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A Review of QTL Mapping in Cotton: Molecular Markers, Mapping Populations and Statistical Methods

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A B S T R A C T

The upland cotton (*Gossypium hirsutum* L.) accounts for about 95% of world cotton production. Improving upland cotton cultivars has been the focus of world-wide cotton breeding programs. In cotton, seed cotton yield, yield contributing and fibre quality traits are under the control of polygenes or quantitative trait locus (QTL), for these traits QTL analysis holds a great promises these are the genomic regions that links the information between phenotypic (trait measurement) and genetic data (molecular markers) and explain the genetic basis of variation in complex traits. The development of appropriate molecular markers in the background of suitable mapping population and construction of genetic linkage maps and QTL identification using statistical programs are earnest for QTL mapping. Present review provides an updates on comparative QTL analysis to obtain a better insight into the genome-wide distribution of QTL and to identify consistent QTL for marker assisted breeding and marker-assisted QTL manipulation to the genetic improvement of quantitative traits in cotton.

Introduction

The primary breeding goal for the worldwide cotton scientists is how to genetically improve both yield and fibre quality. Previous research reports showed that yield, yield contributing and fibre quality traits of interest were negatively associated and controlled by multiple environmental sensitive quantitative genes. Current genetic information and plant breeding methods cannot lead to improvement of such negative association and controlling multiple environmental sensitive quantitative genes for yield and fibre quality. In conventional breeding aim is to develop both high yield and superior quality fibre properties but the quality of fibre can be determined only after harvesting and testing of the fibre. As a result, it is difficult, expensive and time consuming to develop cotton cultivars with high yield and superior quality fibre by these methods. Acceleration of the conventional breeding method has become possible by using biotechnological tool called molecular markers. Construction of genetic linkage maps has been recognized

as an essential tool for plant molecular breeding using molecular markers or DNA markers because they have the properties of neutrality, lack of epitasis and are simply inherited Mendelian characters. Therefore in marker assisted selection (MAS) the use of DNA markers which is highly associated with traits of importance will be an important approach in reaching breeding goal. Various types of DNA markers *viz*., RFLP, the PCR based DNA markers such as AFLP, RAPD, SSR, STS and EST-SSR have been widely used in cotton linkage (*i.e.* Lacape *et al.,* 2003; Zhang *et al.,* 2003) and SNP markers. Recent availability of cotton genome reference sequences for *G. raimondii* (Paterson *et al.,* 2012), draft sequences for *G. arboreum* (Li *et al.,* 2014), *G. raimondii* (Wang *et al.,* 2012) and draft sequences for *G. arboreum* and *G. herbaceum* (Katageri *et al.,*2014) and millions of SNPs were generated in different crops such as Soybean (Lam *et al.,* 2010), Arabidopsis (Zhang *et al.,* 2009), Rice (Subbaiyan *et al.,* 2012; Xu *et al.,* 2012) and other crops (Sim *et al.,* 2012; Sharpe *et al.,* 2013; Delourme *et al.,* 2013), help to cotton scientists for genome based identification efforts and mapping the QTLs. High throughput genome-scale next-generation sequencing (NGS) technologies provide new strategies for sequence-based SNP genotyping. As a result, genotypic data and phenotypic data are widely used in construction of linkage groups and QTL tagging. The F_2, backcross and recombinant inbred (RI) populations have been most popularly used for QTLs mapping. Each population has some advantages and disadvantages (Paterson, 1996).

In cotton crops most traits of economical importance, including seed cotton yield, yield contributing and fibre quality traits are controlled by many genes and are known as quantitative traits (also "polygenic" "multifactorial" or "complex" traits). The term QTL was first coined by Geldermann (1975). The regions within genomes that contain genes associated with a particular quantitative trait are known as QTLs. Conceptually, a QTL can be a single gene, or it may be a cluster of linked genes that affect trait. The procedures for finding and locating the QTLs and analyzing their magnitude of genetic effects and interactions with environment are called QTL mapping. The development of molecular markers and the use of these markers in QTL analysis is increasingly becoming a common approach for evaluating the inheritance and feasibility of accelerating gains from selection for complex quantitative traits in crop plants. Yield contributing and fibre quality traits for which QTL analysis holds great promise.

QTL mapping requires (1) selection of appropriate molecular marker (s) and generation molecular data with adequate number of uniformly-spaced polymorphic markers; (2) Development of appropriate mapping population and phenotyping the population for the trait (s) of interest; (3) Construction of genetic linkage map and identification of QTLs for the trait (s) of interest using statistical programs. Details on molecular markers, mapping population, statistical methods, linkage maps and QTL mapping of agronomics and fibre quality related traits are reviewed here under.

Molecular markers

Until recent advances in molecular genetics, breeders have been improving phenotype through evaluation and selection, which were resource-consuming. Currently, two main types of molecular markers, biochemical markers and DNA based markers are available for genetic studies. Distinguish the molecular markers from morphological markers (1) Distinguish the genotypes at the any part of plants; (2) these markers behave in

a co-dominant manner, allowing the heterozygotes to be differentiated from homozygotes; (4) phenotypic neutrality: deleterious effects are not usually associated with different alleles; (5) alleles at many loci are co-dominant, thus all possible genotypes can be distinguished and (6) few epistatic or pleiotropic effects are observed. All these advantages make molecular genetic markers very important tools in various genetic analyses and crop improvement strategies.

