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Genetic Mapping in Cotton

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Abstract

The genus *Gossypium* provides natural fiber for textile industry worldwide. Genetic improvement in cotton for traits of interest is not up to mark due to scarcity of adequate information about fiber production and quality. Use of DNA markers for overcoming the issues of selection associated with complex traits is the ultimate choice which may lead to initiate breeding by design. Numerous marker-trait associations have been identified for economical traits using linkage analysis in cotton. Currently there is need for developing high-density genetic maps using next-generation sequencing approaches together with genome-wide association studies (GWAS). Efforts have been started in this direction and several QTLs including fiber quality, yield traits, plant architecture, stomatal conductance and verticillium wilt resistance were identified. This chapter narrates genetic diversity, QTL mapping, association mapping and QTLs related to fiber quality traits. The incorporation of various genomic approaches and previously described marker strategies will pave the way for increase in fiber production.

Keywords: cotton, fiber, association mapping, QTLs

1. Introduction

Cotton (*Gossypium spp.*) belongs to the genus *Gossypium*, family Malvaceae and order Malvales, and is known as an ultimate source to produce natural fiber. All over the world, cotton seed is one of the important sources of edible oil. Cotton provides raw material for millions of consumers as well as for industrial products throughout the world. Total impact of cotton in the textile industry continues to excel its importance (presently exceeding 500 billion US$) [1].

Geographically cotton is distributed at 36° South latitude and 46° North latitude in tropical and subtropical regions of the world. The total share of northern hemisphere in global cotton production is 90%. Planting time in the northern hemisphere is the time of harvesting in the southern hemisphere [2].

Cotton is a warm climate crop (cultivated in nearly 100 countries), and is largely grown in Asia, America and Africa. Major emphasis of cotton breeding programs is to improve its lint yield and its quality. It has been thoroughly studied that yield, yield components and fiber quality characters are governed by a number of genes and these are inversely related to each other. Fiber quality and other economic characters have not been refined with conventional breeding strategies as these are adversely influenced by the ecological conditions.

Molecular markers produce variability at genotypic basis and speed up breeding process. Genetic maps are constructed from DNA-based markers information and quantitative trait loci (QTLs) related to trait of interest have been identified. The availability of reference genome of upland cotton (*G. hirsutum* L.). Egyptian cotton (*G. barbadense* L.) and draft genome of *G. arboreum* L., *G. herbaceum* L. [3] and *G. raimondii* [4] has revolutionized the 'omics' studies. The advent of next-generation sequencing with high-throughput sequencing has allowed genotyping at single nucleotide level which are contributing a lot. High uniformity, strength, extensibility, and other fiber quality traits are need of the day worldwide [5, 6]. Fiber development in cotton is a complicated process-comprised of fiber initiation, elongation (primary wall synthesis), wall thickening (secondary wall synthesis) and desiccation (maturation) [7, 8]. Lint and fuzz cover the seed coat of cotton lint serves as a natural textile fiber while fuzz remains on seed coat after ginning.

2. Evolution of genome size in cotton

Polyploidy is a vital evolutionary process in angiosperms; one of the vital factors in creating new plant species [9–11]. Around 70% of the existing angiosperms are polyploids, which include many world-leading crops such as cotton, wheat, potatoes, canola, sugarcane, oats, peanut, tobacco, rose, alfalfa, coffee and banana [11, 12]. Nonetheless, genomic studies in polyploids are lagged behind than diploid species due to their polyploidy nature. It is highly tiresome to create a reference genome in tetraploid cotton owing to involvement of different species. However, advancements in genomic studies like quantitative trait locus (QTL) mapping, association mapping, nested association mapping, cloning, genome sequencing, functional and comparative genomics have laid down the foundation to study such complex organisms for the evolution of highly saturated genetic maps to ascertain the genomic evolution.

In polyploids, after the occurrence of whole genome duplication (WGD), intra and inter-chromosomal rearrangement processes have reallocated both large and small segments across the genome over the evolutionary span. Genome decomposition has given rise to a set of duplicated DNA segments which are dispersed among the chromosomes, with all the duplicate pairs exhibiting a similar degree of sequence discrepancy [11, 12].

