Turkish Journal of Botany

Volume 37 | Number 5 Article 2

1-1-2013

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TÜBİTAK

Turkish Journal of Botany

http://journals.tubitak.gov.tr/botany/

Research Article

Turk J Bot
(2013) 37: 802-810

doi:10.3906/bot-1209-47

QTL mapping of some productivity and fibre traits in *Gossypium arboreum*

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Received: 24.09.2012 • **Accepted:** 29.04.2013 • **Published Online:** 06.09.2013 • **Printed:** 30.09.2013

Abstract: This study explains the construction of an intraspecific genetic linkage map of the A-genome diploid cotton with simple sequence repeat (SSR) and randomly amplified polymorphic DNA (RAPD) markers, using 180 F_2 plants derived from the cross of 2 *Gossypium arboreum* cotton cultivars (Ravi × Entry-17). Polymorphisms between the 2 parents were detected using 1089 pairs of SSR primers and 520 RAPD primers. In total, 34 pairs of SSR primer-amplified and 18 RAPD primer-amplified polymorphic loci were selected to survey the F2 population. In total, 52 polymorphic DNA fragments were generated and used to construct a linkage map with JoinMap 3.0. A total of 45 loci and 5 phenotypic traits were mapped at a logarithm of odds ratio of ≥3.0 on 10 linkage groups. The total length of the map was 346 cM, and the average distance between adjacent markers was 7.7 cM. Chromosome assignments were made according to previous studies. In total, 7 quantitative trait loci (QTLs), including 5 for productivity traits and 2 for fibre traits, were mapped. Identification of these QTLs will set the stage for initiating marker-assisted selection and map-based cloning in cotton.

Key words: Diploid cotton, *Gossypium arboreum*, simple sequence repeats, genetic map, quantitative trait loci, fibre, productivity traits

1. Introduction

A-genome species of cotton including *Gossypium arboreum* L. and *Gossypium herbaceum* L., also called Asiatic cottons, are considered "Old World" cotton crops. In India and Pakistan, Asiatic cotton is still successfully planted in some regions with mediocre soil environments and rough management conditions (Guo, 2006; Rahman et al., 2009, 2011, 2012). In China, *Gossypium arboreum* has also been domesticated and cultivated for almost 2000 years since it was first introduced from India (Xiang, 1989). The significance of *G. arboreum* is derived from several favourable traits for cotton production, which the upland cotton cultivars lack. For example, drought tolerance and resistance to diseases like root rot and insect pests like bollworms and aphids (Mehetre, 2003) make *G. arboreum* well adapted to dry land conditions and low input cultivation practices. Another fascinating characteristic of natural *G. arboreum* fibres is the presence of various colours (e.g., white, milky, beige, and brown). Many Chinese *G. arboreum* accessions produce fibres with high strength and seeds with a high oil content and seed index. For efficient use of *G. arboreum* resources in the development of superior cotton cultivars with favourable agronomic traits, understanding the genetic relationships of *G. arboreum* is important (Liu, 2006), and for efficient use of these gene resources in cotton breeding a regular genetic assessment of the gene resources will help to decrease the redundancy and construct a core germplasm collection (Kantartzi, 2006).

Evaluation of the genetic diversity of landraces in *G. arboreum* L. race *sinense* using simple sequence repeats (SSRs) (Guo et al., 2006, 2007; Liu et al., 2006) has shown a higher level of genetic variation at the DNA level among the *G. arboreum* accessions than among *Gossypium hirsutum* L. accessions. The genetic diversity information for Asiatic cotton is useful for developing mapping populations for construction of an A-genome diploid cotton genetic linkage map and tagging economically important traits (Ma et al., 2008).

Although the A-genome has not been widely explored for mapping, there are few reports on genome mapping in *G. arboreum* and *G. herbaceum* (Desai et al., 2006). The first elaborative intraspecific genetic linkage map of A-genome diploid cotton (*Gossypium arboreum* L.), Jianglingzhongmian × Zhejiangxiaoshanlushu, was developed by Ma et al. (2008). In the present study we have developed an intraspecific genetic linkage map of *G. arboreum* and used it for QTL mapping of productivity traits.

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2. Materials and methods

2.1. Plant materials and population generation

We developed an F_2 population of 180 individuals derived from the intraspecific hybrid between 2 *Gossypium arboreum* cultivated species, namely *Gossypium arboreum* L. 'Ravi' and *G. arboreum* L. 'Entry-17' (AA, 2n = 4x = 26). Ravi and Entry-17 (E-17) were crossed in 2006. F_1 seeds were grown to raise F_2. The 180 F_2 plants were grown in the National Institute for Biotechnology and Genetic Engineering (NIBGE) fields in 2007, and DNA was isolated from F_2 individual plants. The next year, the $F_{2:3}$ of each of the F_2 plants was grown in the cotton field of NIBGE, Faisalabad, Pakistan in randomised complete block design with 3 replications. In each replication we ensured 15 plants with a plant-to-plant distance of 25 cm, and the row-to-row distance was 75 cm. Standard agronomic practices were applied until maturity (Rahman & Zafar, 2012).

2.2. Morphological markers

Five phenotypic traits were scored for the presence of the codominant allele of the 2 *G. arboreum* cultivars' parents segregating in the F_2 and $F_{2:3}$ populations. The morphological markers scored were sympodia length (cm), number of sympodia per plant, and boll weight, as collected at maturity. The average number of sympodial branches was calculated by counting them from all the plants of each family and dividing by the total number of plants in each replication. The average boll weight was calculated by picking the seed cotton from all the plants in each family in each replication. The staple length and uniformity ratio were measured using a high-volume instrument.