A DNA marker is considered as good or powerful if it is easy to detect, amenable for automation, highly polymorphic and distributed across genome at random. These molecular markers include: (i) hybridization-based markers such as restriction fragment length polymorphism (RFLP) (ii) PCR-based markers: random amplification of polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP) and microsatellite or simple sequence repeat (SSR) and (iii) sequence-based markers: single nucleotide polymorphism (SNP). The majority of these molecular markers has been developed either from genomic DNA libraries (e.g. RFLPs and SSRs) or from random PCR amplification of genomic DNA (e.g. RAPDs) or both (e.g. AFLPs). Different types of molecular markers commonly used in cotton breeding programs are presented in table 1, and their application in cotton improvements I as follows:

Restriction Fragment Length Polymorphisms (RFLPs)

It is hybridization based techniques in which organisms are differentiated by analysis of patterns derived from cleavage of their DNA by restriction enzymes. The main steps involve isolation of DNA, digestion with restriction enzymes, separation of restricted fragments by agarose gel electrophoresis, transfer of fragments to nylon membrane,

hybridization with probe and scoring of polymorphism by autoradiography. In various species of cotton, RFLP markers have been used to study the genetic diversity, population genetics, evolution and phylogenetic relationships (Yu *et al.,* 1997). Brubaker *et al.,* 1999; Ulloa and Meredith *et al.,* 2000 and Ulloa *et al.,* 2002 are published genetic mapping of cotton using RFLPs and it was reported that in cotton 64 % RFLPs are co-dominant in nature (Reinisch *et al.,* 1994). Genetic diversity in upland cotton has also been examined using RFLP markers (Brubaker and wendel *et al.,* 1994). Molecular map of the cotton genome was first constructed using 705 RFLP loci and partitioned into 41 linkage groups (Reinisch *et al.,* 1994). Wright *et al.,* 1998, reported utility of RFLP markers in marker assisted selection (MAS) and RFLP linked to resistance allele for pathogen of bacterial blight was validated. RFLP markers are very complex and time and cost intensive technique which restrict it's uses and leads to development of less complicated techniques known as PCR base markers (Agarwal *et al.,* 2008).However, at present, RFLPs are not popular in cotton genome studies because of low ability to detect polymorphism in cotton compared to other plant taxa (Brubaker *et al.,* 2000).

Random amplified polymorphic DNA (RAPD)

In RAPDs, DNA fragments are amplified by the PCR reaction using random primers (usually of 10 bp) (Khanam *et al.,* 2012). Polymorphism is obtained because of sequence variation in the genome for primer binding sites, making RAPDs as dominant marker. RAPD marker system is easy to carry out, needs no prior sequence information, requires very less amount of DNA and is amenable to automation. However, the technique suffers with low reproducibity

(Rafalski *et al.,* 1997).RAPD techniques have been used for many purposes in cotton including assessment of, diversity, genome mapping, phylogentic studies (Rahman *et al.,* 2002; Zhong *et al.,* 2002; Rahman *et al.,* 2008 and Rana and Bhat 2004), genetic variations in population (Chalmers *et al.,* 1992), DNA fingerprinting (Multani *et al.,* 1995) and determining the relationship between the genotypes of different and same species (Wajahatullah and Stewart *et al.,*1997). In cotton RAPDs were used to distinguish the cotton varieties resistant to jassids, aphids and mites (Geng *et al.,* 1995). RAPD marker (R-6592) for the male sterility gene has been identified in cotton (Lan *et al.,* 1999). RAPD techniques were used to evaluate the genetic relationship among cotton genotypes (Shu *et al.,* 2001), to identify the QTLs for stomatal conductance (Ulloa and Meredith 2000) and to construct linkage mapping in cotton.

Amplified Fragment Length Polymorphism (AFLP)

It is a technique which combines reliability of RLFP with the ease of RAPD (Vos *et al.,* 1995). The process involves three simple steps: (i) restriction of genomic DNA and ligation of oligonucleotide adaptors (ii) pre and selective amplification of restriction fragments and (iii) gel analysis of amplified fragments. The polymorphic fragments are detected as present or absent making it a dominant marker system. The technique can be automated and allows the simultaneous analysis of many genetic loci per experiments. AFLP produces more polymorphic loci per primer than RFLPs, SSRs or RAPDs (Maughan *et al.,* 1996).AFLP is an effective tool for the observation of genetic diversity (Murtaza *et al.,* 2006), fingerprinting studies and tagging of agronomic, seed and fibre quality traits (Zhong *et al.,* 2002; Rakshit *et al.,* 2010 and Badigannavar and Myers 2010). AFLP is a great valued technique for gene

mapping studies due to their high abundance and random distribution throughout the genome (Vos*et al.,* 1995). A linkage map of cotton was developed using the AFLP and RAPD markers (Altaf *et al.,* 1997). AFLP markers have also been used for analyzing the genetic diversity (Abdalla *et al.,* 2001 and Rana and Bhat 2004) and map saturation in cotton (Zhang *et al.,* 2005 and Lacape *et al.,* 2003).