The genus *Gossypium* has a long taxonomic and evolutionary history [13]. *Gossypium* is comprised of 52 species, including 46 diploids (2n = 2x = 26) and 5 allotetraploids including one

purporated tetraplod species (2n = 4x = 52) [3]. Out of these, only four species are domesticated. In total, two species are old world diploids (*G. arboreum* L. and *G. herbaceum* L.) and two species are new world allopolyploids (*G. hirsutum* L. and *G. barbadense* L.) which are consisted of a (~1700 Mb) A_t and (~900 Mb) D_t genome. In total four domesticated species contribute toward the production of natural fiber worldwide [14]. *G. hirsutum* L. also known as upland cotton dominates the world's cotton production i.e., > 95%. *G. barbadense* L. known as extra-long staple or sea-island cotton is grown on 2–3% area in the world, but has lower yield/hectare compared to the *G. hirsutum* L. Cultivation of the diploid cotton like *G. arboreum* L. and *G. herbaceum* L. is restricted to a few countries, such as Pakistan and India. Diploid species (2n = 26) are grouped into eight genomic groups (A–G, and K), based on similarities of chromosome pairing [15]. Eight genomes are divided into three different clades as shown in **Figure 1** as A, B, E, and F; D; C, G, K genomes [16], are found naturally in Africa and Asia. D genome clade is indigenous to the Americas and is found in Australia (**Figure 1**).

Tetraploid species evolved ~1–2 million years ago (MYA) as a result of hybridization between "A" and "D" genome species [16], diverged each other from a common ancestor about 4–11 (MYA) [6, 17]. Both "A" & "D" genomes have maintained some level of sequence similarity, resulting in a high transferability of markers among the *Gossypium* species [18, 19]. F_{1s} of mostly cultivated cotton species (*G. hirsutum* L. and *G. barbadense* L.) can further be used in making the crosses with wild tetraploid species (*G. darwinii* G. Watt, *G. mustelinum* Miers ex G. Watt, *G. tomentosum* Nutt. ex Seem.) which produce normal hybrids and some productive off springs [20].

During the last couple of years, major emphasis of genomic research is on comparative analyses of closely related, homoeologous stretch of genomic sequence in plants i.e., maize, rice, and sorghum [21–23]. Cultivated upland cotton has a history of genetic bottlenecks in evolution that have significantly reduced the extent of genetic diversity of the cultivated cotton species, which compelled geneticists to use populations developed by hybridizing two different species for identifying high number of polymorphisms.
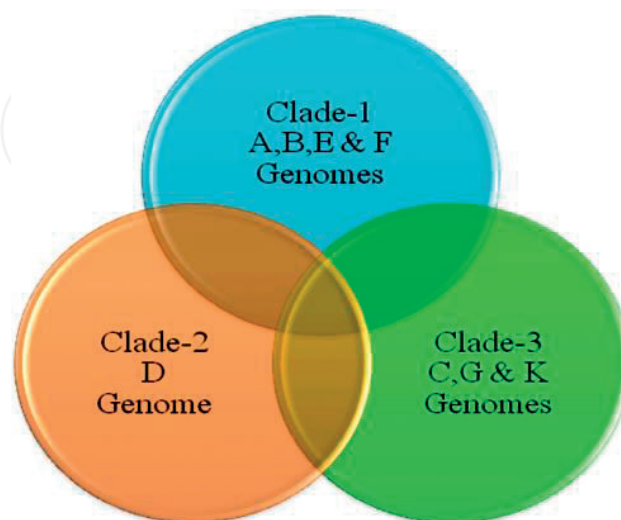
Figure 1. Clades formation in *Gossypium*.

2.1. Genetic diversity in cotton

Cotton has a narrow genetic base which is the main hindrance in sustaining cotton productivity worldwide. Limited genetic diversity and low efficiency of traditional selection methods were the major factors to slow down the process of cultivar improvement from the last three decades [24–26]. One of the major reasons for limited variability of cotton cultivars is the use of adapted cotton germplasm in breeding program. The cotton breeders avoid using the wild genetic resources because of the problem of linkage drags of unwanted characters. The other reason is the lack of innovative tools to mobilize the useful genetic variations from diverse exotic cotton species of *Gossypium* genus into the breeding cultivars. All these factors together led to the genetic bottleneck in evolution [27]. Understanding about the extent of genetic diversity and relationships among breeding materials could pave the way for precise parental selection and germplasm organization for cotton improvement breeding programs [28–34]. Percent Disagreement Values (PDVs) distance matrix, tree clustering diagram and neighbor-joining stars are different statistical techniques to determine the extent of genetic diversity. Polymorphism Information Content (PIC) is another statistical technique that can be deployed to evaluate the polymorphism acquired through different techniques, primers or markers [35–38].

