



Mini-Review

Cotton Fibre Quality Management for Sustainable Textile Industry

Ayesha Latif, Mukhtar Ahmed, Sidra Akhtar, Ammara Ahad, Adnan Iqbal, Amina Yaqoob, Ayesha Imran, Muhammad Usmaan, Naila Shahid, Saira Azam, Aneela Yasmeen, Tahir Rehman Samiullah, Salah ud din, Ambreen Gul, Sana Shakoor, Maria Khawer, Sara Ajmal, Muhammad Azam Ali, Samina Hassan, Mohsin Shad, Sahar Sadaqat, Maira Zahid, Ahmad Ali Shahid, Idrees Ahmad Nasir, Abdul Qayyum Rao and Tayyab Husnain
Centre of Excellence in Molecular Biology, University of the Punjab

Abstract

Cotton fibre is a subject of great interest for scientists and industrialists across the world due to its importance to the textile industry. Fibre quality is attributed to its various characteristics including fibre length, strength, micronaire value, colour, etc. Alteration of one or two of these traits can be interesting to evaluate their impact on quality but, being a multifactorial trait, it is necessary to use a combination approach of genetic modification so as to breed all the desired alleles together to gather as many traits as possible for high-quality cotton fibre. Moreover, the use of genome editing technologies can also be very useful to knockout the traits responsible for inhibiting the expression of fibre related genes. The current study highlights important aspects of genome-based strategies for cotton fibre improvement and their application in detail.

Cotton from Plant to Fabrics

Cotton is one of the most significant crops worldwide. It is a major source of raw material for the production of textile products, cotton seeds (which are used as highly nutritional feed for livestock) and cotton seed oil (which is used in soap making and cooking). Cotton is a member of the family Malvaceae, which contains at least 50 species under the genus *Gossypium*. Amongst these, only four species are commercially used — *Gossypium arboreum*, *Gossypium herbaceum*, *Gossypium hirsutum* and *Gossypium barbadense* (Khan *et al.*, 2016; Iqbal *et al.*, 2001).

Cotton Fibre Development

Development of cotton fibre starts from single cell ovule in four complex overlapping stages:

- Initiation,
- Elongation,
- Primary cell wall synthesis, and
- Secondary cell wall synthesis (Basra & Malik, 1984).

The staple length and fineness of cotton fibre play a very important role for its utilisation in the textile industry (Bajwa *et al.*, 2013). Cotton yield is very important for the cotton growers and this can be achieved by increasing the number of fibres produced on the developing ovules (Xiao *et al.* 2016).

Various factors affect cotton fibre development. Some of these are summarised in this article.

Effects of Abiotic Stresses on Fibre Development

Abiotic stresses affect the overall quality and yield of fibre. The optimum temperature for cotton leaf, stem growth, fruit and seed development is 23.5-32°C. Cellulose formation during fibre cell wall synthesis is slowed down if temperature is decreased (Zheng *et al.*, 2012). During early stages of fibre development, it also inhibits the axial growth (Qiu *et al.*, 2007), whereas Schrader *et al.* (2004) reported that increase in temperature above 38°C will inhibit photosynthesis.

The regular functions of a cotton plant such as metabolism and turgor potential decreases when soil water contents are limited (Wang *et al.*, 2016). Drought, therefore, imparts negative effects on both quality and yield of cotton fibres. There are several studies which showed that water stress not only alters the fibre quality and cotton yield, but also reduces weight and number of cotton bolls (Lokhande and Reddy; 2014). Increasing water supply during square and boll formation stages is reported to enhance boll numbers, boll size and fruit-bearing branches. It has been reported that extreme conditions such as low rains reduce cellulose accumulation and impair photosynthesis while excess rains with cloudy weather decrease photosynthesis and thus fibre quality (Sawan, 2017). Fibre length is also reduced due to nutrient deficiencies (Lokhande and Reddy; 2014).

Genes and Transcription Factors Responsible for Fibre Development

Over 90% of lint is obtained from upland cotton (*G. hirsutum*) but its major disadvantage has been the relatively lower fibre quality in comparison to the superior extra-long-staple (ELS) cotton (*G. barbadense*). Genetic improvement plays a key role in meeting this agricultural challenge. Studies reveal that thousands of genes are responsible for fibre development (Fig. 1). Modern biotechnology focuses on introduction of more than one gene from different sources to one target (Khan *et al.*, 2016; John & Keller, 1996; Iqbal *et al.*, 2016; Ahmed *et al.*, 2018).