Inter Simple Sequence Repeats (ISSR)

It allows the detection of polymorphism in inter SSR loci using primer (16–25 bp long) complimentary to a single SSR and anneal at either the 3' or 5' end (Khanam *et al.,* 2012) which can be di, tri, tetra or pentanucleotide (Reddy *et al.,* 2002). The technique of ISSR markers combines many benefits of AFLPs and SSRs with universality of RAPDs (Bornet and Branchard *et al.,* 2001). Generally the sequence of ISSR primers is larger as compare to RAPD primers, allowing higher annealing temperature which results in greater reproducibility of bands than RAPDs (Reddy *et al.,* 2002, Culley and Wolf *et al.,* 2000). Amplification of ISSRs also revealed larger fragments number per primer than RAPDs (Wang and Yi *et al.,* 2002).

Many earlier studies reported that ISSR markers were more informative than RAPDs for genetic diversity evaluation in different crop species (Nagaoka and Ogihara *et al.,* 1997; Galv´an *et al.,* 2003). The applications of ISSRs for different purposes depend on the diversity and frequencies of SSR within the particular genomes (Shi *et al.,* 2010). It is quickly being utilized by the research community in different areas of plant improvement like in gene tagging, analysis of genetic diversity and estimation of SSR motif [Blair *et al.,* 1999; Bornet *et al.,* 2002 and Sica *et al.,* 2005]. ISSRs have been reported as quite useful markers for revealing

polymorphism in cotton genotypes (Liu and Wendel 2001).

Microsatellites or Simple Sequence Repeats (SSR)

These are di-, tri-, tetra- or pentatandom repeats of nucleotide, scattered abundantly in both noncoding and coding regions of a genome (Kalia *et al.,* 2011; Khanam *et al.,* 2012). Microsatellites are created from sphere where variants of repetitive DNA sequence are previously over represented (Tautz *et al.,* 1986). The loci of these markers are highly transferable about 50% across species (Saha *et al.,* 2004). For SSRs analysis forward and reverse primers are employed in PCR reaction that anneal to the template DNA at the 5' and 3' ends. Short repetitive DNA sequences furnish the basis for multi allelic, co-dominant PCR based molecular marker and found more polymorphic as compare to other DNA markers (Preetha and Raveendr *et al.,* 2008 and Khanam *et al.,* 2012). Due to their greater polymorphism, SSRs are considered as an important marker system in fingerprinting, analysis of genetic diversity, molecular mapping and marker assisted selection (Reddy *et al.,* 2002). Several methods have been pursued to develop SSR markers in cottons, including analysis of SSR-enriched small insert genomic DNA libraries (Richard and Beckman *et al.,* 1995; Udall *et al.,* 2006; Ince *et al.,* 2010 and Kalia *et al.,*2011), SSR mining from ESTs (Shaheen *et al.,* 2009) and large-insert BAC derivation by end sequence analysis (Reddy *et al.,* 2002). Cotton researchers have explored simple sequence repeats (SSRs) for studies of the phylogenetic and diversity analysis (Lacape *et al.,* 2007) genetic mapping (Guo *et al.,* 2007; Lacape *et al.,* 2009; Park *et al.,* 2005; Xiao *et al.,* 2009; Yu *et al.,* 2011; Yu *et al.,* 2012; Yu *et al.,* 2013 and Gore *et al.,* 2014), association mapping (Kantartzi *et al.,* 2008).

Single Nucleotide Polymorphism (SNPs)

To understand the shift to single nucleotide polymorphism (SNP) markers, we must first look into the limitations of SSR markers. First, there are limited numbers of SSR motifs in the genome which becomes a constraint when trying to saturate a region with markers or when trying to identify gene-based markers. In addition, one of the main advantages of SSRs is high information content from multiple alleles per locus and also presents difficulties when merging SSR data from different platforms and curating allele sizes in databases. In addition, gel-based SSRs are labor intensive and automated fragment sizing systems have limited scope for multiplexing. Therefore, SSR genotyping quickly hits a point where the low throughput and higher cost becomes a limiting factor which is in contrast to recent SNP genotyping techniques. The main advantages of SNP markers relate to their ease of data management along with their flexibility, speed and cost-effectiveness. Bi-allelic SNP markers are straight forward to merge data across groups and create large databases of marker information, since there are only two alleles per locus and different genotyping platforms will provide the same allele calls once proper data QC has been performed. A major factor in the advantages of SNP markers for flexibility, speed and cost-effectiveness is the range of genotyping platforms available to address a variety of needs for different marker densities and costs per sample. Variations of single nucleotide (A, T, C, and G) in sequence of individual genome are known as single nucleotide polymorphism or SNPs (Agarwal *et al.,* 2008). These may occur in the non-coding, coding and intergenic regions of the genome, so allowing the detection of the genes due to the variations in the sequences of nucleotides (Agarwal *et al.,* 2008, Ayeh 2008) and these are either non synonymous or synonymous

