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 worldwide 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.

Keywords
QTL, Molecular markers, Genetic linkage maps, Marker assisted breeding.

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 epistasis 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 F2, 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 reproducibility
RAPD techniques have been used for many purposes in cotton including assessment of diversity, genome mapping, phylogenetic 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 RFLP 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; Galvan 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 and Yu 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 F2, 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 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     | Platform         | Operating system | Experimental designs                                                                 | Availability                                      | Reference                              |
|---------|-------------------|------------------|------------------|--------------------------------------------------------------------------------------|--------------------------------------------------|----------------------------------------|
| 1.      | AntMap            | DOS and UNIX     |                  | F₂ intercross, F₂ backcross, RIL (self), DH                                          | http://cse.naro.affrc.go.jp/iwatah/antmap/index.html | Iwata and Ninomiya (2006)             |
| 2.      | CarthaGe'ne      | C++              |                  | F₂ intercross, F₂ backcross, RIL                                                      | http://www.inra.fr/mia/T/CarthaGene/             | Schiex and Gaspin (1997)              |
| 3.      | DGMAP             | UNIX             |                  | Various including F₂ backcross                                                       | No longer available                               | Newell et al., (1995)                 |
| 4.      | JoinMap           | MS-Windows       |                  | BC₁, F₂ intercross, RILs (self), DH, DH₁, DH₂, HAP, HAP₁ 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     |                  | F₂ intercross, F₂ backcross, RIL (self), F₃ intercross (self), RIL (sib)          | http://www.broadinstitute.org/ftp/distribution/software/mapmaker3/ | Lander et al., (1987)                 |
| 7.      | Map Manager QTX  | Windows and Mac OS |                  | Advanced intercross, advanced backcross, RILs                                        | http://www.mapmanager.org/                        | Manly and Olson (1999)               |
| 8.      | MSTMAP            | C++ and Linux    |                  | BC₁, DH, HAP, RIL                                                                     | http://www.138.23.191.145/mstmap/               | Wu and Huang (2008)                  |
| 9.      | RECORD            | DOS              |                  | BC₁, F₂, F₃, RIL                                                                      | http://www.plantbreeding.wur.nl/UK/software_record.html | Van et al., (2005)                  |
| 10.     | THREaD Mapper     | Web- Browser enable tool |                  | F₂ intercross, F₂ 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/NT4.0/2000/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**                                                                                 |           |                      |
| 1       | Fiber quality                 | FS, FL, FF               | F₂         | 216 RFLP, 139 RAPDs                                                                      | 13        | Kohel et al., 2001  |
|         |                               |                          |            | **Size**                                                                                 |           |                      |
| 2       |                               | F₂                       | 171        | 217 SSRs, 800 RAPDs UBC and 1040 OPERON                                                   | 2         | Zhang et al., 2003  |
| 3       |                               | LY, LP, SW, NS, UQ, SF, FL, FE, FT, FF and IF | F₂         | 120 144 AFLPs, RFLPs and 150 SSRs                                                       | 28        | Mei et al., 2004    |
| 4       |                               | FS, FE, FF, FU and FL    | F₂         | 200 448 RFLP                                                                              | 28        | Zhang et al., 2011  |
| 5       |                               | FS, FE, FL, FU, LP and FF | F₂         | 117 290 SSRs and 9 AFLPs                                                                 | 16        | Zhang et al., 2005  |
| 6       |                               | FF                       | BC₃F₂       | 3,662 262 RFLPs                                                                          | 41        | Drayee et al., 2005 |
| 7       |                               | FL, FLU and SFC          | BC₃F₂       | 3,662 262 RFLPs                                                                          | 45        | Cheet et al., 2005  |
| 8       |                               | FS, FL, FF, FE          | RIL's       | 95 SSRs, 72 CSR                                                                          | 13        | Park et al., 2005   |
| 9       |                               | FS, FS, FF and FE       | R₂         | 1378 SSRs                                                                                | 39        | Shen et al., 2005   |
| 10      |                               | FS, FL, FF, MFT, FE and SFI | RIL’s     | 4106 SSRs, AFLPs, RAPDs and SRAPs                                                        | 48        | Wang et al., 2006   |
| 11      |                               | FS, FE, FU, FL and FF   | RIL’s       | 7508 SSRs, 384 SRAPs and 740 IT-ISJs                                                      | 13        | Zhang et al., 2009  |
| 12      |                               | FE, FL, FS, FF and FU   | CP          | 172 16052 SSRs                                                                            | 63        | Zhang et al., 2012  |
| 13      |                               |                          |            | **Type**                                                                                 |           |                      |
| 14      | Fiber and agronomical         | SCY, LY, LP, BW, SI, MFT, PER, WF,WT, FF, FL, FE, FS | RIL’s     | 188 141 SSRs                                                                             | 36        | Wu et al., 2009     |
| 15      | Yield and fiber               | SCY, LI, SI, LY, no. of seeds per boll, FS, FL and FF | F₂         | 69 834 SSRs, 437 SRAPs, 107 RAPDs, 16 REMAPs                                              | 57        | He et al., 2008     |
| 16      |                               | FS, FL, FF, FE, LP, SI, NB, SCY and LY | RIL’s     | 258 2131 SSRs                                                                            | 53        | Shen et al., 2007   |
| 17      |                               | LI, SI, LY, SCY, NSB and FS | F₂         | 69 834 SSRs, 437 SRAPs, 107 RAPDs, 16 REMAPs                                              | 52        | He et al., 2007     |
| 18      |                               | 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    |
| 19      |                               | SCY, LY, NB, BW, LP, SI, LI and FBN | RIL’s and IF₂ | 180 2675 EST-SSRs                                                                 | 111       | Liu et al., 2012    |
| 20      |                               | PH, FBN, BW, LP, LI, SI, LY, FL, FS, FE, FF and FU | G. hirsutum accessions | 81 121 SSRs                                                                              | 180       | Zhang et al., 2013  |
| 21      |                               | SCY, LY, LI, BW, FL, FS, FU | BIL's      | 146 2,041 SSRs                                                                            | 67        | Yu et al., 2013     |
| 22      |                               | LI, LY, PH, FL, FS, FS, FU | RIL's      | 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, 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 F2 mapping population. Till date, fifty linkage mapping studies done using intra or interspecific mapping populations (F2/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 F2 interspecific 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 F2 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., 2005). 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., 2005).
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 girded 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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