2.3. DNA extraction, SSR amplification, and electrophoresis

DNA was isolated from young leaf tissues from both parents and every individual F_2 in the mapping population, following the methods of Iqbal et al. (1997). PCR amplifications were done on a Master Gradient Thermal Cycler, and products were analysed by electrophoresis. A total of 1089 pairs of SSR primers were used to screen polymorphisms between Ravi and E-17. These SSR primers included BNL, JESPR, CIR, TM, CM, and PGMB (Reddy et al., 2001; Han et al., 2004, 2006; Qureshi et al., 2004; Park et al., 2005; Shaheen et al., 2013); they are available at http://www.cottonssr.org.

2.4. Data analysis

The maternal (Ravi), paternal (E-17), and F_1 heterozygous genotypes of the F_2 population were scored as 1, 2, and 3, respectively. Missing data were designated as 0. The computer software JoinMap 3.0 (Van Ooijen & Voorrips, 2001) was used for the chi-square test, used to test markers for the 1:2:1 segregation ratio expected in the F_2 population with codominant markers or for the 3:1 segregation ratio expected with dominantly scored markers and map construction. First, a subset of markers with a minimum of missing data, excluding those without significant segregation ratio distortion, was used to construct an initial framework using a logarithm of odds ratio (LOD) score threshold of 3.5–15.0. The Kosambi (1994) mapping function was used for calculation of the pairwise distance. Chromosome assignments were done according to the method of Wang et al. (2006) using the similar SSR loci.

For quantitative trait loci (QTL) mapping, composite interval mapping (CIM) was utilised using Windows QTL Cartographer software (Wang et al., 2007). A LOD score of ≥3.0 was used to declare the presence of a putative QTL in a given genomic region in the CIM analysis, considering that high environmental effects could have influenced the power of detection of the QTLs.

3. Results

A total of 1089 SSR primer pairs including 74 EST-derived (prefix MGHES) and 1015 genomic sequence-based SSRs (prefix JESPR: 200, TM: 334, CIR: 150, BNL: 280, PGMB: 23, and CM: 28) were used to detect potential polymorphic markers in parent genotypes that could be used in genetic map construction and QTL analysis. In total, 2.7% of MGHES (EST-SSRs), 0.5% of JESPR, 2.37% of TM, 4.6% of CIR, 5% of BNL, and 2% of CM primer pairs were polymorphic. Twenty-three SSR primer pairs, developed in our laboratory (prefix PGMB; Plant Genomics and Molecular Breeding Laboratories, NIBGE, Faisalabad, Pakistan) were also surveyed in parents, revealing no informative primer pairs. A total of 1245 alleles were produced from 1089 amplified primer pairs, producing 1.14 alleles per primer. In total, 34 (3.12%) polymorphic SSR primer pairs were identified out of 1089 successfully amplified SSR primer pairs in parental lines. These informative SSR primer pairs generated a total of 52 different loci (19 primer pairs each amplified a single locus, 13 primer pairs each produced 2 loci, 1 primer pair generated 3 loci, and 1 primer amplified 4 loci) with an average of 1.52 loci per primer pair. Among the 34 SSRs surveyed on the mapping population, 33 loci segregated codominantly, whereas 1 of the markers was dominant. A total of 6 loci (17%) showed distorted segregation when subjected to a chi-square goodness-of-fit test for the expected Mendelian segregation ratio of 1:2:1 and 1:3 for codominant and dominant markers, respectively.

In randomly amplified polymorphic DNA (RAPD) analysis using arbitrary decamer oligonucleotide primers, a total of 520 RAPD primers were employed to screen Ravi and E-17, parents of the intraspecific F_2 population. As a result, 18 primers were informative, indicating a low level of polymorphism (3.46%). The surveyed RAPD primers produced 2466 amplicons with an average of 4.74

amplicons per primer. The 18 DNA markers identified through RAPD profiling, varying in size from 270 to 1000 bp, were used for genotyping 180 F_2 individuals. All the loci segregated dominantly. Around 20% of the loci showed distorted segregation in the mapping population.

A total of 52 DNA markers including 34 SSR and 18 RAPD were genotyped on the F_2 mapping population, and data were utilised for linkage analysis and map construction. Linkage analysis resulted in the mapping of 45 loci (27 SSRs, 18 RAPDs) on 10 different linkage groups (LGs) ranging from 10 to 68 cM in length. The remaining 7 markers were unlinked. The resulting linkage groups were numbered LG1–LG10 in descending order of length (Figure 1). The 10 linkage groups ranged from 2 to 10 markers with an average length of 33.9 cM. The map spanned a total of 346.3 cM, covering about 10% of the total *G. arboreum* genome, and the average distance between adjacent markers was 7.7 cM (Table 1). The linkage groups LG5 and LG9 were composed entirely of SSRs. Other groups comprised both RAPDs and SSRs. Nine of the linkage groups were assigned to 9 chromosomes of the cotton genome based on the presence of SSRs (BNL3008, BNL3582, BNL1162, BNL827, BNL3255, BNL1438, CIR222, CIR19, CIR141, CIR156, CIR272) mapped to specific chromosomes by aneuploid analysis (Liu et al., 2000) or assigned to chromosomes by linkage analysis (Lacape et al., 2003; Nguyen et al., 2004; Song et al., 2005). The haploid genome sizes are estimated to be approximately 880 Mb for *G. raimondii* Ulbrich, 1.75 Gb for *G. arboreum*, and 2.5 Gb for *G. hirsutum* (Hendrix & Stewart, 2005). Interval mapping analysis was employed to determine chromosomal location of genes impacting productivity traits and yielded 6 QTLs for 4 traits. Composite interval mapping located 3 QTLs for 3 traits (Table 2).