within the coding regions of the genome. Synonymous changes can alter mRNA splicing that result the changes in the phenotype of an individual (Richard and Beckman 1995). SNP markers are important tool for linkage mapping, map based cloning and marker assisted selection due to the high level of polymorphism. The co-dominant nature of SNPs makes these markers able to distinguish the heterozygous and homozygous alleles (Shaheen *et al.,* 2009).In cotton, many research have been conducted to observe diversity, characterization and mapping of SNPs in the nucleotide sequence of *Gossypium* genome (An *et al.,* 2008, Deynze *et al.,* 2009). Recently, an international collaborative effort has developed 70K SNP chip based on Illumina Infinium genotyping assay (Unpublished data; http://www.cottongen.org/node/ 1287616). This high-throughput genotyping assay will be a resource that will be used globally by public and private breeders, geneticists and other researchers to enhance cotton genetic analysis, breeding, genome sequence assembly and many other uses.

Mapping population

To study genotypes diversity, finger printing, gene tagging, map construction and QTLs identification all these requires appropriate mapping population and is very critical for the success of QTL mapping project. These populations are developed by crossing between two inbred parents with clear contrasting difference in their phenotypic traits of interest. In auto gamous species, QTL mapping studies make use of F_2 or segregating generation derived families, backcross (BC), recombinant inbred lines (RILs), near isogenic lines (NILs) and double haploids (DH). The primary mapping populations for QTLs mapping is F_2, backcross (BC), recombinant inbred lines (RILs) and double haploid (DH) populations. Both F_2 and BC populations are the simplest

types of mapping populations because they are easy to construct and require only a short time to produce. F_2 is more powerful for detecting QTLs with additive effects and can also be used to estimate the degree of dominance for detected QTLs. In cotton several studies used F_2 as mapping population (Reinisch *et al.,* 1994; Jiang *et al.,* 1998; Jiang *et al.,* 2000; Kohel *et al.,* 2001; Saranga *et al.,* 2001; Rong *et al.,* 2007 and Yu *et al.,* 2007). When dominance is present, backcrosses give biased estimates of the effects because additive and dominant effects are completely confounded. However, both F_2 and BC populations have three limitations. First, development of these populations require relatively few meioses such that even markers that are far from the QTLs remain strongly associated with it. Such long-distance associations hamper precise localization of the QTLs. Second, F_2 and BC populations are temporary populations as they are highly heterozygous and cannot be propagated indefinitely through seeds (*i.e.,* these populations can't be evaluated several times in different environmental conditions, years, locations, *etc.*). Finally, epistatic interactions could hardly be studied in both F_2 and BC populations. RILs are derived from an F_2 population by generations of selfing (bulk or single seed descent) (Soller and Beckman, 1990 and Xu and Crouch, 2008). RILs are advanced homozygous lines that have undergone several rounds of inbreeding (Darvasi and Soller, 1995). Such multiple generations of mating increases the potential number of recombination events and improves map resolution (*i.e.,* sufficient meioses have occurred to reduce disequilibrium between moderately linked markers). In cotton a considerable number of studies have used RILs as mapping population for mapping yield and fibre quality related and other traits (Park *et al.,* 2005; Shen *et al.,* 2007; Wang *et al.,* 2006; Abdurakhmonov *et al.,* 2007; Wu *et al.,* 2008;

Zhang *et al.,* 2009; Lacape *et al.,* 2009, 2010; Yu *et al.,* 2012; Gore *et al.,* 2014 andYu *et al.,* 2013).DH populations have also been used for QTL mapping in several species (Bao *et al.,* 2002; Mahmood *et al.,* 2003; Behn *et al.,* 2005; Semagn *et al.,* 2006; Semagn *et al.,* 2007 and Xu and Crouch, 2008).

The DH production methodology improves breeding efficiency by generating inbred lines with 100 per cent purity and genetic uniformity in just two generations. DH lines make it easy to carry genetic studies and shorten the breeding time significantly. DH populations are quicker to generate than RILs and NILs but the production of DHs is only possible for species with a well-established protocol for haploid production. RILs, NILs and DHs are permanent populations because they are homozygous or 'true-breeding' lines that can be multiplied and reproduced without any occurrence of genetic change. Seeds from RILs, NILs and DHs can be transferred between different laboratories for mapping to ensure that all collaborators examine identical material (Young, 1994 and Lekgari, 2010). So that genetic result from phenotyping, genotyping and QTL mapping can be accumulated across laboratories. In spite of the availability of various papers on genetic mapping, specific studies relating to the ideal number of individuals in a given population required to establish accurate genetic maps have yet been inconclusive. Simulation studies performed using a sample size ranging from 50 to 1000 individuals of F_2, BC, RILs and DHs populations have shown that the type and size of mapping populations can exert an influence on the accuracy of genetic maps.