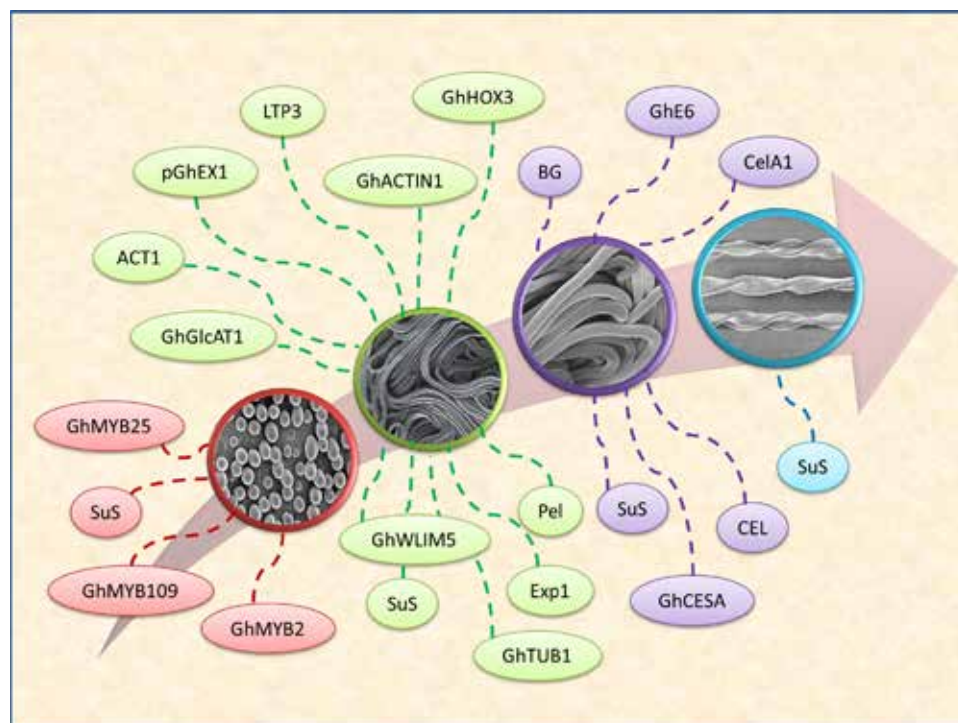


Figure1: Genes involved in development of cotton fibre

Epidermal cells of ovules are the source of single cellular cotton fibre origination; as a result, alterations in the genetic makeup of these epidermal cells can improve the quality of the originating fibres (Shi *et al.*, 2001). Genes are controlled by master regulators known as transcription factors (TFs). (Pati *et al.*, 2006). GhMYB25-like transcription factors are very important in fibre cell initiation and differentiation whereas GhMYB25, GhMYB109 and GhMYB2 transcription factors play significant role in fibre development (Huang *et al.*, 2013).

GhHox3 genes play a vital role in production of fine-quality elongated fibres (Shan *et al.*, 2014). GhWLM5 gene belongs to cotton LIM-domain proteins which have the ability to bind with actin cytoskeleton and bundling of F-actin filaments, therefore these are reported to be widely

expressed in fibre elongation (Li *et al.*, 2013). GhHOX3 is involved in the cotton fibre elongation and its silencing results in 80% reduction in fibre length (Shan *et al.*, 2014). Pectin methyl esterase enzyme (PME) plays an important role in different developmental stages of fibre (Li *et al.*, 2016). Plant LIM proteins have been reported as one of the key actin-binding proteins (ABP's) (Thomas *et al.*, 2007). The nuclear LIM-domain proteins act primarily in tissue-specific gene regulation and cell fate determination, whereas the cytoplasmic LIM-domain proteins function mainly in cytoskeletal organisation (Han *et al.*, 2013). It has been reported that GhLIM5 protein has a role in actin filament bundling (Li *et al.*, 2013) and down-regulation

of the *GhACTIN1* gene resulted in shortening the length and weakening the strength of cotton fibres (Li *et al.*, 2005). Therefore, it is surmised that over-expression of *GhACTIN1* and *GhWLM5* genes would result in increased fibre length and strength respectively.

