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REVIEW

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Genetic improvement of fiber quality in tetraploid cotton: an overview of major QTLs and genes involved in and edited for the quality of cotton fibers

BAGHYALAKSHMI Kari[1*], PRIYANKA Rajendran Ariyapalayam[1], SARATHAPRIYA Govindaraj[1], RAMCHANDER Selvaraj[2] and PRAKASH Arkalgud Hiriyannaiah[1]

Abstract

Cotton, an important industrial crop cultivated in more than 70 countries, plays a major role in the livelihood of millions of farmers and industrialists. Cotton is mainly grown for its fiber, an economic component that can be differentiated from its epidermal cells in the outer integument of a developing seed. Fiber length, fiber strength, and fiber fineness are three main attributes that contribute to the quality of cotton fibers. Recent advancements in genomics have identified key genes, which are the most important factors that govern these three traits, can be introduced into cultivars of interest via gene editing, marker-assisted selection, and transgenics, thus the narrow genetic background of cotton can be addressed and its fiber quality traits can be enhanced. Over the past two decades, quantitative trait loci (QTLs) have been mapped for different fiber traits, approximately 1 850 QTLs have been mapped for fiber length, fiber strength, and fineness among which a few genes have been edited for quality improvement in cotton. In this background, the current review covers the development and the factors that influence these traits, along with the reported genes, QTLs, and the edited genomes for trait improvement.

Keywords Cotton, Fiber length, Fiber strength, Micronaire, Quantitative trait locus, Genome editing

Introduction

Cotton is an important agricultural product that holds a prominent place in the global market for natural textile fibers. It also continues to be a vital source of income for a large part of the farming community. However, the intense conflict between natural and synthetic fibers has created a tense situation to enhance the quality and productivity of cotton fibers. The cotton genus contains eight genomes denoted as A, B, C, D, E, F, G, and K. The genomes of the Old-World diploids of two species (*Gossypium arboreum* and *G. herbaceum*) have limited access to the A genome. The D genome is found in South and Central America, while the B, E, and F genomes are prevalent in Africa and Arabia (Fryxell 1992). Australia has diploid species such as Kimberly cotton (K), Grandicalyx (K), Sturtia (C), and Hibiscoidea (G (Craven et al. 1994). These species have evolved into five species such as the commercially important *G. hirsutum* and *G. barbadense*, both belonging to the AD genome group. *G. barbadense* is also known as Egyptian cotton, Sea Island cotton, Peruvian cotton, and superior cotton whereas *G. hirsutum* is referred to as American cotton or upland cotton. The main species, *G. hirsutum*,

*Correspondence:
Baghyalakshmi Kari
kauverik@gmail.com
[1] ICAR-Central Institute for Cotton Research, Coimbatore 641004, India
[2] School of Agricultural Sciences, Karunya Institute of Technology and Sciences, Coimbatore 641004, India

contributes approximately 90% of the global cotton production. In India, four species such as *G. hirsutum*, *G. arboreum*, *G. herbaceum*, and *G. barbadense*, are commercially cultivated.

Cotton fibers are simple trichomes that are unicellular and unbranched and they differentiate from the epidermal cells in the outer integument of a developing seed. According to Bradow et al. (1996), single-seed fibers show continuity in shape, physical maturity, cell wall thickness, and length. Cotton fiber development includes four distinct yet overlapping stages such as initiation, elongation (with primary cell wall synthesis), secondary cell wall (SCW) synthesis, and maturation. Among these, cotton fiber formation and elongation are intricate processes that involve numerous genes and pathways. Lint fibers begin to elongate at the anthesis stage whereas the fuzz fibers begin to elongate 5–10 days post-anthesis (DPA); linear growth continues for approximately 20 days or until a length of 25–30 mm is reached (Pesch et al. 2013). After this point, the elongation gets stopped and the deposition of cellulose gets started. However, these two processes frequently overlap with each other (Hinchliffe et al. 2010). After five to ten days of anthesis, the second wave of fibers begins to elongate, producing fuzz fibers—also known as 'linters' (Salih et al. 2016). These are typically short and adhere to the seed when ginned. Improving the production and quality of cotton fiber and reducing the fuzz content has long been a primary objective of cotton domestication since it directly affects the quality of textiles. In addition to yield and the quality of fiber, other factors that are deemed to be significant include fiber composition, vegetative cycle duration, and tolerance to various biotic and abiotic stressors.

Genomics-assisted breeding process utilizes high-throughput genotyping to predict multiple complex traits. The key genes are then introduced into cultivars of interest via gene editing, marker-assisted selection, and transgenics processes, helping to mitigate the narrow genetic background, caused by the utilization of fewer parents in cotton breeding programs. Although wild cotton species possesses exceptional fiber traits and adaptive mechanisms to withstand a variety of detrimental influences, its application in breeding programs is limited due to the breakdown of hybridity. At present, over 20 different wild cotton species such as *G. tomentosum*, *G. darwinii*, and *G. mustelinum* have been employed in genetic breeding and development programs (Chang et al. 2023). In the realm of cotton, molecular markers have proven to be invaluable genetic tools for constructing genetic, and physical maps. Technological advancements have simplified the screening of large plant populations for rare, abnormal, or normal genetic variations in specific target genes that are crucial for key traits. Traditional cotton breeding methods, involving interspecific hybridization for stable genetic transformation, encountered a lot of challenges. However, numerous genomic tools and biological protocols, including polymorphic genetic markers, linkage maps, and diverse mapping populations, have been developed so far to overcome these challenges. In this context, the aim of the current study is to present a comprehensive overview of significant quantitative trait loci (QTLs) and the genes associated with the quality of cotton fibers, identified in previous research.