Statistical methods for QTL analysis and mapping

QTL analysis looks for co-segregation between the quantitative trait and marker allele in a segregating population. Undoubtedly, the development of statistical methods has played an important role for the detection of the association between DNA markers and quantitative characters. The first report of an association between a morphological marker and a quantitative trait was reported by Sax (1923).QTL mapping programs can be roughly classified into different groups according to the number of markers or genetic models and analytical approaches applied. According to the number of markers, models can be classified as single-QTL models and multiple-locus models (Liu, 1998). According to the analytical technology, the methods can be grouped into one-way analysis of variance (ANOVA) or simple t-test, simple linear regression, multiple linear regression, nonlinear regression, log-linear regression, likelihood functions, MCMC (Markoff Chain Monte Carlo) and mixed linear models (Wang *et al.,* 1999).

Briefly, the statistical analyses of associations between phenotype and genotype in a population to detect QTLs include single-marker mapping (Luo and Kearsey, 1989), simple interval mapping (SIM) (Lander and Botstein, 1989) and composite interval mapping (CIM) (Zeng, 1994), multiple interval mapping (MIM) (Jiang and Zeng 1995; Ronin *et al.,* 1995) as follow:

Single Marker Analysis (SMA)

The simplest method for QTL mapping is single-marker mapping, includes t-test, ANOVA and simple linear regression, which assess the segregation of a phenotype with respect to a marker genotype (Soller and Brody, 1976). According to this principle progeny is classified by marker genotype and phenotypic mean between classes is compared (t-test or ANOVA). A significant difference indicates that a marker is linked to a QTL. The difference between the phenotypic mean

provides an estimate of the QTL effect. This approach can indicate which markers linked to potential QTLs are significantly associated with the quantitative trait investigated. In short, QTL location is indicated only by looking at which markers give the greatest differences between genotype group averages. Depending on the density of markers, the apparent QTL effect at a given marker may be smaller than the true QTL effect as a result of recombination between the marker and the QTL. The advantage of this method is that it is a simple procedure that can be accomplished by a standard statistical analysis software package, such as SAS and Minitab. In contrast the main weakness of single-marker tests is the failure to provide an accurate estimate of QTL location or recombination frequency between the marker and the QTL because the evaluation of individual markers is independent and without reference to their position or order (Doerge and Churchill, 1996).

Simple Interval Mapping (SIM)

Lander and Botstein, (1989) developed interval mapping, which overcomes the three disadvantages of analysis of variance at marker loci. Interval mapping is currently the most popular approach for QTL mapping in experimental crosses. The method makes use of a genetic map of the typed markers and like analysis of variance, it also assume assumes the presence of a single QTL. Each location in the genome is posited, one at a time, as the location of the putative QTL.

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of a genetic map of the typed markers and, like analysis of variance, it also assumes the presence of a single QTL. Each location in the genome is posited, one at a time, as the location of the putative QTL. Interval mapping has several advantages over analysis of variance at the marker loci. (1) It provides a curve which indicates the evidence for QTL location. (2) It allows for the inference of QTLs to positions between markers. (3) It provides improved estimates of QTL effects. (4) And perhaps most important, appropriately performed interval mapping makes proper allowance for incomplete marker genotype data. The key disadvantage to interval mapping, in comparison to analysis of variance, is that it requires some increase in computation time and the use of specially designed software. The principle behind interval mapping is to test a model for the presence of a QTL at many positions between two mapped marker loci. The model is fit and its goodness is tested using the method of maximum likelihood. If it is assumed that a QTL is located between two markers, the 2-locus marker genotypes contain mixtures of QTL genotypes each. Maximum likelihood involves searching for QTL parameters that give the best approximation for quantitative trait distributions that are observed for each marker class. Models are evaluated by computing the likelihood of the observed distributions with and without fitting a QTL effect. The LOD (logarithm of the odds) score is the log of the ratio between the null hypothesis (no QTL) and the alternative hypothesis (QTL at the testing position). Large LOD scores correspond to greater evidence for the presence of a QTL. The best estimate of the location of the QTLs is given by the chromosomal location that corresponds to the highest significant likelihood ratio. The LOD score is calculated at each position of the genome.

Table.1 Different types of molecular markers, their advantages and disadvantages

Sl. No.	Feature	RFLP	RAPD	AFLP	SSR	SNP
1.	Genomic abundance	High	High	High	Moderate to high	Very high
2.	Genomic coverage	Low copy coding region	Whole genome	Whole genome	Whole genome	Whole genome
3.	Expression/inheritance	Codominant	Dominant	Dominant / co-dominant	Co-dominant	Co-dominant
4.	Number of loci	Small (<1,000)	Small (<1,000)	Moderate (1,000s)	High (1,000s – 10,000s)	Very high (>100,000)
5.	Type of polymorphism	Single base changes, indels	Single base changes, indels	Single base changes, indels	Changes in length of repeats	Single base changes, indels
6.	Reproducibility/reliability	High	Low	High	High	High
7.	Genotyping throughput	Low	Low	High	High	High
8.	Ease of use	Not easy	Easy	Moderate	Easy	Easy
9.	Ease of automation	Low	Moderate	Moderate to high	High	High
10.	Primary application	Genetics	Diversity	Diversity and genetics	All purposes	All purposes
11.	Type of probes/primers	Low copy DNA or cDNA clones	10 bp random nucleotides	Specific sequence	Specific sequence	Allele-specific PCR primers
12.	Cloning and/or sequencing	Yes	No	No	Yes	Yes
13.	PCR-based	Usually no	Yes	Yes	Yes	Yes
14.	Radioactive detection	Usually yes	No	Yes or no	Usually no	No
15.	Effective multiplex ratio	Low	Moderate	High	High	Moderate to high
16.	Amount of DNA required	Large (5 – 50 μg)	Small (0.01 – 0.1 μg)	Moderate (0.5 – 1.0 μg)	Small (0.05 – 0.12 μg)	Small (≥ 0.05 μg)
17.	Quality of DNA required	High	Moderate	High	Moderate to high	High
18.	Technically demanding	Moderate	Low	Moderate	Low	High
19.	Time demanding	High	Low	Moderate	Low	Low
20.	Development/start-up cost	Moderate to high	Low	Moderate	Moderate to high	High