In cotton, the developing cotton boll acts as a sink and breakdown of sucrose into its component hexoses and is the first step for utilisation of sucrose for fibre development. Sucrose cleavage is essential as it results in production of UDP-glucose (Li *et al.*, 2019). Sucrose synthases (SuS) and invertases control the degradation of sucrose in most plants (Shua *et al.*, 2009). Invertases hydrolyse sucrose into fructose and glucose (Gou *et al.*, 2007; Kleczkowski, 2010; Brill *et al.*, 2011). UDPG plays a vital role in cytosolic formation of sucrose and syn-

thesis of polysaccharides (e.g. hemicelluloses) and pectin, and components of cell wall (Amor *et al.*, 1995; Gibeau, 2000; Johansson *et al.*, 2002). Studies have revealed that decreased SuS activity at fibre initiation stage affects fibre development (Ruan *et al.*, 2003; Ahmed *et al.*, 2019). During secondary cell wall synthesis, SuS channelises UDPG to cellulose synthase (CES) located in cell membranes of fibres. Toward the end of the elongation phase, cellulose synthesis is hastened and leads to secondary wall deposition (Haigler *et al.*, 2001). The high SuS activity at different stages of fibre development has a potential towards sucrolysis of sucrose into component hexoses, which are used for cell elongation. The increased cellulose contents will result in improved fibre smoothness and strength.

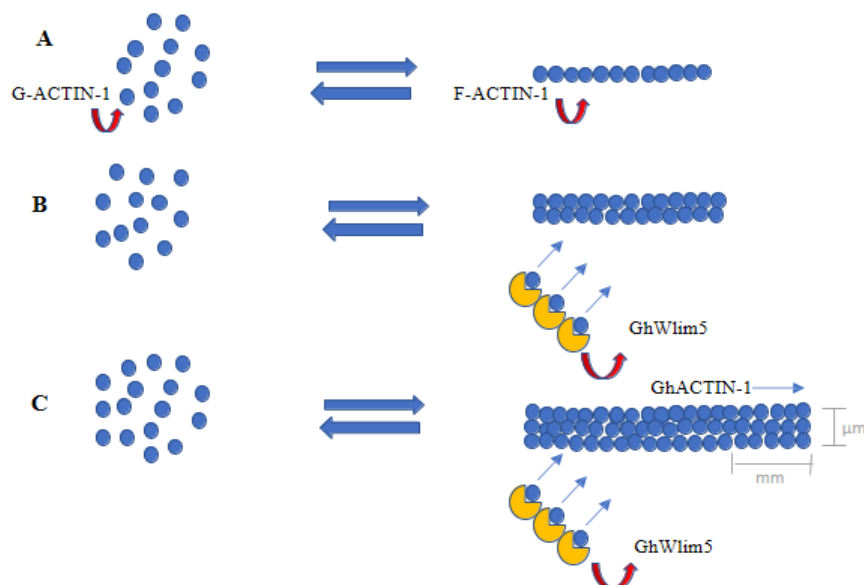


Figure 2: Schematic diagram of actin filament elongation and bundling by *GhACTIN-1* and *GhWlim5* in cotton fibre

(A) Cotton fibre elongation by *GhACTIN-1* gene when expressed under normal condition (B) Actin filaments bundling by *GhWlim5* gene when expressed under normal condition (C) Actin filament elongation and bundling by over-expression of *GhACTIN-1* and *GhWlim5* genes resulted in increased cotton fibre length and strength respectively (Iqbal *et al.*, 2019).

Effect of Cellulose Content on Fibre Development

The process of cellulose synthesis is catalysed by the enzyme cellulose synthase (Saxena *et al.*, 1994). A number of bacteria such as *Agrobacterium*, *Azotobacter*, *Pseudomonas* and *Acetobacter* are naturally found to be pronounced cellulose producers (Wong *et al.*, 1990). Among these the most efficient cellulose synthesising bacteria come from the genus *Acetobacter*, especially *Acetobacter xylinum* which was later on reclassified as *Gluconacetobacter xylinus* by Yamada *et al.* (1997). Bacterial cellulose (BC) is known to possess several unique characteristics in comparison to plant celluloses such as ultra-fine network of cellulose microfibrils, increased water holding capacity, high strength and high moldability (Nishi *et al.*, 1990). Hence, transformation of the Bacterial cellulose synthase (*Bcs*) genes in cotton can play a significant role in improving the cotton fibre quality. In *G. xylinus* strains the process of cellulose synthesis was found to be regulated by an operon consisting of four genes, *acsA*, *acsB*, *acsC* and *acsD*. Out of these, *acsA* and *acsB*, were reported to be essential for the production of cellulose in-vitro (Lu *et al.*, 2002).