Three important traits of quality fiber

Over the past two centuries, progress has been achieved in both yield and quality through extensive traditional quantitative genetic research. However, improvement in both yield and quality was achieved at a cost of genetic diversity, thereby increasing the susceptibility to biotic and abiotic stresses (Maqbool et al. 2010). Cotton fiber quality attributes can be categorized into seven industrially significant categories: fiber length (FL), fiber strength (FS), fineness, maturity, fiber entanglement (Neps), length uniformity index, and color, among which FL, FS, and fineness have been extensively investigated so far. The average FL of the longer half of the combed single seed cotton bundle is called as Upper-half-mean length (UHML). FS is determined based on the force required to break a bundle of fibers per unit mass (tex) using a High-Volume Instrument (HVI). In general, micronaire (MIC) is used to assess the fiber's maturity and fineness. It measures the air permeability of a compressed cotton fiber mass. Easy-to-compress fibers have lower air permeability, resulting in a lower MIC value whereas mature or coarse fibers are resistant to compression and hold a higher MIC value. The *G. barbadense* fiber has an average FL of 36 mm, 45 $cN{\cdot}tex^{-1}$ in FS combined with 3.8 in MIC, whereas the *G. hirsutum* fiber has an average FL of 30 mm, FS of 30 $cN{\cdot}tex^{-1}$ with an improved MIC value of 4.2 (Constable et al. 2015). In general, *G. barbadense* is exploited for its length, while *G. hirsutum* is exploited for its micronaire and yield stability. Table 1 shows the classification of each trait.

There exists three main fiber types based on tip morphology such as narrow, tapered, and hemisphere/blunt (Graham and Haigler 2021). *G. barbadense* has narrow fibers, while *G. hirsutum* has either one of two types, i.e., blunt/hemisphere tips or tapered tips (Stiff and Haigler 2016). To be specific, the hemisphere-tipped fibers have a large diameter that is twice to that of the narrowed tips, thus potentially influencing the FL and FS characteristics. The two tip morphologies of *G. hirsutum* result in heterogeneous fibers on single seed and boll with slightly different characteristics (Graham and Haigler 2021). Moreover, the presence of two populations of fiber tip

Table 1 Classification of cotton based on fiber traits

Trait	Classification	Description
Upper half mean length /mm	Short staple	≤ 20.0
	Medium staple	20.5–24.5
	Medium long staple	25.0–27.0
	Long staple	27.5–32.0
	Extra long staple	≥ 32.5
Fiber strength /(cN·tex^{-1})	Very Strong	≥ 31.0
	Strong	29.0–30.0
	Average	26.0–28.0
	Intermediate	24.0–25.0
	Weak	≤ 23.0
Micronaire	Very fine	< 3.0
	Fine	3.0–3.9
	Average	4.0–4.9
	Coarse	5.0–5.9
	Very coarse	> 6.0

types in *G. hirsutum*, with many fibers having a larger diameter, might contribute to the lower fineness. In contrast, the single narrow tip morphology of *G. barbadense* produces homogeneous fibers with greater uniformity and smaller diameters, thus potentially contributing to its greater quality (Stiff and Haigler 2016). Some of the accessions studied so far have shown hemisphere-tipped fiber initials in diploid domesticated species, thus producing higher-diameter fibers, although tip refinement is seldom studied in these species (Butterworth et al. 2009).

Mechanism and the influencing factors of fiber development

Inheritance and genetic analysis of fiber quality

The genetics of fiber traits is evaluated by estimating the variations in genetic components such as the dominance and additive effects. Most studies have shown that FL and fineness exhibited additive gene action, whereas FS showed an additive genetic effect with partial dominance (Ali et al. 2008; Iqbal et al. 2003; Basal and Turgut 2005). The environment has less impact on fiber properties than the additive gene effects do (Cui et al. 2014; Zhang et al. 2017). Therefore, traits whose phenotypic variation is mostly governed by genetic impacts can be enhanced through genetics and breeding processes. On the other hand, those traits that are more influenced by the environment can be efficiently altered by modifying the cultivation methods. In general, high additive effects favor early selection whereas non-additive effects frequently point to the possibility of using heterosis breeding. Both FL and FS showed a substantial, broad or narrow-sense heritability in most studies, thus inferring that allopatric selection and shuttle breeding techniques can improve these traits (Shahzad et al. 2019). In recent years, association mapping has often been used to elucidate the genetic basis of these traits. Heritability is one important aspect that influences the accuracy of this association mapping. When the heritability (H^2) value is higher than 50%, then it is regarded as highly heritable and is generally used to assess the stability of the hereditary traits. High heritability levels are typically observed in the fiber quality traits of the upland cotton. For instance, the H^2 values of these traits ranged between 86%–93%, 84%–92%, 69.54%–91.05%, and 72.06%–91.38% in the studies conducted by Nie et al. (2016), Huang et al. (2017), Dong et al. (2018), and Liu et al. (2020), respectively. The analysis of variance (ANOVA) results from the same experiments showed that the variances of the tested traits attributed to both genotype and the environment while their interaction was found to be statistically significant. This implies that the environment indeed influenced these traits, although genotype remains the primary influencing factor.