Table.2 Software availability for genetic map construction

Sl. No.	Software name	Plat form operating system	Experimental designs	Availability	Reference
1.	AntMap	DOS and UNIX	F_2 intercross, F_2 backcross, RIL (self), DH	http://cse.naro.affrc.go.jp/iwatah/antmap/index.htmlhttp://cse.naro.affrc.go.jp/iwatah/antmap/index.html	Iwata and Ninomiya (2006)
2.	CarthaGe'ne	C++	F_2 intercross, F_2 backcross, RIL	http://www.inra.fr/mia/T/CarthaGene/	Schiex and Gaspin(1997)
3.	DGMAP	UNIX	Various including F_2 backcross	No longer available	Newell *et al.,* (1995)
4.	JoinMap	MS-Windows	BC_1, F_2 intercross, RILs (self),DH, DH_1, DH_2, HAP, HAP_1 CP	http://www.kyazma.nl/	Stam (1993)
5.	MadMapper	Python scripting language	Specializes in RILs but flexible scoring scheme can be employed for many other design types	http://cgpdb.ucdavis.edu/XLinkage/MadMapper/	Kozik and Michelmore (2006)
6.	MAPMAKER/EXP	DOS and UNIX	F_2 intercross, F_2 backcross, RIL (self), F_3 intercross (self), RIL (sib)	http://www.broadinstitute.org/ftp/distribution/software/mapmaker3/	Lander *et al.,* (1987)
7.	Map Manager QTX	Microsoft Windows and Mac OS	Advanced intercross, advanced backcross, RILs	http://www.mapmanager.org/	Manly and Olson (1999)
8.	MSTMAP	C++ and Linux	BC_1, DH, HAP, RIL	http://www.138.23.191.145/mstmap/	Wu and Huang (2008)
9.	RECORD	DOS	BC_1, F_2, F_3, RIL	http://www.plantbreeding.wur.nl/UK/software_record.html	Van *et al.,* (2005)
10.	THREaD Mapper	Wed- Browser enable tool	F_2 intercross, F_2 backcross, RIL (self), DH	http://cbr.jic.ac.uk/dicks/software/threadmapper/index.html	Cheema *et al.,* (2008)

Table.3 The commonly used QTL mapping statistical programs

Sl. No.	Name	Platform (operating system)	Description	References
1.	Map Manager QTX (Version b29)	Windows, Mac OS	A graphic, interactive program to map QTL using intercrosses, backcrosses or recombinant inbred strains in experimental plants or animals	Manly and Olson (1999)
2.	Mapmaker/ QTL (Version 1.1)	UNIX, VMS, DOS, Mac OS	A package containing a program for genetic linkage analysis and a program for mapping genes underlying complex traits.	Lander and Bostein, 1989; Lincoln *et al.,*(1992)
3.	MapQTL (Version 5)	Windows ® (95/98/ME/N T4.0/2000/XP/Vista 32-Bit	Mapping of QTL for several types of experimental mapping populations.	Van Ooijen (2005)
4.	PlabQTL (Version 1.2)	DOS	A program characterizing loci that affect the variation of quantitative traits.	Utz and Melchinger (2003)
5.	QGene (Version 4.0)	Any computer	An entirely rebuilt Java application that will run on any computer.	Nelson (1997)
6.	QTL Cartographer (Version 2.5)	For Windows UNIX, DOS, Windows, Mac OS	A program to map quantitative traits using a map of molecular markers.	Basten*et al.,*(1994); Wang *et al.,*(2010)