2.2. Genomic studies in cotton

The discoveries made through exploring the genome would set a firm foundation for initiating breeding by design for improvement programs in cotton. Over the last two decades, multiple genomic tools have been utilized for exploring the cotton genome. Different types of DNA markers such as restriction fragment length polymorphism (RFLP) [39, 40], randomly amplified polymorphic DNA (RAPD) [41–48], amplified fragment length polymorphism (AFLP) [27, 49], simple sequence repeat (SSR) or microsatellites [37, 50, 51], single nucleotide polymorphism (SNPs) [52–55], physical maps, genetic maps, mapped genes and QTLs, microarrays, gene expression profiling, BAC and BIBAC libraries, QTL fine mapping, resistance gene analogs (RGA), genome sequencing, non-fiber and non-ovule EST development, gene expression profiling, and association studies for various traits have been extensively used for understanding the cotton genome. Finally, the genome sequence information of *G. hirsutum* L. and its progenitor species will considerably expedite the cotton genomic research toward identifying new genes conferring various traits of interest, and would also help in identifying DNA markers linked with traits which can be used in MAS.

2.3. Mapping population

The group of individuals used for the determining variation on genetic basis, phylogenetic analysis, development of genetic map, assigning of loci to the trait of interest is known as mapping population; which are of vital importance for mapping. Mapping populations are obtained using two contrasting parents for the desired trait. In self-pollinated crops; usually mapping populations include F_2 [56, 57]; $F_{2:3}$ [58, 59], recombinant inbred lines (RILs) [60, 61], backcross (BC) [62, 63], Backcross inbred lines (BILs) [64], near isogenic lines [65, 66], double-haploids [67, 68], chromosome substitution lines (CSILs) [69, 70]. F_2, BC, RILs and double-haploids have been highly used for linkage mapping studies in cotton.

The easiest developed populations include F_2 and BC as less duration is required. F_2 population has more cons for detecting QTLs with additive effects and can also be utilized for assessing the dominance pattern. A number of QTLs for cotton has been found using this population [56, 71–73]. Backcross population produce false results if dominant factors are allowed as additive and dominance are overlapped. Nonetheless, these two populations have demerits including (i) owing to less meiosis some markers which are present at a distance from QTL are also counted; (ii) non-allelic interaction cannot be analyzed; (iii) F_2 and BC have got more heterozygosity and also temporary as cannot be repeated at different locations. In-contrast RILs have gone through number of selfings and are highly homozygous [63]. Moreover, RILs are populations which produce finely saturated genetic maps as recombination frequency is high. RILs have been used in cotton for identifying traits related to agronomic and fiber [5, 53, 74]. Doubled-haploids are the best populations for improving any trait as these are the ones having 100% purity. These can be obtained in less duration compared to RILs and BILs but needs to be developed in a fully sterile environment with high skill [75]. By using these, it's convenient to reduce the variety development duration and analyze genetic behavior. BILs, RILs and double-haploids are the permanent populations and the inferences can be analyzed in detail of QTLs after phenotypical screening, genotyping and genetic map construction.

2.4. Association mapping

During the last decade, interest of plant geneticists is increasing to use the nonrandom associations of loci in haplotypes, a powerful high-resolution mapping tool for studying the complex quantitative traits as compared to the conventional linkage mapping. Association between chromosomal fragments and phenotype can be determined through exploiting genotypic data. Genotypic and phenotypic data are collected from a population with unknown relatedness followed by the estimation of marker-trait association in the experimental population. Association mapping is an open system model that helps in developing high-resolution maps while in linkage mapping, fine mapping is required to reach near the loci [76], but understanding about the time and place of recombination in the genome is very tricky. Single-marker analysis, interval mapping, multiple interval mapping, and Bayesian interval mapping, have been widely used in conventional linkage mapping studies. Association mapping is an influential approach to map genes for QTLs using genomic tools together with robust statistical methods. Association mapping is an imperative way to investigate the genetic structure of QTLs which can lay down a foundation to study the different traits like insect resistance, disease resistance, earliness, fiber quality etc. [77]. Zhu et al. [78] reviewed status and prospects of association mapping in comparison to linkage analysis. However, recent advances in association of DNA markers with the fiber quality traits paves the way to understand the mechanism of cotton fiber development.

Linkage disequilibrium mapping (LD) commonly named as association mapping is a method to detect and locate QTLs based on marker-trait association study and it anticipates a relatively new method to dissect the complex traits. Methods for linkage disequilibrium were initially developed for undertaking human genetic studies [79, 80]. These methods have been successfully translated on crop plants for exploring the linkage disequilibrium (LD). Association mapping offers a uniquely high-resolution mapping strategy based upon historical

recombination events at population scale which can empower mapping at gene level in less studied organisms where conventional QTL mapping would not be practical [81].