Internal hormonal factors

Fiber development undergoes four different sequential phases, as mentioned earlier. Auxin is carried into fiber cells from ovules while several phytohormones, for instance, brassinosteroids, abscisic acid, and jasmonic acid, regulate the initiation phase (Jareczek et al. 2023). Altering the phytohormones either through exogenous application or by triggering the genes responsible for fiber initiation tends to affect the number of emerging fibers. Higher yields can be attained by adjusting the quantity of fiber initiated on the ovule's surface through hormone modification, especially in low-producing cultivars. However, this phenomenon should be kept under control with physical limitations inside the locule. Both elongation and primary cell wall deposition in fiber growth cease at approximately 16 DPA, whereas it universally stops after 25 DPA (Tuttle et al. 2015). Secondary cell wall deposition begins during the transition stage and continues for the next 20–30 days, resulting in a cell wall that is composed of approximately 98% pure cellulose (Kim 2018). This phase involves significant changes in the regulation of reactive oxygen species (ROS), gene expression, and phytohormones, especially auxin and gibberellic acid since it plays a crucial role in the transition phase (Zhang et al. 2020). The secondary wall synthesis period further influences the FS and determines the width of the fiber cell wall. It is an established fact that plant hormones such as auxin, gibberellins, and brassinosteroids play a significant role in fiber development. Exogenous auxin application can lengthen as well as strengthen the fibers whereas auxin signaling interference results in shorter fibers (Xiao et al. 2019). Gibberellic acid, another phytohormone, has

been demonstrated to enhance FL, FS, and MIC (Xiao et al. 2019). Hence, both fiber length and strength are controlled by same hormones and are positively correlated with each other. Cotton fibers typically reach maturity between 40 and 50 DPA after several weeks of cell wall thickening, resulting in death and drying of fiber cells and boll dehiscence. During this maturation phase, unknown mechanisms cause the fiber to shrink into a hollow cellulose tube as it dries (Kim 2018). Throughout the phases of fiber development, phytohormones such as auxin, gibberellic acid, and ethylene significantly impact both quantities as well as the quality of the developed fiber. Additionally, the second and third phases primarily determine FL and FS, while the fourth phase is solely responsible for the fineness of the fiber.

External factors

Although fiber traits are strongly influenced by genetic factors, environmental factors also play a significant role in controlling these traits to a certain extent. Maturity, elongation, and short fiber index are main fiber quality attributes, whereas the MIC (fineness), FL, and FS are critical spinning factors. Crop management and climate have an impact on MIC and FS whereas genotype has a significant influence on FL. Temperature is one of the most significant environmental variables that influences the MIC value during the growth of bolls because it affects the secondary cell wall thickening process. The variations in temperature during the fiber thickening process also result in MIC variations (Darawsheh et al. 2022). A combination of crop management, a favorable growth environment, and cotton variety determines the length of the fiber. The length of the fiber also depends on factors during developmental stage, such as insufficient supply of nutrients, biotic stress, temperature extremes, and water stress. On the other hand, the cleaning or drying process during the post-harvest period further affects FL. To develop the management strategies that result in high-quality fiber production, it is necessary to comprehend numerous mechanisms by which cotton responds to its surroundings. Many studies have been conducted despite the intricacy of these mechanisms in terms of fiber development, yield, and quality; nonetheless, there is a dearth of literature on the critical interpretation of data regarding the impact of geography on lint quality in cotton.

Interrelation of fiber quality parameters

The domestication of considerably longer and stronger fibers in contemporary cotton is believed to have resulted from strong evolutionary pressure, involving genetic and epigenetic alterations in the cotton genome (Huang et al. 2021). Having been known for its quality traits, the cotton species *G. barbadense* has a good FL and an excellent FS. Both qualities are positively correlated with yield and the agronomical traits of *G. barbadense* (Bechere et al. 2014) and *G. hirsutum*. However, in terms of fiber fineness, *G. barbadense* possesses a low value, indicating its negative correlation with the FL and FS. Gnanasekaran et al. (2020) reported that a positive correlation between fiber fineness and staple length in upland cotton. During the fiber maturity stage, functional studies have also been conducted with a particular focus on cell wall thickening. Several genes were found to be responsible for fiber development while many of them overlapped among the four stages of fiber development.