Role of Flavonoids Pathway on Cotton Fibre Improvement

Flavonoids, along with various pigments and co-pigments, contribute to different flower colours (Grotewold, 2006).

The role of flavonoid pathway in cotton colour development and its potential in improvement of fibre quality was reported by Liu *et al.*, (2018). Therefore, it is possible that fibre quality parameters can be enhanced through over expression of flavonoid genes (Ahad *et al.*, 2018).

Marker-assisted Selection for Fibre Quality Improvement

The majority of fibre properties are under genetic control and are inherited quantitatively. For example, the length, strength and fineness of cotton fibre are influenced by 12 to 21 Quantitative Trait Loci (QTLs) (Park *et al.*, 2005). Significant improvement in fibre length and fibre strength (~70%) can be achieved by transgene exploitation through breeding but the later remain unstable in inheritance (May *et al.*, 2002). Until now, 28 different QTLs for fibre quality have been identified (Zhang *et al.*, 2011).

Effects of Phytohormones on Fibre Development

Plants use different hormones to regulate different stages of fibre development (Hao *et al.*, 2012; Tan *et al.*, 2012). Auxin and gibberellins in combination enhanced the fibre growth (Ji *et al.*, 2003, Seagull *et al.*, 2004). Indole acetic acid and phenyl acetic acid improve the fibre length in some cultivars (Gokani & Thaker, 2002). Some hormones like ABA (abscisic acid) have a negative impact on fibre growth (Haigler *et al.*, 2012).

Management of Cotton Fibre Quality through Combined Approach

Fibre quality traits are controlled by several genes. Because of the polygenic control of fibre quality, it is difficult to achieve all the desired characteristics of fibre quality through a single approach, such as plant breeding and or the introduction of a few fibre trait-related genes through transgenic modification — or even through knockout of a few genes responsible for inhibition of fibre related gene expression (Sawant *et al.*, 2018). Expression of individual fibre traits in cotton could lead to improvement in a step-wise manner, thereafter the scope of which can be increased through gene pyramiding of different transgenic traits into a single plant variety through conventional plant breeding combined with knockout of inhibitors in-