Table.4 Details of QTLs identified trait-wise in cotton

Sl. No.	Traits	Descriptor	Population		Marker (number and Type)	QTLs No.	Reference
			Type	Size			
1	Fiber quality	FS, FL, FF	F$_2$	171	216 RFLP, 139 RAPDs	13	Kohel*et al.,* 2001
		FS	F$_2$	186	217 SSRs, 800 RAPDs UBC and 1040 OPERON	2	Zhang *et al.,* 2003
		LY, LP, SW, NS, UQ, SF, FL, FE, FT, FF and IF	F$_2$	120	144 AFLPs, RFLPs and 150 SSRs	28	Mei *et al.,* 2004
		FS,FE, FF, FU and FL	F$_2$	200	448 RFLP	28	Zhang *et al.,* 2011
		FS, FE, FL, FU, LP and FF	F$_2$	117	290 SSRs and 9 AFLPs	16	Zhang *et al.,* 2005
		FF	BC3F$_2$	3,662	262 RFLPs	41	Draye*et al.,* 2005
		FL, FLU and SFC	BC3F$_2$	3,662	262 RFLPs	45	Chee*et al.,* 2005
		FS, FL, FF, FE	RILs		95 SSRs, 72 CSR	13	Park*et al.,* 2005
		FL, FS, FF and FE	F$_2$	—	1378 SSRs	39	Shen*et al.,* 2005
		FS, FL, FF, FMT, FE and SFI	RIL's	180	4106 SSRs, AFLPs, RAPDs and SRAPs	48	Wang *et al.,* 2006
		FS, FE, FU, FL and FF	RIL's	270	7508 SSRs, 384 SRAPs and 740 IT-ISJs	13	Zhang *et al.,* 2009
		FE, FL, FS, FF and FU	CP	172	16052 SSRs	63	Zhang *et al.,* 2012
2	Fiber and agronomical	SCY, LY, LP, BW, SI, FMT, PER, WF,WT, FF, FL, FE, FS	RIL's	188	141 SSRs	36	Wu *et al.,* 2009
3	Yield and fiber	SCY, LI, SI, LY, no. of seeds per boll, FS, FL and FF	F$_2$	69	834 SSRs, 437 SRAPs, 107 RAPDs, 16 REMAPs	57	He *et al.,*2008
		FS, FL, FF, FE, LP, SI, NB, SCY and LY	RIL's	258	2131 SSRs	53	Shen*et al.,* 2007
		LI, SI, LY, SCY, NSB and FS	F$_2$	69	834 SSRs, 437 SRAPs, 107 RAPDs and 16 REMAPs	52	He *et al.,* 2007
		NB, BW, SI, LP, LI, SCY, LY, FL, FS, FF, FE and FU	4WC and inbred lines	280	6123 SSRs and EST-SSRs	31	Qin *et al.,* 2008
		SCY, LY, NB, BW, LP, SI, LI and FBN	RIL's and IF$_2$	180	2675 EST-SSRs	111	Liu *et al.,* 2012
		PH, FBN, BW, LP, LI, SI, LY, FL, FS, FE, FF and FU	*G. hirsutum* accessions	81	121 SSRs	180	Zhang *et al.,* 2013
		SCY, LY,LI, BW, FL, FS, FU	BILs	146	2,041 SSRs	67	Yu *et al.,* 2013
		LI, LY, PH, FL, FF, FS, FU	RILs	98	2,183	28	Gore *et al.,* 2014

NB: number of bolls per plant, BW: boll weight, SI: seed index, LP: lint percent, LI: lint index, SI: seed index, SCY: seed cotton yield per plant, LY: lint yield per plant, FL: fiber length, FS: fiber strength, FE: fiber elongation, FU: fiber uniformity ratio, FY: fiber yellowness, FF: fiber fineness, FMT: fiber maturity, PH: plant height, FBL: fruit branch length, FBN: fruit branch number, FBA: fruit branch angle, FLU: fiber length uniformity, SFC: short fiber content, FR: fiber reflectance, SW: seed weight, NS: number of seeds per bolls, UQ: upper quartile length, SF: short fiber content, FT: fiber tenacity, IF: immature fiber content, SFI: short fiber index, NSB: number of seeds per boll

In case of many missing genotypes and large gaps on the map, the missing data are replaced by probabilities estimated from the nearest flanking markers (Broman, 2001). Until now, many software packages based on interval mapping were developed for QTL mapping, such as MAPMAKER/QTL (Lincoln *et al.,* 1992) and Q Gene (Nelson, 1997) (Table 2).

Composite Interval Mapping (CIM)

There are two problems with SIM; one is that the effects of additional QTL will contribute to sampling variance. The other is that combined effects of two linked QTLs will cause biased estimates. The ideal solution would be to fit a model that contains the effects of all QTL. Jansen (1993), Zeng (1993) and Zeng (1994) independently proposed combining SIM with multiple regression analysis in mapping, which is termed as "composite interval mapping" (CIM). Like SIM, CIM evaluates the possibility of a target QTL at multiple analysis points across each intermarker interval. However, at each point, it also includes the effect of one or more background markers that are often referred as cofactors. The purpose of using cofactors is to minimize the effects of QTLs in the remainder of the genome when attempting to identify a QTL in a particular region.

The inclusion of cofactors in the analysis helps in one of two ways, depending on whether the background markers and the target interval are linked. If they are not linked, inclusion of the background markers makes the analysis more sensitive to the presence of a QTL in the target interval. If they are linked, inclusion of the background marker may help to separate the target QTL from other linked QTL on the far side of the background marker (Zeng, 1993; Zeng, 1994).