Molecular breeding for fiber-related traits

The recent advancements attained in molecular marker technology reduced the cost involved in collecting the data and also increased the application of molecular information. Traditional breeding and biotechnological methods have contributed to genetic advancements, leading to the increased lint output (Prakash et al. 2022). However, without modern genomic technologies, the traditional breeding programs struggle to achieve the desired genetic gains. The introduction of genetically-modified cotton has accelerated research on cotton genomics whereas additional strategies such as marker-assisted selection (MAS) are now used to accelerate the breeding process. Genetic variability in fiber quality attributes limits the ability of the cultivated cotton to significantly enhance its quality. Many global cotton breeding projects focus on lint quality improving. The traditional breeding programs have made a significant contribution in terms of increased productivity and fiber quality of upland cotton (Morales et al. 2024). The use of molecular markers enables the plant breeders to modify the economic and agronomic traits rapidly and precisely. High-density genetic maps, anchored with fiber-associated genes, have a substantial impact on cotton fiber growth research and it also accelerates the MAS to improve the fiber quality. The identification of new genes in wild germplasm and its introduction into adapted cultivars hold sufficient potential to genetically enhance both the production as well as the quality of seed cotton fiber (Chang et al. 2023). The most common challenges encountered in breeding cotton cultivars for fiber quality traits are the multigenic regulation of fiber quality QTLs and the negative correlation among fiber quality traits while the latter is primarily influenced by linkage drag (Ijaz et al. 2019). Furthermore, the development of new cultivars through conventional selection techniques is an expensive, time-consuming, and a resource-intensive process (Kushanov et al. 2021). Molecular breeding or MAS technique is used in genetics and plant breeding programs to transfer the

desirable traits in a targeted way using DNA-based molecular markers. Evidences shows that fiber quality improvement has been achieved through molecular breeding approaches. Liu et al. (2022) investigated the molecular basis of 226 FL-related genes from 198 advanced breeding lines and found that all the genes were highly correlated with the trait. They also identified a breeding line that accumulated 51% of these FL genes and expressed the best fiber traits. Suvin is a *G barbadense* cultivar, released from the Indian Council of Agricultural Research-Central Institute for Cotton Research (ICAR-CICR), with fiber quality comparable to Pima cotton (Prakash et al. 2022). This genotype has been used to create nested association mapping (NAM) population by crossing with eight germplasm genotypes for fiber quality improvement at ICAR-CICR. Further research was also conducted to improve the quality parameter of *G hirsutum* lines through *G. hirsutum* × *G. barbadense* crosses (Baghyalakshmi et al. 2024). Li et al. (2022) found 21 genes that are closely related to fiber development using RNA-seq analysis of the progeny of Xinhai 16 and Landy cotton line 9 backcrossed populations at different stages of fiber development. An immature fiber mutant (*im*), identified during the 1970s, was used in the hybridization program (F_2 and $F_{2:3}$ populations) to verify its detrimental effects on lint yield and other fiber quality attributes (Wang et al. 2022). Li et al. (2024) identified 15 key genes that can decode the differences in fiber development between an immature fiber mutant (*xin w 139*) and wild-type (Xin W 139). All the identified genes can be incorporated into popular cultivars to further enhance the production of cotton quality through molecular breeding programs. In previous study, 3 157 high-throughput single nucleotide polymorphism (SNP) markers were acquired using specific-locus amplified fragment sequencing (SLAF-seq) and identified 91 QTLs that associated with fiber quality traits in three environments, according to the linkage analysis outcomes, with phenotypic variance explained (PVE) rates ranging between 4.53% and 20.92% (Chang et al. 2023). Using different chromosome segments from *G. tomentosum* on a *G. hirsutum* cultivar background, a population of 559 chromosome segment substitution lines (CSSLs) was developed and five fiber quality traits were found to have a total of 89 QTLs (Hao et al. 2024).

QTL and the genes responsible for fiber quality

Cotton fiber quality characteristics have been mostly investigated using linkage studies with biparental segregation populations before the publication of cotton genomes. This mapping technique has been used for a known time to identify almost 1 000 QTLs associated with fiber quality traits, spreading across 26 cotton chromosomes (Liu et al. 2020). The identification of QTL for fiber quality traits began as early as 1998 and several QTLs have been identified so far by segregating the populations. Since constructing segregating mapping populations is a time-consuming process, researchers utilized the available germplasms to study the fiber quality traits through genome-wide association mapping in the previous decade. In the past two decades, numerous QTLs have been mapped for different fiber traits which approximately 1 850 QTLs have been mapped for FL, FS, and MIC (www.cottongen.org). The number of QTLs for each trait are shown in Fig. 1.

Many QTLs that contribute to fiber quality in cotton have been identified so far while most of the QTLs have been located on the D sub-genome than the A sub-genome. The D sub-genome contains more QTLs associated with FL whereas the A genome harbors a greater number of QTLs contributing to FS. The chromosomes A7, D1, and D12 have a relatively high concentration of QTL (Fig. 2). QTL identification helps in establishing the connections between markers and measurable traits at the genomic level and also in understanding trait genetics. Various populations such as F_2, recombinant inbred lines (RILs), backcross inbred lines (BILs), and multiparent advanced generation inter cross (MAGIC) are commonly used in cotton research. F_2 and RIL populations are widely used to identify QTLs for fiber quality traits in cotton. At present, approximately 775 QTLs, 957 QTLs, and 178 QTL have been identified for FL, FS, and MIC, respectively. The studies indicate that chromosomes 14, 25, 19, and 7 carry most of the QTLs for FL while the chromosomes 7, 25, 21, and 5 for FS, and chromosomes 15, 5, and 1 for MIC (www.cottongen.org), respectively. In summary, chromosomes 14, 7, and 25 host numerous QTLs for these three fiber quality traits.