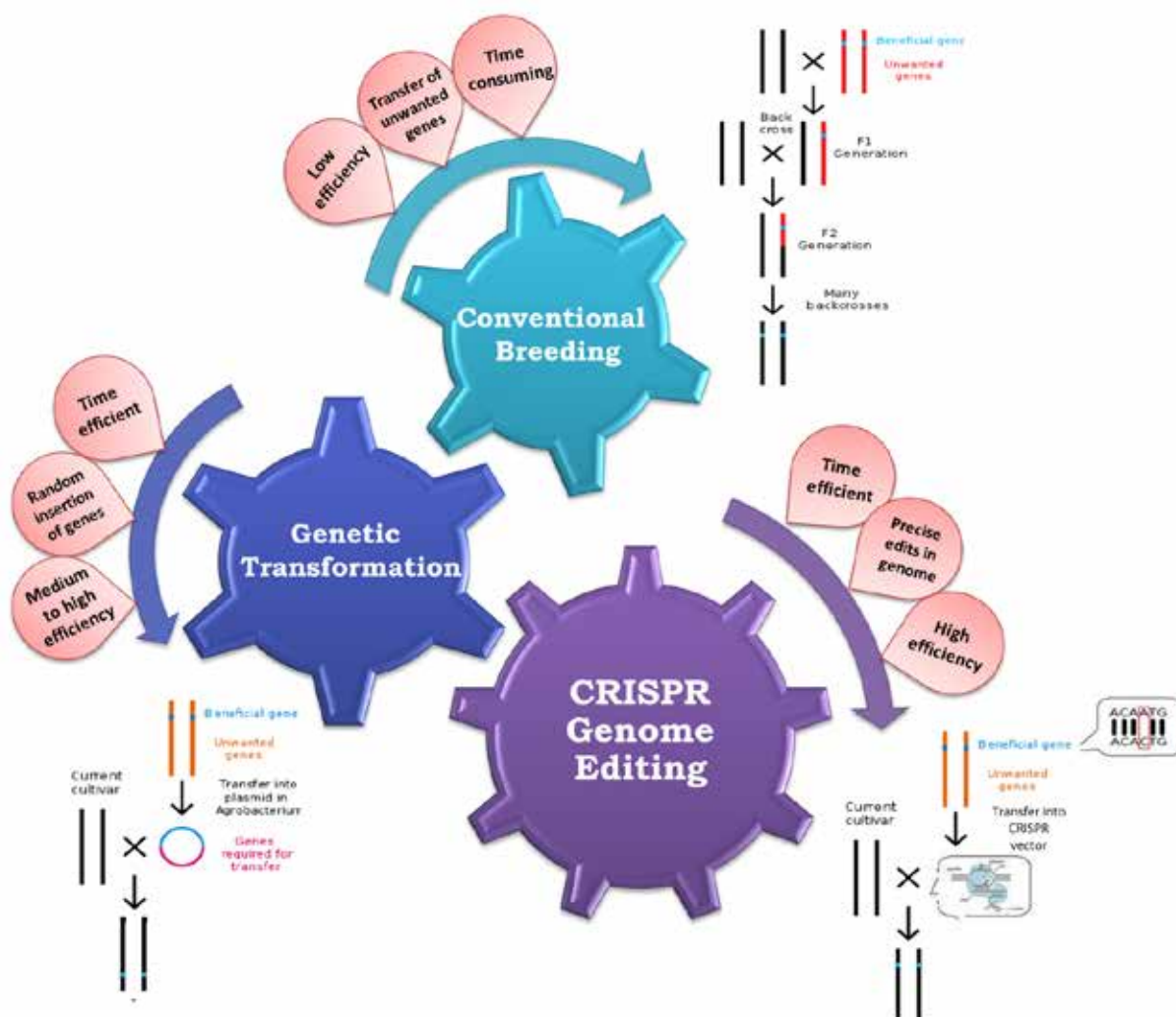


Figure 3: Schematic representation of combinational approach for cotton fibre quality management (Akhtar *et al.*, 2019)

involved through a genome editing technology, like CRISPR/Cas system to develop varieties harbouring all these traits to meet the growing demands of consumers and the textile industry. It will be helpful to achieve these difficult tasks in a short time by improving fibre properties using a combination of approaches that could save economic losses due to poor quality fibre waste that are generally incurred by textile industry (Li *et al.*, Morello *et al.*, 2019).

Conclusion

Improvement of cotton fibre quality is a topic of great interest for scientists and the textile industry. Any efforts to improve fibre traits will lead to greater success for the cotton sector. Scientists are trying to work on various factors that may enhance quality of cotton fibres. With the advent of new technologies, a combined approach to target more than one aspect simultaneously will be more fruitful.

References

- Ahad A., Tahir S., Ali MZ, Iqbal A., Ahmed M., Akhtar S., Nawaz R., Rao AQ, Shahid AA., Rahman Z, Husnain T. 2018. Functional prediction of F3'5'H in color alteration in cotton: an in-silico comparative analysis between cotton and viola. *Int. J. Biosci.* 13(3), 185-197, September 2018.
- Ahmed M., Shahid AA., Din US., Akhtar S., Ahad A., Rao AQ, Bajwa SS, Khan MAU, Sarwar MB and Husnain T. 2018. An Overview Of Genetic And Hormonal Control Of Cotton Fibre Development *Pak. J. Bot.*, 50(1): 433-443
- Ahmed, M., Akhtar, S., Fanglu, M. *et al.* 2019. *Russ J Plant Physiol.* 66: 41.
- Akhtar S., 2018. PhD dissertation submitted to Higher education commission of Pakistan
- Amor, Y., Haigler, C. H., S. Johnson, S., Wainscott, M., and Delmer, D. P. 1995. A membrane-associated form of sucrose synthase and its potential role in synthesis of cellulose and callose in plants. *Proc. Natl. Acad. Sci.* 92:9353-9357.