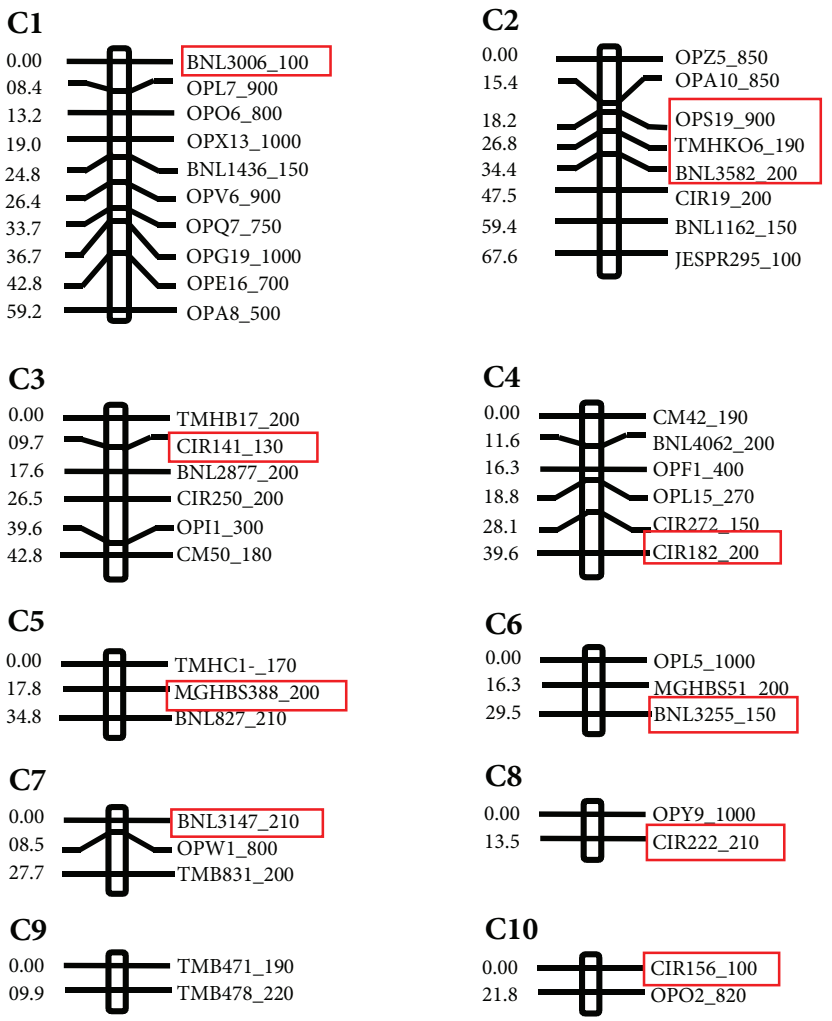

Figure 1. Genetic linkage map of *G. arboreum* constructed using the F_2 population derived from intraspecific cross Ravi × E-17. Marker names are given on the right and the position of 27 SSR and 18 RAPD loci on the left (in cM) (Kosambi, 1944). The fragment sizes of RAPDs (in base pairs) are given next to the marker name. SSR markers used to assign the chromosomes are boxed.

Table 1. Distribution of molecular markers on the genetic map of cotton constructed using the F_2 population derived from intraspecific cross Ravi × E-17.

Linkage group	Assigned chromosome	No. of marker loci	Percentage of marker loci	Length (cM)	Marker density
1	Chr. 16 or D07	10	22.2	59.2	6
2	Chr. 9 or A09	8	17.7	67.6	8.5
3	Chr. 7 or A07	6	13.4	42.8	7.13
4	A12 or Chr. 12	6	13.4	39.6	7
5	Chr. 25 or D6	3	6.7	34.8	11.6
6	A02 or Chr. 2	3	6.7	29.5	9.8
7	A03 or Chr. 3	3	6.7	27.7	9.2
8	Chr. 4 or A04	2	4.4	13.5	7
9	-	2	4.4	9.9	4.95
10	D02 or Chr. 14	2	4.4	21.7	11
Total		45	100	346.3	7.7

Table 2. Information regarding the putative QTLs detected (QTL Cartographer v. 2.5).

Trait	QTL	LG[(1)] (chrom)	Nearest marker	QTL[(2)] position	LOD[(3)] score	Additive effect	$R^{2(4)}$ (%)
Sympodia length	*Sm*	1(16)	OPX13_1000	19.03	3.27	–0.8918	5.0
Nodes to sympodia	*Ns*	1(16)	BNL1438_150	24.8500	4.0577	–5.19	31.0
Staple length	*Sla*	2(9)	BNL1438_150	40.7100	16.2	–1.04	14.9
	Slb	2(9)	OPV6_900	53.4900	20.2	–1.04	14.9
Uniformity index	*Ua*	2(9)	BNL1438_150	40.7100	4.4	–3.67	9.7
	Ub	2(9)	OPV6_900	55.4900	4.6	–4.23	15.4
Boll weight	*B*	9	TMB471_190	0	4	0.65	22.4

[1]: Linkage group/chromosome.
[2]: Position (in cM) from top of the linkage group/chromosome.
[3]: Log of odds scores.
[4]: Phenotypic variation explained.