During cotton fiber elongation, a variety of proteins get expressed, including those associated with the tonoplast, plasma membrane, and some aquaporins (Ferguson et al. 1997). Aquaporins are essential for the passage of water through the plasma membrane and tonoplasts of the fiber cells (Arpat et al. 2004). In Ligon-lintless mutants (*Li1, Li2*), the RNA-seq revealed that aquaporins are the most significantly down-regulated genes in growing fibers (Naoumkina et al. 2015). The synthesis of secondary walls and cotton fiber maturity is influenced by various factors including genes, transcription factors, phytohormones, and environmental challenges (Ayele et al. 2017). So, fiber quality can be improved by modifying different genes and promoters involved in the production of SCW (Qin and Zhu 2011). Tables 2 and 3 show QTLs and genes that are important for fiber quality and their possible functions.

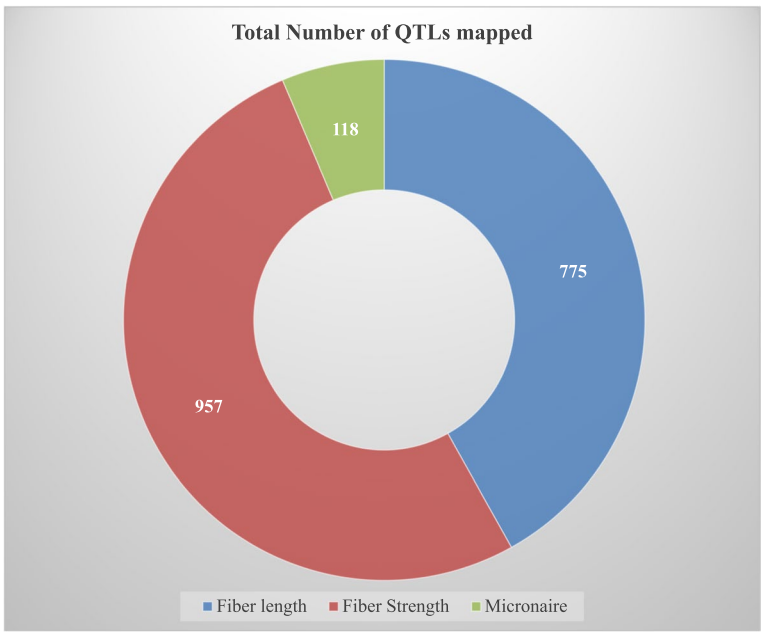

Fig. 1 Number of QTL mapped so far for fiber length, fiber strength, and micronaire

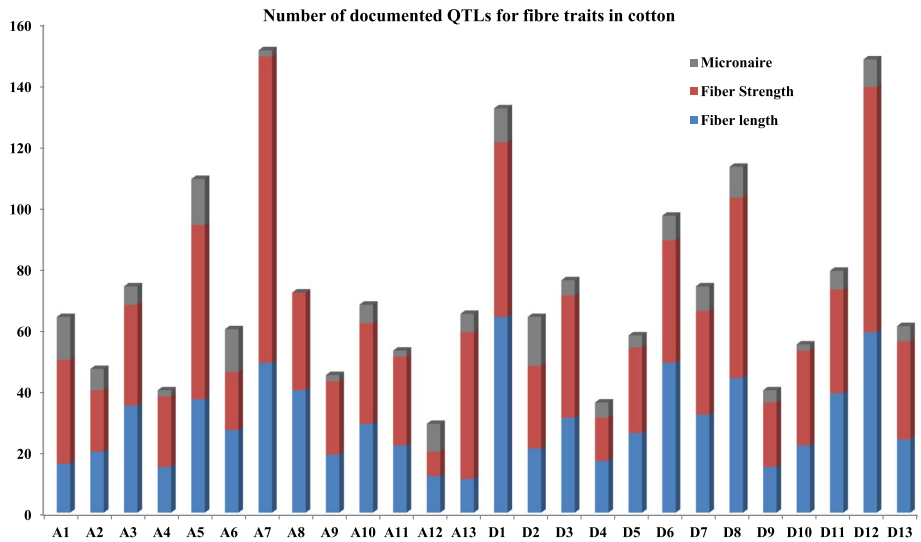

Fig. 2 Number of QTL for the fiber length, strength, and fineness traits in cotton

Impact of the modifications on gene expression

The formation of aliphatic polyester poly-d-(2)-3-hydroxybutyrate (PHB), a thermoplastic polymer in cotton, can change the properties of the fibers. The enzymes β-ketothiolase (phaA), polyhydroxyl alkanoate synthase (phaC), and acetyl-CoA reductase (phaB) catalyze the reaction that produces PHB from acetyl-CoA. In general, the cotton fibers exhibit endogenous phaA activity. The protein, expressed in fiber cells, was ascertained using transgenic cotton plants with the latter expressing phaB and phaC coupled with β-glucuronidase (GUS). The cotton fibers with *PHB* genes showed better insulating qualities. The successful application of transgenic technology for altering certain fiber properties has a significant impact on the textile industry (John and Keller 1996). According to the previous findings, during cell wall biosynthesis, high expression levels of *GhGluc1*, *GhCeSA1*, and *GhCeSA2* result in high rates of cellulose deposition (Ruan et al. 2003). Ca^{2+} conductance, regulated by *ghFAnnxA* during SCW production, causes an increase in cell wall