- Bajwa, K.S., A.A.Shahid, A.Q. Rao, M.S. Kiani, M.A. Ashraf, A.A. Dhab, A. Bakhsh, A. Latif, M.A.U. Khan and A.N. Puspito. 2013. Expression of *Calotropis procera* expansin gene *CpEXPA3* enhances cotton fibre strength. *Aust. J. Crop Sci.*, 7(2): 206.
- Basra AS, Malik CP (1984) Development of the cotton fibre. *Int Rev Cytol* 89: 65-113. doi:10.1016/S0074-7696(08)61300-5.
- Brill, E., van, M., White, R. G., Llewellyn, D., Campbell, P. M., Engelen S., Ruan, Y.L, Arioli, T., Furbank, R.T. 2011. A novel isoform of sucrose synthase is targeted to the cell wall during secondary cell wall synthesis in cotton fibre. *Plant Physiol.* 157, 40–54.
- Gibeaut, D. M. 2000. Nucleotide sugars and glucosyltransferases for synthesis of cell wall matrix polysaccharides, *Plant Physiol. Biochem.* 38: 69 – 80.
- Gokani, S. J., & Thaker, V. S. 2002. Physiological and biochemical changes associated with cotton fibre development: IX. Role of IAA and PAA. *Field crops research*, 77(2-3), 127-136.
- Gou, J. Y., Wang, L. J., Chen, S. P., Hu, W. L., & Chen, X. Y. 2007. Gene expression and metabolite profiles of cotton fibre during cell elongation and secondary cell wall synthesis. *Cell research*, 17(5), 422.
- Grotewold, E. 2006. The genetics and biochemistry of floral pigments. *Annu Rev Plant Biol.* 57: 761–780.
- Haigler, C.H., Ivanova-Datcheva, M., Hogan, P.S., Salnikov, V.V., Hwang, S., Martin, K. and Delmer, D.P., 2001. Carbon partitioning to cellulose synthesis. In *Plant Cell Walls* (pp. 29-51). Springer, Dordrecht.
- Han, L. B., Li, Y. B., Wang, H. Y., Wu, X. M., Li, C. L., Luo, M., ... & Xia, G. X. 2013. The dual functions of WLIM1a in cell elongation and secondary wall formation in developing cotton fibres. *The Plant Cell*, 25(11), 4421-4438.
- Hao, J., Tu, L., Hu, H., Tan, J., Deng, F., Tang, W., ... & Zhang, X. 2012. GbTCP, a cotton TCP transcription factor, confers fibre elongation and root hair development by a complex regulating system. *Journal of experimental botany*, 63(17), 6267-6281.
- Huang, G. Q., Gong, S. Y., Xu, W. L., Li, W., Li, P., Zhang, C. J., ... & Li, X. B. 2013. A fasciclin-like arabinogalactan protein, GhFLA1, is involved in fibre initiation and elongation of cotton. *Plant physiology*, 161(3), 1278-1290.
- Iqbal A. 2019. PhD dissertation submitted to Higher education commission of Pakistan
- Iqbal M. J., Reddy O. U. K., El-Zik K. M., Pepper A. E. 2001. A genetic bottleneck in the 'evolution under domestication' of upland cotton *Gossypium hirsutum* L. examined using DNA fingerprinting. *Theor. Appl. Genet.* 103 547–554. 10.1007/PL00002908
- Iqbal, N., A. Khatoon, M. Asif and A. Bashir. 2016. Expression analysis of fibre related genes in cotton (*Gossypium hirsutum* L.) through real time PCR. *Pak. J. Bot.*, 48(3): 1099-1106.
- Ji, S. J., Lu, Y. C., Feng, J. X., Wei, G., Li, J., Shi, Y. H., ... & Zhu, Y. X. 2003. Isolation and analyses of genes preferentially expressed during early cotton fibre development by subtractive PCR and cDNA array. *Nucleic acids research*, 31(10), 2534-2543
- Johansson, H., Sterky, F., Amini, B., Lundberg, J and Kleczkowski, L. A. 2002. Molecular cloning and characterization of a cDNA encoding poplar UDP-glucose dehydrogenase, a key gene of hemi-cellulose/pectin formation, *Biochim.Biophys.Acta.* 1576 : 53 – 58.
- John, M.E. and G. Keller. 1996. Metabolic pathway engineering in cotton: biosynthesis of polyhydroxybutyrate in fibre cells. *Proc. Natl. Acad. Sci.*, 93(23): 12768-12773.