There are several ways for the determination of LD [82] but the most popular statistic parameter for the calculation of marker-trait association is "r^2". Theoretically Pearson's correlation coefficient narrates the polymorphism of allele at one locus to other allele at another while "r^2" is known as "coefficient of determination" being the squared value of Pearson's coefficient. As a whole "r^2" elaborates the magnitude of individual variance independent variable with the dependent variable when linear regression is accomplished.

LD is described by another common statistic parameter termed as "Lewontin's D". If two loci are segregated randomly then "D" measures the disequilibrium as the distinction among coupling and repulsion gametes frequencies [83]. D is used for calculating $D^/$ for determination of association among loci using the formula:

$$D = 2 P_{AB} - P_A \times P_B \tag{1}$$

P_{AB} is the observed extent of a set of closely linked alleles of two loci inherited to offspring with allele A in the 1st locus and B in the 2nd while PA is allele A frequency in 1st site and PB is allele B frequency on 2nd. Owing to base on allelic magnitude the D calculated value is not a precise approach for determining power and distinction of nonrandom association. $D^/$ was developed by Lewontin [83] for determining the LD which is less related to allelic magnitude. Varshney and Tuberosa [81] revealed that LD variance values were often high but $D^/$ had minimum variance nonetheless the individuals were evaluated from populations under equilibrium. He also pointed out that population size had significant impact upon association as $D^/$ can produce problematic outcomes for the studies.

Ersoz et al. [84] devised other approaches based on kinship which deals with the determination of probability of independence among two loci through individual spreading instead of using LD statistics summary. These statistical tools are also known as model-based LD methods which allow determination of population recombination measure from sequence information in an unbiased equilibrium model [85–87]. Besides these models there are other ways which are model-based using diverse population structures for the calculation of LD for differentiation among different individuals origin [88].

The applications of association mapping are receiving major attention for genomic studies of quantitative traits in all major crops. However, association mapping achieved for crop improvement is not comparable to that in human genomics [89]. Over the decades, many QTLs have been identified using bi-parental populations for yield, yield components and other traits of interest [90, 91]. However, only few were successfully used in plant improvement programs. The recent advancements in genomic science has provided the opportunity of identifying more QTLs through various approaches including GWAS. Similarly, low cost genotyping methods also complemented the aforementioned in identifying more QTLs which can be used in breeding programs. A genome-wide association study (GWAS) was conducted for yield components and fiber quality traits on a diversity panel of 103 cotton accessions. They identified 17 SNP associations for fiber length and 50 for micronaire value [191]. In another report, GWAS

was conducted on 318 genotypes. They found that 54.8% of the GWAS detected alleles were transferred from three founder parents; Deltapine15, Stoneville 2B and Uganda Mian [192].

DNA markers linked to QTLs contributing toward traits of agronomic importance are invaluable resources for cotton (*Gossypium* sp.) improvement. In spite of the existence of potential diversity in the *Gossypium* genus, it is mainly underutilized due to barriers of photoperiodism and stringency of advanced technologies to deal with these challenges. Linkage disequilibrium (LD) mapping is a powerful tool for dissecting genetic diversity. Abdurakhmonov et al. [92] used association mapping in 208 exotic *G. hirsutum* L. accessions, containing 208 landrace accessions and 77 photoperiodic accessions. A significant genetic diversity within exotic germplasm stock was found. About 11–12% of SSR loci showed significant LD. Estimates of LD declined at significant threshold (r^2 = 0.1) found in the range of 10 cM genetic distance in landraces and 30 cM in varieties. LD calculated at r^2 = 0.2 was estimated on an average 6–8 cM in cotton varieties and ~1–2 cM in land races, providing evidence for potential associations for important traits. A significant relatedness and population structure was found in the germplasm. Mixed linear model (MLM) detected between 13 and 6% of SSRs associated with major fiber quality parameters in cotton. The study demonstrated the potential application of association mapping in cotton to exploit new sources of genetic variation.

Utility of the diploid Asiatic cotton species in breeding programs depend upon the understanding of the ancestry and genetic relatedness. A collection of 56 *G. arboreum* L. accessions collected from nine different zones of Asia, Africa and Europe were assessed for eight fiber quality parameters (strength, lint color, lint percentage, micronaire, elongation, maturity, 50% span length and 2.5% span length) and genotyped with 98 microsatellites. Majority of the SSRs were found polymorphic. The analysis of population structure identified six major clusters for accessions representing distinct geographic regions. Marker-trait association estimates were assessed by general linear model method. This study illustrated the potential of association mapping in diploid cotton, because a modest number of SSRs, phenotypic data and strong pioneering statistical interpretation, identified interesting associations [93].