Table 2 List of fine-mapped and stable QTLs across the cotton genome

QTL	Chromosome	Position	Strategies	Reference
Trait: fiber length				
qFL-A08-1	A08	156.5–162.5 cM	Fine mapping by simple sequence repeats (SSR)	Liu et al. (2019)
qFLD03-1	D03	2.43–2.54 cM		
qFL-c10-1	10	1.01–7.01 cM	QTL mapping	Wang et al. (2016)
qFL21.2	21	109–189 cM	CottonSNP80K array	Tan et al. (2018)
qFL06.1	6	35.14 cM	Specific locus amplified fragment sequencing (SLAF-seq)	Ali et al. (2018)
qFL-c7-1	7	10.4–12.7 cM	Fine mapping by SSR markers	Chen et al. (2018)
qFL-chr5-2	5	44.29 cM	QTL mapping	Liang et al. (2013)
		38.92 cM		
		54.29 cM		
		42.67 cM		
qFL-chr14-2	14	83.85 cM		
		88.52 cM		
		91.93 cM		
		84.44 cM		
Trait: fiber strength				
	A08	157.5–162.5 cM	Construct linkage map and QTL mapping	Feng et al. (2020)
	A07	62.6 kb		
qFS-chr.D02	D02	21.30–38.13 cM		
qFS-chr01-2	1	27.41 cM	Linkage mapping	Liu et al. (2018)
qFS-chr07-2	7	69.01 cM		
qFS-chr16-3	16	15.61 cM		
qFS-A02-1	A02	81.75–82.67 Mb	SLAF-seq and Llinkage mapping	Chang et al. (2023)
qSCI-A02-1	A02			
Trait: micronaire				
qFM-chr19-1	19	67.87 cM	Linkage mapping	Liang et al. (2013)
		65.87 cM		
qFM-chr-3–1	3	39.95 cM		
qFM-chr25-1	25	47.11–47.21 cM	QTL mapping using SSR and SNP	Zhang et al. (2015)
qFM-chr25-3		64.01–64.81 cM		
qMIC-A03-1	A03	90.56 Mb	SLAF-seq and linkage mapping	Chang et al. (2023)
qMIC-A04-1	A04	59.45 Mb		
qMIC-A07-1	A07	50.02 Mb		
qMIC-A08-1	A08	69.93 Mb		
qMIC-D01-1	D01	42.61 Mb		

loosening and intracellular turgor pressure (Qin and Zhu 2011). On the other hand, FL gets inhibited by the down-regulation of *GhAnne* as a result of a decline in Ca^{2+} flow at the cell apex (Tang et al. 2014).

Enhanced FL is one of the most desirable qualities in the fiber growth process. The actin-binding proteins increase the degree of fiber elongation (Wang et al. 2010). F-actin arrays are important for Arabidopsis root hair development and staple elongation. When the F-actin decreases, it inhibits the fiber cell elongation process by silencing *GhACTIN1* (Qin and Zhu 2011). Both actin filaments and MTs, connected by kinetin, work together to change fiber length (Xu et al. 2009). Increased FL can be observed in *G. hirsutum*, when fiber-specific α-expansins *GbEXPA2* and *GbEXPATR* get overexpressed. *GhEXPA8* is another significant gene linked to fiber quality enhancement. The combined results of the studies conducted on three generations of the local cotton variety NIAB 846 showed a significant improvement in staple length and MIC values in transgenic cotton plants (Bajwa et al. 2015). Potassium (K) is the main osmotic agent that causes fiber elongation and increases the cell turgor pressure. In case of potassium deficiency, the cotton

Table 3 Successful examples of fiber quality improvement through biotechnology

Gene	Accession no	Annotation	Reference
Fiber length			
GhE6	BM356398	Fiber protein E6, fiber elongation, and secondary wall biosynthesis	John et al. (1996)
pGhEX1	AF043284	Found abundantly in cotton fiber cells and regulated during fiber elongation	Orford et al. (1998)
GhTUB1	AF487511	Plays a role in polar elongation of cotton fiber	Zhang et al. (2003)
Exp1	DQ204495	Alpha expansin1, cell wall extension and effect on length and quality of fiber	Zhu et al. (2012)
ACT 1	AY305723	Actin1, plays a major role in fiber elongation	Zhu et al. (2012)
Pel	DQ073046	Pectate lyase, degradation of de-esterified pectin and helps in normal fiber elongation	Zhu et al. (2012)
Ghir_D10	G025770	Hypothetical protein	Prasad et al. (2022)
Fiber strength and fineness			
GhCESA1	U58283	Upregulated at the onset of secondary wall synthesis	Pear et al. (1996)
GhGlcAT1	AY346330	Glucuronosyl transferase-like protein involved in the synthesis of non-cellulosic cell wall components during fiber elongation	Wu et al. (2006)
CelA1	GHU58283	Cellulose synthase	Zhu et al. (2012)
Ghir_D05	G003410	Serine threonine-protein kinase transcript	Prasad et al. (2022)
BG	DQ103699	Beta 1,4-glucanase, loosening of primary wall and promotion of secondary cell wall synthesis	Zhu et al. (2012)
LTP3	AF228333	Lipid transfer protein-encoding gene, cutin synthesis during fiber primary cell wall synthesis stage	Zhu et al. (2012)
Ghir_A09	G012990	Glycerol-3-phosphate dehydrogenase and bifunctional epoxide hydrolase 2-like transcripts	Prasad et al. (2022)
WLIM1a	JX648310	Fiber elongation and secondary wall synthesis in developing fibers	Han et al. (2013)
GbEXPATR	DQ912951	Enhances cotton fiber elongation through reorganizing secondary cell wall synthesis	Li et al. (2016)
Ghir_A02G012730, Ghir_A02G012790, and Ghir_A02G012830	-	Cellulose and cell wall biosynthesis	Chang et al. (2023)

FL reduces (Yang et al. 2014). A recent development in the field of green revolution research involves the regulation of a plant's natural biological cycle mechanism to promote desirable features.