4. Discussion

In the construction of genetic maps and molecular tagging, SSRs have been extensively utilised (Zhang et al., 2002; Nguyen et al., 2004; Song et al., 2005; Han et al., 2006; Abdurakhmonov et al., 2007; He et al., 2007; Shen et al., 2007; Zhang et al., 2008; Wu et al., 2009; Doğan et al., 2011; Achrem et al., in press). About 92% of SSR primer pairs used in this study amplified a single amplicon from both parents, which was expected because multiple-locus amplification is a common phenomenon in allopolyploids like *Gossypium hirsutum* and may be related to fusion of the A and D genomes and chromosome duplication events during evolution (Buteler et al., 1999) because this is a diploid species. Dominant loci may result from null alleles. By definition, a microsatellite null allele is an allele at a microsatellite locus that consistently fails to amplify during PCR and, thus, is not detected when individuals are genotyped (Dakin & Avis, 2004; Ma et al., 2008). In this study we observed 3.12% polymorphism intraspecifically with SSRs, which is comparable to findings of a study by Ma et al. (2008) in which 4.4% polymorphism was observed intraspecifically in *G. arboreum* Jianglingzhongmian × Zhejiangxiaoshanlushu.

RAPD analyses also showed results similar to SSR analysis and revealed a relatively low percentage of polymorphism (3.64%) between the parent genotypes used to develop mapping populations in this study. The low level of polymorphism revealed in the present study by SSR and RAPD analyses illustrated the narrow genetic base of modern cotton cultivars. This finding is supported by some earlier studies on genetic diversity in cotton that showed high similarity among *G. arboreum* cultivars/genotypes (Rana & Bhat, 2004; Vafaie-Tabar et al., 2004; Rahman et al., 2008). This low level of polymorphism can be attributed to the processes of domestication and selection, which have resulted in a drastic narrowing of genetic variation in cotton (Rahman et al., 2008).

Interspecific linkage maps of diploid cottons have been constructed for the A-genome (*G. herbaceum* × *G. arboreum*), D-genome (*Gossypium trilobum* × *Gossypium raimondii*) (Brubaker et al., 1999; Rong et al., 2004; Desai et al., 2006; Niu et al., 2008), and G-genome (*Gossypium nelsonii* × *Gossypium australe*) taxa (Brubaker & Brown, 2003). A-genome *Gossypium* species exhibit low levels of polymorphism in comparison with the D-genome species, which is a major constraint in the development of a high-density A-genome map (Brubaker et al., 1999; Rong et al., 2004). A larger number of SSR markers are now available to overcome the constraint of low levels of polymorphism in the A-genome. To better understand the cotton genome and facilitate genomic research, Ma et al. (2008) developed the first intraspecific Asiatic cotton genetic map using 267 SSR loci in an F_2 population derived from a cross of *G. arboreum* cultivars.

In the present study, an intraspecific F_2 population consisting of 180 plants was used to generate a genetic map. A linkage map of 27 SSR and 18 RAPD markers scored in the mapping population was developed to facilitate QTL analysis. The map comprised 10 linkage groups and spanned 346 cM, around 10% of the total 3260 cM of recombinational length of the *G. arboreum* genome (Ma et al., 2008). In an earlier intraspecific genetic map of *G. arboreum* reported by Ma et al. (2008), 2508.71 cM of the *G. arboreum* genome was covered by 268 polymorphic SSRs. Interspecific maps of A-genome map coverage ranged from 1216 cM to 1147 cM (Desai et al., 2006; Niu et al., 2008).

The average distance between adjacent markers on the map was 7.7 cM, which is in agreement with the best confidence interval of 10 cM proposed for QTL detection (Kearsey, 1998; Kearsey & Farquhar, 1998). Nine of the linkage groups have been assigned to 9 chromosomes of the cotton genome based on the presence of SSRs mapped to specific chromosomes by aneuploid analysis (Liu et al., 2000) or have been assigned to chromosomes by linkage to such SSRs (Lacape et al., 2003; Nguyen et al., 2004; Song et al., 2005). One linkage group could not be assigned to any chromosome due to a lack of reference marker. Three of the linkage groups were assigned to the Dt genome while 6 were assigned to the At genome, according to the modern classification of tetraploid cotton chromosomes (Wang et al., 2006). A-genome chromosomes are largely collinear with the At and Dt subgenome chromosomes. Similar results were obtained by Desai et al. (2006) and Ma et al. (2008). The interchromosomal duplicated loci supply molecular evidence that A-genome diploid Asiatic cotton is paleopolyploid (Desai et al., 2006; Ma et al., 2008).

In the present study, 17% of polymorphic SSR loci and 20% of RAPD loci showed skewed segregation in the mapping population. Skewed segregation ratios have been reported frequently in cotton (Ulloa et al., 2002, 2005; Lacape et al., 2003; Mei et al., 2004; Desai et al., 2006).

