2 contingency chi-square test was used to identify whether these differences were significant. Compared to Pop 3, four MLs were significantly different in Pop 2, which were caused by male gametes. One shorter ML was located on LG38/Chr19, and three longer MLs on LG31/Chr21, LG37/Chr22 and LG41/Chr24, respectively (Table 2). In Pop 3, a total of 13 MLs were significantly different compared to Pop 2, which were caused by female gametes. There were 11 shorter MLs: two located on LG03/Chr02, one on LG13/Chr09, one on LG20/Chr13, five on LG34/Chr19, one on LG39/Chr23, one on LG41/Chr24; two longer MLs located on LG24/Chr14 (Table 2). In addition, some obviously different MLs such as TMB2557-BNL3867 on LG18/Chr12, BNL2443-BNL3460 on LG31/Chr17, BNL0341-MUCS064 on LG44/Chr26 and STV067-CM140b on LG36/Chr21 were observed in Fig. 1, however, their differences were not significant by 2×2 contingency chi-square test, which indicated that these differences were not caused by male and female gametes.

Table 2 Marker intervals with significant differences between the recombinant rates of female and male gametes (P<0.05)

Population	LG/Chr	Marker interval	Genetic distance		male/ female
			Pop 2	Pop 3	
Pop 2	LG31/Chr17	BNL3371-BNL2443	23.2	17.7	1.31
	LG37/Chr21	BNL2895-TMB0628b	31.1	5.7	5.46
	LG38/Chr22	HAU086a-MUSB1112a	12.7	13.9	0.91
	LG41/Chr24	MUCS113-BNL3638	15.7	13.6	1.15
Pop 3	LG03/Chr02	DPL674-BNL1410	9.6	20.6	0.47
	LG03/Chr02	BNL1410-BNL2651	22.3	36.7	0.61
	LG13/Chr09	DPL395-BNL290	29.7	41.0	0.72
	LG20/Chr13	MUCS145-BNL0569	16.8	39.7	0.42
	LG24/Chr14	TMB1176-BNL3034	59.6	39.7	1.50
	LG24/Chr14	BNL3034-STV097	31.1	28.1	1.11
	LG34/Chr19	DPL247-DPL140	20.1	29.4	0.68
	LG34/Chr19	BNL1611-BNL0285	8.7	26.8	0.32
	LG34/Chr19	BNL0285-BNL3492a	7.7	33.5	0.23
	LG34/Chr19	BNL3492a-EMS21	13.7	43.2	0.32
	LG34/Chr19	EMS21-BNL0852	8.7	28.1	0.31
	LG39/Chr23	STV164b-BNL2690	29.7	35.0	0.85
	LG41/Chr24	DPL461-MUSS250	24.7	35.0	0.71

Discussion

In order to study the impacts of the recombination rate of male and female gametes on the map construction in cotton, another two genetic maps were constructed based on constructed backbone interspecific linkage map (Zhang *et al*., 2008). Because both recurrent parents were homozygous, these two maps represent the recombination rates of the male and female gametes. One co-dominant SSR markers every 10-20cM was picked out on the backbone genetic map and a total of 347 markers were selected. The resulting male and female maps both included 30 linkage groups and 313 loci, and covered 83.1% and 81.9% of the backbone genetic map, respectively. So, these two maps could reflect the genome-wide recombination rate of the male and female gametes. The total map length, sub-genomic marker distribution, average marker interval and big gaps were

similar between the two maps, which showed that the recombination rate of the male versus female gametes had no significant influence on the whole genetic map construction in cotton. Similar results were also reported by Busso *et al*., (1995).

Although no significant differences on the entire maps were detected between the recombination rate of the male and female gametes, some LGs/Chrs were significantly influenced. Among the two maps, differences existed on almost all of the LGs/Chrs and every MLs on each LGs/Chrs. LGs/Chrs with relatively small differences were due to the complementary results of larger-difference MLs. While, LGs/Chrs with greatly differences were directly caused by larger-difference MLs or by the accumulation of small-difference MLs. However, LGs/Chrs with big differences were not all caused by recombination rate of the male and female gametes, t-test revealed that only 6 LGs/Chrs were significantly different, indicating that the recombination rate of the male and female gametes only affected some LGs/Chrs in cotton genetic linkage map construction.

The LGs/Chrs affected by the recombination rate of male and female gametes respectively were all 3, indicating that there was no proneness for them to the genetic length of chromosomes, which was not in consistent with the results in tomato (de Vicente & Tanksley 1991) and barley (Wang *et al*., 1995). Although the impacts of male and female gametes on At and Dt sub-genome were not specific, affected LGs/Chrs in Dt sub-genome were more than in At sub-genome; In addition, MLs the affected by male and female gametes were significantly more in Dt sub-genome than in At sub-genome. This phenomenon is related to the origin of the 2 sub-genome of tetraploid cotton. Previous studies conclude that At sub-genome origins from the cultivated species of *Gossypium herbaceum* or *G. arboretum* which have been domesticated for a long time, and more selection pressure was imposed which lead the species to a more stable genome; while Dt sub-genome origins from the wild species of *G. raimondii* and its' genome is still active (Guo *et al*., 2007).

Among all of the MLs with great difference of genetic distance, their differences were not all caused by male and female gametes. Only 17 MLs were due to gamete recombination rate by 2×2 contingency chi-square test. By comparing genetic distances of corresponding MLs in the two maps, we found that the genetic distances of some MLs were similar, but the 2×2 contingency chi-square test showed that it was significantly different; however, genetic distances in some MLs were greatly different, but their differences were not significant. So, the recombination rate of male and female gametes were not the only causes for the differences of MLs as well as the chromosomes, there should be some other factors, such as the environment (Wang *et al*., 1995).

In traditional breeding, backcross breeding is an important breeding method. Generally, (A × B) × A or × B cross is used in cotton breeding. The results of this study showed that male gametes usually resulted in a longer genetic distance of cotton genetic linkage map, i.e., increase the recombination rates; female gametes usually resulted in a shorter genetic distance of cotton genetic linkage map, i.e., decrease the recombination rates. Therefore, the cross of A or B × (A × B) is more beneficial to produce more recombinant genotypes, and to produce more variation in cotton breeding. However, for molecular marker-assisted selection, the cross of (A × B) × A or × B is conducive to decrease recombination rates, and the higher linkage between the target traits and the selection marker, which can improve the efficiency of molecular-assisted selection.

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