Cotton fiber traits edited through CRISPR-Cas9

At present, clustered regularly interspaced short palindromic repeats/CRISPR-associated protein (CRISPR-Cas) is a commonly used genetic engineering technique owing to its adaptability, efficiency, and simplicity. A CRISPR array, with unidentified biological characteristics, was discovered in the *Escherichia coli* genome in 1987 (Ishino et al. 1987). Based on the availability of homologous spacers to viral and plasmid sequences, investigation was successfully conducted and the results demonstrated the involvement of a CRISPR array in adaptive immunity (Pourcel et al. 2005). Jinek et al. (2012) developed an RNA-guided DNA cleavage system with a high target efficiency. The CRISPR-Cas9 system is a key player in enhancing the genetic architecture of the crops (Yang et al. 2020). This approach has been used to increase both fiber quality and resilience to both biotic as well as abiotic stimuli in cotton (Sattar et al. 2019). A successful breeding program also requires the presence of robust genetic variations and wild relatives. However, these resources appear to be limited because the basic and applied research is progressing slowly, and the collection of mutants, especially in crops, is limited. On the other hand, the genetic engineering tools effectively overcome these challenges by causing specific genetic alterations. Through genetic editing techniques and epigenetic alterations, the cotton breeding programs may benefit from the production and evaluation of cotton crops with improved fiber quality, yield, and seed quality, as well as resistance to biotic and abiotic stressors (Qin et al. 2020).

Initially, the primary aim of developing CRISPR-Cas9 genome editing technology in cotton was to investigate the role of the MYB-25-like transcription factors in the formation of cotton fibers (Li et al. 2017). Previous research has demonstrated that *MYB-25-like* gene is expressed predominantly during the early stages of cotton fiber growth and initiation (Walford et al. 2011).

Additionally, the MYB-25-like transcription factor and CRISPR-Cas9-mediated knockouts were unable to initiate the production of cotton fibers (Li et al. 2017; Zhang 2019). Therefore, two gRNAs were created in this work to target two distinct *MYB25-like* gene sites, shared by the A and D subgenomes. It was shown that both gRNAs functioned extremely well both as separate entities as well as in combination to produce a large number of deletion/insertion mutations with high efficacy and no off-target effects (Li et al. 2017). The 14-3-3 proteins are members of a class of conserved regulatory molecules and are found in a wide variety of plant species. Cotton has a minimum of 25 14-3-3 proteins (Sun et al. 2011). These proteins are essential for initiation and elongation of cotton fibers (Zhang et al. 2010; Zhou et al. 2015). According to Zhou et al. (2015), the overexpression of *Gh14-3-3L* in transgenic cotton increased FL of the cotton, whereas inhibiting expression of *Gh14-3-3* prevented the process of fiber commencement and elongation. Zhang et al. (2010) suggested that 14-3-3 proteins altered the brassinosteroid signaling pathway. CRISPR-Cas9 technology was recently used to eliminate two copies of the *14-3-3d* gene (Zhang et al. 2018). The cotton fibers preferentially express the ALARP protein, which is rich in alanine and is encoded by *ALARP* gene. Table 4 shows the list of genes edited for cotton fiber improvement.

Homologous and repetitive sequences may be important targets for improving the fiber quality in transgenic plants. Highly repetitive DNA sequences can be found in tetraploid A- and D-diploid genomes of *G. hirsutum* (Li et al. 2015). Consequently, it is necessary to select numerous homeo-alleles for a particular region using the CRISPR-Cas9-based method. Furthermore, it also has a few experimental validations because of the presence of highly homologous genes and gene redundancy. However, stable homozygous mutants and targeted mutations can be produced by the efficient use of the CRISPR-Cas9 system. The appropriate choice of sgRNA remains a crucial factor since it has a direct impact on the effectiveness of using CRISPR-Cas9 (Ma et al. 2016).