We have detected 4 QTLs for fibre traits placed on chromosome 9 or A09 according to the classification by Wang et al. (2006) of tetraploid cotton chromosomes: 2 for staple length, accounting for 29.8% of phenotypic variation, and 2 for uniformity index, accounting for 25.1% of the total phenotypic variation. QTLs *sla* and *Ua* for the fibre traits of staple length and uniformity index, respectively, were placed in the same chromosome region; QTLs *Slb* and *Ub* for staple length and uniformity index, respectively, were also placed in the same chromosome region (Figure 2). In earlier studies, QTLs affecting different fibre-related traits were detected within the same chromosome regions, suggesting that genes controlling fibre traits may be linked or the result of pleiotropy. Abdurakhmonov et al. (2007) reported that QTLs associated with lint percentage were located on chromosomes 12, 18, 23, and 26 in tetraploid cotton. The studies of Park et al. (2005) on genetic mapping of fibre loci using EST-derived microsatellites in an interspecific recombinant inbred line population of *G. hirsutum* suggested that chromosomes 2, 3, 15, and 18 may harbour genes for traits related to fibre quality. Further investigation by Frelichowski et al. (2006) revealed that, apart from the above-mentioned chromosomes, loci on chromosome 12 may also affect variation in fibre quality traits. Our results indicate that fibre-related traits may also be present on *G. arboreum* chromosome A09, which corresponds to chromosome 9 of *G. hirsutum*.

Despite the fact that the *G. arboreum* genome has not been extensively utilised for QTL mapping, QTLs controlling fibre traits have also been identified and mapped to progenitor subgenomes At and Dt (Jiang et al., 1998; Han et al., 2004; Mei et al., 2004; Lin et al., 2005).

A total of 2 QTLs were determined for sympodial length, accounting for 6% of the variability of the trait, and nodes to sympodia, accounting for 30% variability of the trait on linkage group 1, corresponding to chromosome 16 or D07. The results obtained in the present study are congruent with the study of Guo et al. (2008), in which

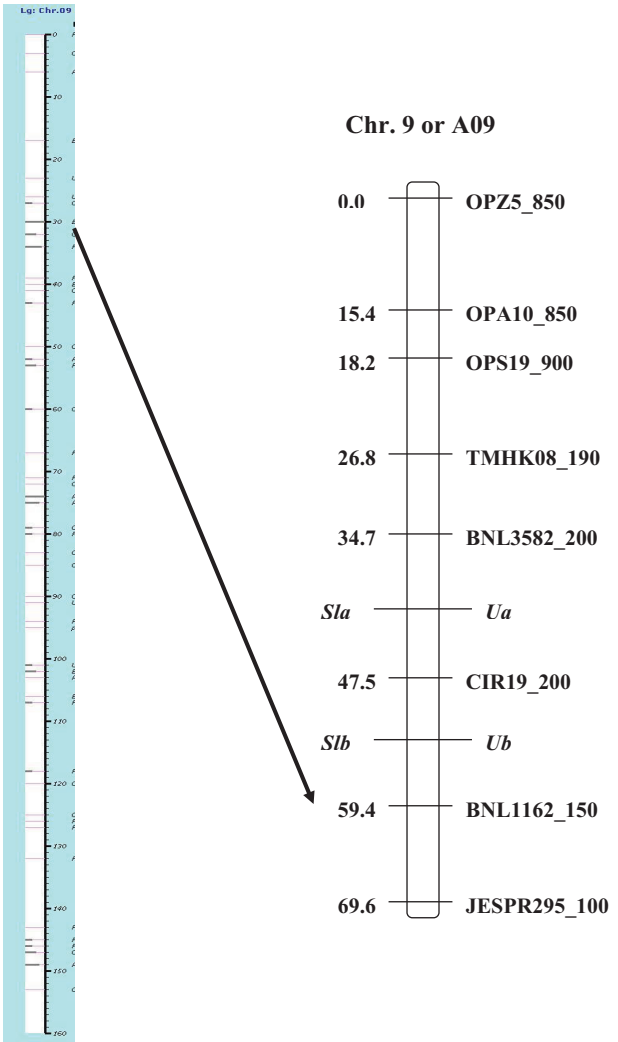

Figure 2. Position of QTLs associated with staple length (*Sl*) and uniformity index (*U*) on genetic linkage map of cotton constructed using the F_2 population derived from intraspecific cross Ravi × E-17. Positions of QTLs were identified with log of odds ratio of ≥3.0 in QTL Cartographer v. 2.5.