The use of marker-assisted breeding (MAB) in cotton improvement is limited, as compared to the other commercial crops due to its narrow genetic base and limited polymorphisms. This scenario urges a need for tagging, characterization and utilization of naturally existing polymorphisms in *Gossypium* germplasm collections. Estimates of genetic diversity, population structure, LD magnitude and association mapping were explored for cotton fiber quality trait in a set of 335 *G. hirsutum* L. germplasm cultivated under two distinct environments by surveying 202 SSRs. Genome-wide LD at $r^2 \geq 0.1$, extended up to 25 cM in tested cotton accessions. However, at a threshold of $r^2 \geq 0.2$, genome-wide was reduced to ~566 cM, highlighting the potential application of association mapping studies in cotton. Preliminary findings suggested inbreeding, linkage, selection, genetic drift and population stratification as the key LD-generating players in cotton. Using a kinship and unified MLM on an average ~20 SSR markers were observed to be associated with major fiber quality traits in two environments. These significant associations were further confirmed for permutation based multiple testing and population structure by applying linear model and structured association test. The identified association provided a strong evidence for the use of association mapping studies in cotton germplasm resources [94].

In another report, association studies were undertaken to identify SSR markers linked with fiber traits in the exotic germplasm population derived from multiple crosses among tetraploid species of *Gossypium*. After 12 generations of continuous selfing, a total of 260 lines were selected for evaluation of fiber-related traits in three environments from species polycross (SP) population. A total of 314 polymorphic fragments were amplified by surveying with 86 SSRs. The SSRs showing 6% allele frequency were evaluated for associations. A total of 59 markers have substantial ($P < 0.05$, 0.01, or 0.001) association with six fiber traits. Structure analysis grouped the population in six groups with allelic frequency ranged from 0.11 to 0.27. The correction for population structure and kinship analysis identified 39 out of 59, significant marker-trait associations. Population sub-structure was highly significant for boll weight. The results clearly indicated that marker-trait associations have a promising potential in determining the genetics underlying interrelationships among fiber traits [95].

The discovery of valuable alleles for fiber quality traits and also the novel germplasm exhibiting high fiber quality features are important for accelerating the breeding progress for improving the lint quality. An association mapping study was conducted for fiber quality traits using 99 *G. hirsutum* L. accessions with diverse origins. A total of 97 polymorphic microsatellite marker were used which detected 107 significant marker-trait associations for three fiber quality traits under three diverse environments. A total of 70 marker-trait significant associations were detected in two to three environments while 37 identified in only one environment. Out of the 70 marker-trait associations, 52% were found similar with earlier reports, indicating the stability of these loci for the target traits. Further, a large number of elite alleles conferring two or three traits were also detected. These results pointed out the potential of using germplasm for mining elite alleles and their use in breeding for improving the lint quality [71].

Knowledge about population structure and linkage disequilibrium in association mapping studies can help in minimizing the appearance of false positive associations. Association mapping of verticillium wilt resistance in cotton was reported in the panel of 158 cotton genotypes. The studied germplasm was genotyped with 212 markers covering the whole genome and phenotyped with disease nursery and screening method in green house. In total 480 alleles were identified, ranged 2–4 alleles/locus. A total of two major groups and seven subgroups were identified through model-based analysis. The LD level of the linked markers was considerably higher than the unlinked markers, indicating that physical linkage heavily affected LD in this panel and LD level increased when the studied germplasm was divided into groups and subgroups. In total, 42 marker loci were associated with verticillium wilt resistance, which were mapped on 15 chromosomes. In total, 10 out of 42 marker loci were found to be constant with already known QTLs while 32 were new marker loci. This study paved the way for marker-assisted selection of verticillium wilt resistance in cotton [96].

Baytar et al. [97] used SSRs in a germplasm collection consisting of 108 genotypes for association analysis and analyzing genetic diversity, population stratification and linkage disequilibrium in upland cotton. 967 alleles were used for population construction and differentiated into 4-subgroups. Linkage disequilibrium showed the decay in 20–30 cM ($r^2 \leq 0.5$) and association was observed via general linear model and mixed linear model for verticillium disease resistance. As a whole 26 markers were observed associated with this disease on

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