Multiple Interval Mapping (MIM)

MIM (Kao *et al.,* 1999) is the extension of interval mapping to map multiple QTLs simultaneously, just as multiple regression extends analysis of variance. MIM allows one to infer the location of QTLs to positions between markers, makes proper allowance for missing genotype data and can allow interactions between QTLs. The idea of MIM is to fit multiple putative QTL effects and associated epistatic effects directly in a model to facilitate the search, test and estimation of positions, effects and interactions of multiple QTLs (Semagn *et al.,* 2010). MIM consists of four components: (1) an evaluation procedure designed to analyze the likelihood of the data given in a genetic model (number, positions and epistatic terms of QTL); (2) a search strategy optimized to select the best genetic model (among those sampled) in the parameter space; (3) an estimation procedure for all parameters of the genetic architecture of the quantitative traits (number, positions, effects and epistasis of QTL; genetic variances and covariance's explained by QTL effects); and (4) a prediction procedure to estimate or predict the genotypic values of individuals and their offspring based on the selected genetic model and estimated genetic parameter values (Zeng *et al.,* 1999). When compared with methods such as SIM and CIM, therefore, MIM tends to be more powerful and precise in detecting QTLs. The MIM model is based on Cockerham's model for interpreting genetic parameters and the method of maximum likelihood for estimating genetic parameters ((Kao *et al.,* (1999) and Satagopan *et al.,* (1996)) used a Bayesian approach relying on a Markov chain Monte Carlo simulation to map multiple QTLs.

All the different QTL mapping methods described above share a common assumption that the phenotype follows a normal distribution with equal variance in both

parents. Based on these statistical principles different QTL mapping programs have been developed. Details of each statistical program are given in table 3.

Genetic linkage maps in cotton

Genetic mapping refers to the determination of the relative position and distances between markers along chromosomes. Genetic map distances between two markers are defined as the mean number of recombination events, involving a given chromatid, in that region per meiosis. Genetic linkage maps are fundamental for the localization of genes conferring biotic and abiotic stress tolerance. Linkage maps of organisms are constructed to map genomic regions controlling qualitative and quantitative traits, to exercise indirect selection for several agronomic, fibre quality traits and to isolate the genes involved based on their map position. Genetic maps based on molecular markers have several advantages over classical maps (Subudhi and Nguyen, 2000).In cotton, the first molecular linkage map was constructed by Reinisch *et al.,* (1994) using RFLPs molecular markers in F_2mapping population. Till date, fifty linkage mapping studies done using intra or interspecific mapping populations (F_2/RILs/BIL) and SSRs/RAPD/AFLPs/RFLPs/SRAP markers have been found. The range of markers mapped in different studies mapped 19 to 1306 SSR/RAPD/RFLP/AFLP markers. However, Rong *et al.,* (2004) developed consensus genetic maps using different molecular linkage studies and mapped 2584 markers. This low number of markers maps in different studies indicates the presence of low number of polymorphic markers (Zhang *et al.,* 2009; Wang *et al.,* 2007; Wang *et al.,* 2006; Rong *et al.,* 2007 and Yu *et al.,* 2007). In cotton there is only one study available on developing a linkage map using F_2interspecific maps and SNP markers

(Hulse-Kemp *et al.,* 2015b). So, they were able to map so many markers on cotton chromosomes with an average 0.23 cM distance between the markers, which is the very finest map available in cotton. In the present study also it was attempted to map SNP markers using recombinant inbred lines derived from interspecific cross. 63K SNP chips were used in the present study which were also used by Hulse-Kemp *et al.,* (2015b).

QTL mapping for yield, yield contributing and fibre quality trait in cotton

The regions in genomes to have genes linked with a quantitative trait are known as quantitative trait loci, QTLs (Collard *et al.,* 2005) and the process of developing linkage maps and performing QTL analysis is referred to as QTL mapping (Paterson *et al.,* 1996). QTL analysis stands on the principal of identifying a connection among phenotype and genotype of markers. Over last twenty years, twenty studies on QTL mapping for various traits have been carried out (Table 4). Out of these, seven mapping populations use F_2 and only seven mapping populations used recombinant inbred lines. All these previous studies on QTLs mapping were based on RFLP/RAPD/AFLP/ SRAPs/ REMAPs /SSRs/ EST-SSRs markers genotyping. In all these studies, the number of QTLs identified ranged from two to one hundred and eighty for yield, yield contributing and fibre quality traits.

Marker-Assisted Selection (MAS)

Marker assisted selection (MAS) is a procedure by which a phenotype is selected on the basis of genotype of a marker (Collard *et al.,* 2005). Selecting the plants in the segregating population that have the suitable gene combinations is the important component of plant breeding (Weeden *et al.,*

1993). Once the markers tightly linked to the genes that are to be detected, breeders may use particular DNA marker to identify the plants carry the genes. The effectiveness and cost of MAS are influenced by the marker technique; therefore, it must be selected carefully (Young *et al.,* 1996). During the past two decades, RAPDs techniques have been used for MAS for getting the glanded plants and glandless seeds in the interspecific population of *G. sturtianum* and other species (Mergeai *et al.,* 1998). It was exposed that DNA markers connected to the major QTL (QTLFS1) for fibre strength could be utilized in MAS to increase fibre strength of commercial varieties in segregating populations (Zhang *et al.,* 2003). Identified tightly linked QTL used for marker assisted breeding and marker-assisted QTL manipulation to the genetic improvement of quantitative traits in cotton.

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