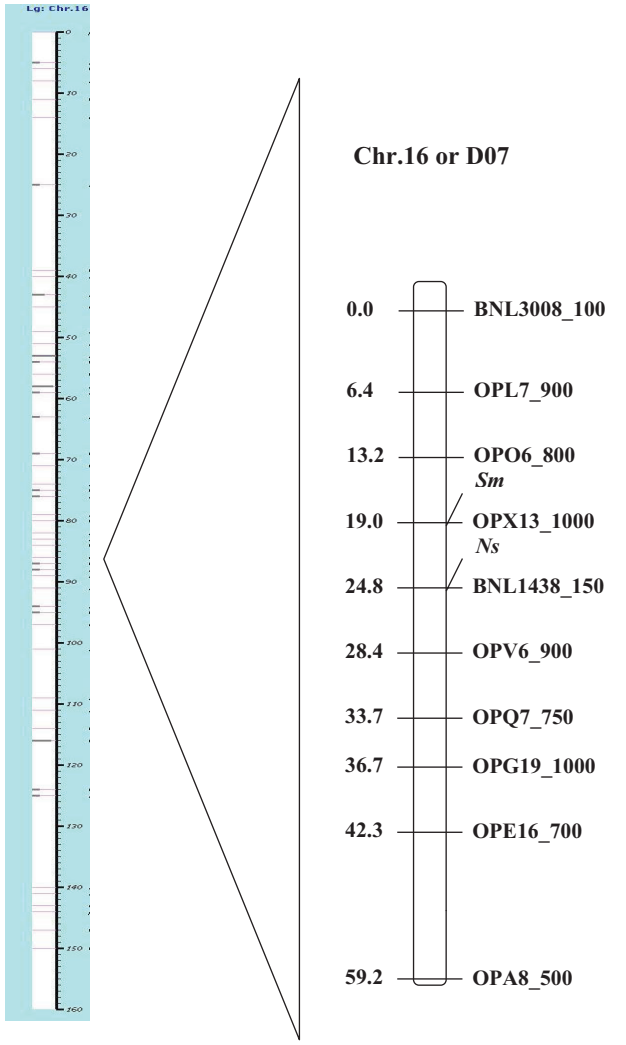

Figure 3. Position of QTLs associated with sympodia length (*Sm*) and nodes to sympodia (*Ns*) on genetic linkage map of cotton constructed using the F_2 population derived from intraspecific cross Ravi × E-17. Positions of QTLs were identified with log of odds ratio of ≥3.0 in QTL Cartographer v. 2.5.

molecular markers were used to locate QTLs for the node of first fruiting branch in *G. hirsutum*, and 3 significant QTLs were mapped to chromosomes 16, 21, and 25 while 2 suggestive QTLs were mapped to chromosomes 15 and 16 using interval mapping and multiple QTL mapping. The presence of QTLs for both traits, sympodia length and nodes to sympodia, on the same chromosome (Figure 3) highlights the presence of related traits on the same chromosomes, as reported earlier for fibre traits and yield traits (Guo et al., 2008).

Mapping of yield components yielded 1 QTL for boll weight in LG9, explaining 22.4% of the total phenotypic variance (Figure 4). This is in agreement with results of Jiang (2004) in *G. hirsutum*, in which only 1 QTL for the trait, explaining 8.5% of the total phenotypic variance, was detected. Correspondence of the *G. arboreum* linkage group with the Dt genome chromosome suggests that there are complex evolutionary relationships among the A, At, D, and Dt genomes.

In conclusion, QTLs are considered to be an effective means to assess genetic control of quantitative traits. QTLs identified in the present study will not only be useful in cotton breeding programs but will also be instrumental in identifying genes conferring staple length using map-based cloning strategies. The information regarding the QTLs discovered in *G. arboreum* is important because there are few QTLs identified using intraspecific populations, and the species is one the progenitors of the cultivated cotton

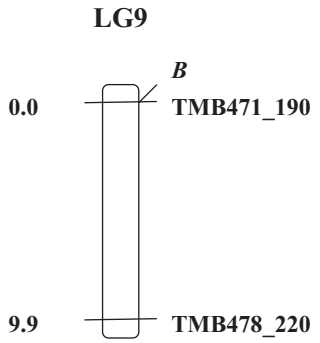

Figure 4. Position of QTLs associated with boll weight (*B*) on genetic linkage map of cotton constructed using the F_2 population derived from intraspecific cross Ravi × E-17. Positions of QTLs were identified with log of odds ratio of ≥3.0 in QTL Cartographer v. 2.5.

species *G. hirsutum*. The cotton genome of *G. raimondii* has been released by 2 independent laboratories. The genome sequence of another important cotton species, *G. arboreum*, will be released next year. Thus, genetic information about these 2 species will not only be instrumental in helping us understand the complex genetics of fibre, but will also pave the way for drawing evolutionary conclusions about fibre traits.

Acknowledgements
We are grateful to the Higher Education Commission (HEC), Islamabad, Pakistan, for funding this study through a PhD student grant. This research has also been supported through a PYI project entitled "Finding Single Nucleotide Polymorphism in Cotton Genome" by the HEC of Pakistan.

References

Abdurakhmonov IY, Buriev ZT, Saha S, Pepper AE, Musaev JA, Almatov A, Shermatov SE, Kushanov FN, Mavlonov GT, Reddy UK, Yu JZ, Jenkins JN, Kohel RJ & Abdukarimov A (2007). Microsatellite markers associated with lint percentage trait in cotton, *Gossypium hirsutum*. *Euphytica* 156: 141–156.

Achrem M, Kalinka A, Rogalska SM (in press). Assessment of genetic relationships among *Secale* taxa by using ISSR and IRAP markers and the chromosomal distribution of AAC microsatellite sequence. *Turkish Journal of Botany* 38: doi: 10.3906/bot-1207-26.

Brubaker CL & Brown AHD (2003). The use of multiple alien chromosome addition aneuploids facilitates genetic linkage mapping of the *Gossypium* G genome. *Genome* 46: 774–791.

Brubaker CL, Paterson AH & Wendel JF (1999). Comparative genetic mapping of allotetraploid cotton and its diploid progenitors. *Genome* 42: 184–203.

Buteler MI, Jarret RL & LaBonte DR (1999). Sequence characterization of microsatellites in diploid and polyploid Ipomoea. *Theoretical and Applied Genetics* 99: 123–132.

Dakin EE & Avis JC (2004). Microsatellite null alleles in parentage analysis. *Heredity* 93: 504–509.

Desai A, Chee PW, Rong JK, May OL & Paterson AH (2006). Chromosome structural changes in diploid and tetraploid A genomes of *Gossypium*. *Genome* 49: 336–345.

Doğan B, Ünal M, Özgökçe F, Martin E & Kaya A (2011). Phylogenetic relationships between *Malcolmia*, *Strigosella*, *Zuvanda*, and some closely related genera (Brassicaceae) from Turkey revealed by inter-simple sequence repeat amplification. *Turkish Journal of Botany* 35: 17–23.