Future directions

Understanding the characteristics of fiber quality is crucial, especially in the textile industry. So, it is essential to enhance the quality of cotton fiber to ensure its superiority over synthetic yarn. There is a need to thoroughly study the cotton fiber characteristics in order to improve the accuracy of the measurements. To improve the cotton fiber quality, four key traits should be focused such as Neps, FL, MIC, and fiber maturity, measured using the advanced fiber information system (AFIS) method. By accurately and quickly determining these traits, cotton breeders can identify the crucial features for creating multiple varieties with enhanced fiber quality, suitable for industrial use. To achieve this goal, there exists a need to discover a substantial number of highly significant SNP markers and validate them through gene expression analysis. The genes that are closely associated with these important SNPs are considered as candidate genes as it allow mechanistic investigations to be conducted to understand the relationships among traits, genes, and cell types. Through introgression and marker-assisted breeding techniques, the breeders can use these newly discovered genetic markers to enhance fiber quality and restore the lost genetic characteristics in cotton. Worldwide, scientists are exploring various genetic engineering techniques to improve fiber quality and identify critical genes for different cotton fiber properties. By altering the expression of genes, especially the ones related to fiber, transcription factors, and phytohormones, positive outcomes can be achieved. The process of improving the

Table 4 Potential edited and target genes in cotton

Code	Gene name	Role of edited gene	Sequence change	Gene modification	Reference
1	*GhMYB25-like A* and *GhMYB25-like D*	Fiber development	small nucleotide mutations – 1 bp/ – 3 bp/ – 7 bp nucleotide deletions	Non-homologous end joining (NHEJ)	Li et al. (2017)
2	*GhALARP-A and GhALARP-D*	Alanine-rich protein which is expressed in cotton fibers	(1) a single nucleotide insertion (+ 1 bp), (2) one or multiple nucleotide deletions, and (3) a mixture of nucleotide deletion and insertion	NHEJ	Zhu et al. (2018)
3	*GhPRP5*[a]	Proline rich protein, a cell wall structure protein	one or multiple nucleotide deletions	NHEJ	Katageri (2017)
4	*GhCDS*[a]	D-Cysteine desulphydrase	one or multiple nucleotide deletions	NHEJ	Katageri (2017)
5	*GhTLP*[a]	Thaumatin like protein	one or multiple nucleotide deletions	NHEJ	Katageri (2017)

[a] work not yet published

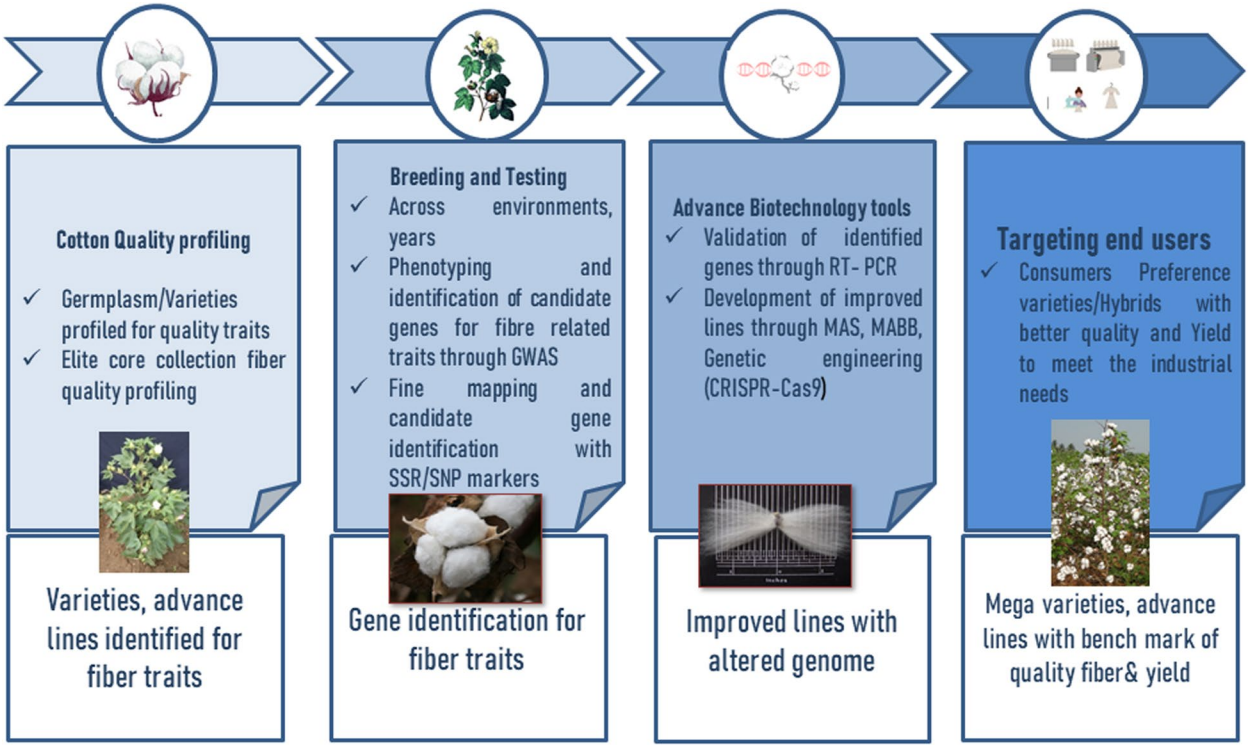

Fig. 3 Cotton improvement for fiber traits through advanced techniques

fiber traits starts with screening the germplasm and utilizing the CRISPR-Cas9 technology to study the most effective genes and drive improvements.

The successful enhancement of cotton fiber quality has also been achieved through the introduction of foreign genes relevant to fiber production. However, more research is required in addition to the advanced techniques previously discussed (Fig. 3). Discovering additional distant genes related to fiber production and incorporating them into cotton can further improve fiber properties. Understanding the molecular basis of various mechanisms involved in fiber formation requires further investigation to improve fiber traits.

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