Frelichowski JE, Palmer MB, Main D, Tomkins JP, Cantrell RG, Stelly DM, Yu J, Kohel RJ & Ulloa M (2006). Cotton genome mapping with new microsatellites from Acala 'Maxxa' BAC-ends. *Molecular Genetics and Genomics* 275: 479–491.

Guo W, Cai C, Wang C, Han Z, Song X, Wang K, Niu X, Wang C, Lu K, Shi B & Zhang T (2007). A microsatellite-based, gene-rich linkage map reveals genome structure, function and evolution in *Gossypium*. *Genetics* 176: 527–541.

Guo W, Wang W, Zhou B & Zhang T (2006). Cross species transferability of *G. arboreum*- derived EST-SSRs in the diploid species of *Gossypium*. *Theoretical and Applied Genetics* 112: 1573–1581.

Guo Y, McCarty JC, Jenkins JN & Saha S (2008). QTLs for node of first fruiting branch in a cross of an upland cotton, *Gossypium hirsutum* L., cultivar with primitive accession Texas 701. *Euphytica* 163: 113–122.

Han ZG, Guo WZ, Song XL & Zhang TZ (2004). Genetic mapping of EST-derived microsatellites from the diploid *Gossypium arboreum* in allotetraploid cotton. *Molecular Genetics and Genomics* 272: 308–327.

Han ZG, Wang CB, Song XL, Guo WZ, Guo JY & Zhang TZ (2006). Characteristics, development and mapping of *Gossypium hirsutum* derived EST-SSR in allotetraploid cotton. *Theoretical and Applied Genetics* 112: 430–439.

He DH, Lin ZX, Zhang XL, Nie YC, Guo XP, Zhang YX & Li W (2007). QTL mapping for economic traits based on a dense genetic map of cotton with PCR-based markers using the interspecific cross of *Gossypium hirsutum* × *Gossypium barbadense*. *Euphytica* 153: 181–197.

Hendrix B & Stewart JM (2005). Estimation of the nuclear DNA content of *Gossypium* species. *Annals of Botany* 95: 789–797.

Iqbal MJ, Aziz N, Saeed NA, Zafar Y & Malik KA (1997). Genetic diversity of some elite cotton varieties by RAPD analysis. *Theoretical and Applied Genetics* 94: 139–144.

Jiang B (2004). Optimization of *Agrobacterium* Mediated Cotton Transformation Using Shoot Apices Explants and Quantitative Trait Loci Analysis of Yield and Yield Component Traits in Upland Cotton (*Gossypium hirsutum* L.). PhD, Louisiana State University and Agricultural and Mechanical College, USA.

Jiang C, Wright RJ, El-Zik KM & Paterson AH (1998). Polyploid formation created unique avenues for response to selection in *Gossypium* (cotton). *Proceedings of the National Academy of Sciences of the United States of America* 95: 4419–4424.

Kantartzi S, Ulloa M & Stewart JM (2006). Genetic diversity of A-genome cotton. In: Oosterhuis DM (ed.) *Summaries of Arkansas Cotton Research*, pp. 112–116. Arkansas Agricultural Experiment Station Research Series 552.

Kearsey M & Farquhar AGL (1998). QTL analysis in plants: where are we now? *Heredity* 80: 37–142.

Kearsey MJ (1998). The principles of QTL analysis (a minimal mathematics approach). *Journal of Experimental Botany* 49: 1619–1623.

Kosambi D (1944). The estimation of map distance from recombination values. *Annals of Eugenia* 12: 172–175.

Lacape JM, Nguyen TB, Thibivilliers S, Bojinnov TB, 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 Informatics* 46: 612–626.

Lin Z, He D, Zhang X, Nie Y, Guo X, Feng C & Stewart JM (2005). Linkage map construction and mapping QTL for cotton fibre quality using SRAP, SSR and RAPD. *Plant Breeding* 124: 180–187.

Liu DQ, Guo XP, Lin ZX, Nie YC & Zhang XL (2006). Genetic diversity of Asian cotton (*Gossypium arboreum* L.) in China evaluated by microsatellite analysis. *Genetic Resources and Crop Evolution* 53: 1145–1152.

Liu S, Saha S, Stelly D, Burr B & Cantrell RG (2000). Chromosomal assignment of microsatellite loci in cotton. *Journal of Heredity* 91: 326–332.

Ma X, Zhou B, Lu Y, Guo W & Zhang T (2008). Simple sequence repeat genetic linkage maps of A-genome diploid cotton (*Gossypium arboreum*). *Journal of Integrative Plant Biology* 50: 491–502.

Mehetre SS, Aher AR, Gawande VL, Patil VR & Mokate AS (2003). Induced polyploidy in *Gossypium*: a tool to overcome interspecific incompatibility of cultivated tetraploid and diploid cottons. *Current Science* 84: 1510–1512.

Mei M, Syed NH, Gao W, Thaxton PM, Smith CW, Stelly DM & Chen ZJ (2004). Genetic mapping and QTL analysis of fibre related traits in cotton. *Theoretical and Applied Genetics* 108: 280–291.

Nguyen TB, Giband M, Brottier P, Risterucci AM & Lacape JM (2004). Wide coverage of the tetraploid cotton genome using newly developed microsatellite markers. *Theoretical and Applied Genetics* 109: 167–175.

Niu C, Lister HE, Nguyen BZ, Wheeler TA & Wright RJ (2008). Resistance to *Thielaviopsis basicola* in the cultivated A-genome cotton. *Theoretical and Applied Genetics* 117: 1313–1323.

Park YH, Alabady MS, Ulloa M, Sickler B, Wilkin TA, Yu J, Stelly DM, Kohel RJ, El-Shiny OM & Cantrell RG (2005). Genetic mapping of new cotton fibre loci using EST-derived microsatellites in an interspecific recombinant inbred (RIL) cotton population. *Molecular Genetics and Genomics* 274: 428–441.

Qureshi SN, Saha S, Kantety RV & Jenkins JN (2004). EST-SSR: a new class of genetic markers in cotton. *Journal of Cotton Science* 8: 112–123.

Rahman M, Asif M, Shaheen T, Tabbasam N, Zafar Y & Paterson AH (2011). Marker-assisted breeding in higher plant taxa. In: Lichfouse E (ed.) *Sustainable Agriculture Reviews 6; Alternative Farming Systems, Biotechnology, Drought Stress and Ecological Fertilisation*, pp. 39–76. Dordrecht: Springer.

Rahman M, Shaheen T, Tabbasam N, Iqbal MA, Ashraf M, Zafar Y & Paterson AH (2012). Cotton genetic resources. A review. *Agronomy for Sustainable Development* 32: 419–432.

Rahman M, Yasmeen T, Tabassum N, Ullah I, Asif M & Zafar Y (2008). Studying the extent of genetic diversity among *Gossypium arboreum* L. genotypes/cultivars using DNA fingerprinting. *Genetic Resources and Crop Evolution* 55: 331–339.

Rahman M & Zafar Y (2012). Registration of NN-3 cotton. *Journal of Plant Registrations* 6: 342–347.

Rahman M, Zafar Y & Paterson AH (2009). Gossypium DNA markers: types, numbers and uses. In: Paterson AH (ed.) *Genetics and Genomics of Cotton,* pp. 101–139. Dordrecht: Springer.

Rana MK & Bhat KV (2004). A comparison of AFLP and RAPD markers for genetic diversity and cultivar identification in cotton. *Journal of Plant Biochemistry and Biotechnology* 13: 19–24.

Reddy OUK, Pepper AE, Abdurakhmonov I, Saha S, Jenkins JN, Brooks T, Bolek Y & El-Zik KM (2001). New dinucleotide and trinucleotide microsatellite marker resources for cotton genome research. *Journal of Cotton Science* 5: 103–113.

Shaheen T, Zafar Y, Stewart M & Rahman M (2013). Development of short gSSRs in *G. arboreum* and their utilization in phylogenetic studies. *Turkish Journal of Agriculture and Forestry* 37: 288–299.

Shen X, Guo W, Lu Q, Zhu X, Yuan Y & Zhang T (2007). Genetic mapping of quantitative trait loci for fiber quality and yield trait by RIL approach in Upland cotton. *Euphytica* 155: 371–380.

Song X, Wang K, Guo W, Zhang J & Zhang T (2005). A comparison of genetic maps constructed from haploid and BC1 mapping populations from the same crossing between *Gossypium hirsutum* L. and *Gossypium barbadense* L. *Genome* 48: 378–390.

Ulloa M, Meredith WR, Shappley ZW & Kahler AL (2002). Genetic linkage maps from four F2:3 populations and a join maps of *Gossypium hirsutum* L. *Theoretical and Applied Genetics* 101: 200–208.

Ulloa M, Saha S, Jenkin N, Meredith WR, McCarty JC & Stelly DM (2005). Chromosomal assignment of RFLP linkage groups harboring important QTL on intraspecific cotton (*Gossypium hirsutum* L.) join map. *Journal of Heredity* 96: 132–144.

Vafaie-Tabar M, Chandrashekaran S, Rana MK & Bhat KV (2004). RAPD analysis of genetic diversity in Indian tetraploid and diploid cotton (*Gossypium* spp). *Journal of Plant Biochemistry and Biotechnology* 13: 81–84.

Van Ooijen JW & Voorrips RE (2001). JoinMap Version 3.0, Software for the Calculation of Genetic Linkage Maps. Wageningen: Plant Research International.

Wang K, Song X, Han Z, Guo W, Yu JZ, Sun J, Pan J, Kohel RJ & Zhang T (2006). Complete assignment of the chromosomes of *Gossypium hirsutum* L. by translocation and fluorescence in situ hybridization mapping. *Theoretical and Applied Genetics* 113: 73–80.

Wang S, Basten CJ & Zeng ZB (2007). Windows QTL Cartographer 2.0. Raleigh, NC, USA: Department of Statistics, North Carolina State University.

Wu J, Gutierrez OA, Jenkins JN, McCarty JC & Zhu J (2009). Quantitative analysis and QTL mapping for agronomic and fiber traits in an RI population of upland cotton. *Euphytica* 165: 231–245.

Xiang XL & Shen DZ (1989). Chinese Asian Cotton (*Gossypium arboreum*). Beijing: China Agricultural Press.

Zhang J, Guo W & Zhang T (2002). Molecular linkage map of allotetraploid cotton (*Gossypium hirsutum* L. × *Gossypium barbadense* L. with a haploid population. *Theoretical and Applied Genetics* 105: 166–1174.

Zhang Y, Lin Z, Xia Q, Zhang M & Zhang X (2008). Characteristics and analysis of simple sequence repeats in the cotton genome based on a linkage map constructed from a BC1 population between *G. hirsutum* and *G. barbadense*. *Genome* 51: 534–546.