- Khan, M.A.U., A.A. Shahid, A.Q. Rao, K.S. Bajwa, A. Muzaffar, T. Rehman-Samiullah, I.A. Nasir and T. Husnain. 2016. Molecular and biochemical characterization of cotton epicuticular wax in defense against cotton leaf curl disease (CLCuD). *Iran J. Biotechnol.*, 13(4): 3-9.
- Kleczkowski, L. A., Kunz, S., Wilczynska, M., 2010. Mechanisms of UDP-glucose synthesis in plants. *Crit. Rev. Plant. Sci.* 29: 191–203.
- Li, C., Unver, T., & Zhang, B. 2017. A high-efficiency CRISPR/Cas9 system for targeted mutagenesis in cotton (*Gossypium hirsutum* L.). *Scientific reports*, 7, 43902.
- Li, M., Wang, S., Liu, Y., Zhang, Y., Ren, M., Liu, L., Lu, T., Wei, H. and Wei, Z., 2019. Overexpression of *PsnSuSy1*, 2 genes enhances secondary cell wall thickening, vegetative growth, and mechanical strength in transgenic tobacco. *Plant molecular biology*, 100(3), pp. 215-230.
- Li, W., Shang, H., Ge, Q. *et al.* *BMC Genomics*. 2016. 17: 1000. <https://doi.org/10.1186/s12864-016-3365-z>
- Li, W., Shang, H., Ge, Q., Zou, C., Cai, J., Wang, D., ... & Song, W. 2016. Genome-wide identification, a phylogeny, and expression analysis of pectin methylesterases reveal their major role in cotton fibre development. *BMC genomics*, 17(1), 1000.
- Li, Y., Jiang, J., Li, L., Wang, X.L., Wang, N.N., Li, D.D., & Li, X.B. 2013. A cotton LIM domain-containing protein (GhWLIM5) is involved in bundling actin filaments. *Plant physiology and biochemistry*, 66, 34-40.
- Liu HF, Luo C., Song W., Shen H., Li G., He ZG.....Liu Hailang. 2018. Flavonoid biosynthesis controls fibre color in naturally colored cotton. *PeerJ* 6:e4537; DOI 10.7717/peerj.4537
- Lokhande S, Reddy K.R. 2014. Quantifying temperature effects on cotton reproductive efficiency and fibre quality. *Agron J* 106:1275–1282
- Lu, Y C., Wei, G. and Zhu, Y X. 2002. Cloning whole cellulose synthesizing operon (ayacs operon) from *Acetobacter xylinum* and transforming it into cultivated cotton plants. *Acta Botanica Sinica*, 44 (4): 441-445.
- May, O. L. 2002. Quality improvement of upland cotton (*Gossypium hirsutum* L.). *Journal of crop production*, 5(1-2), 371-394.
- Morello, L., Pydiura, N., Galinovsky, D., Blume, Y. and Breviaro, D., 2019. Flax tubulin and Cesa superfamilies represent attractive and challenging targets for a variety of genome- and base-editing applications. *Functional & integrative genomics*, pp.1-14.
- Nishi, Y., Uryu, M., Yamanaka, S., Watanabe, K., Kitanuma, N., Iguichi, M. and Mitsuhashi, S. 1990. The structure and mechanical properties of sheets prepared from bacterial cellulose and improvement of the mechanical-properties of sheets and their applicability to diaphragms of electroacoustic transducers. *I Mazer Sci*, 25: 2997-3001.
- Park, Y. H., Alabady, M. S., Ulloa, M., Sickler, B., Wilkins, T. A., Yu, J., ... & Cantrell, R. G. 2005. Genetic mapping of new cotton fibre loci using EST-derived microsatellites in an interspecific recombinant inbred line cotton population. *Molecular Genetics and Genomics*, 274(4), 428-441.

- Pati, A., Vasquez-Robinet, C., Heath, L. S., Grene, R., & Murali, T. M. 2006. XcisClique: analysis of regulatory bicliques. *BMC bioinformatics*, 7(1), 1.
- Qiu, C.X., F.L. Xie, Y.Y. Zhu, K. Guo, S.Q. Huang, L. Nie and Z.M. Yang. 2007. Computational identification of microRNAs and their targets in *Gossypium hirsutum* expressed sequence tags. *Gene*, 395(1): 49-61.
- Ruan, Y.L., Llewellyn, D.J. and Furbank, R.T., 2003. Suppression of sucrose synthase gene expression represses cotton fibre cell initiation, elongation, and seed development. *The Plant Cell*, 15 (4), pp.952-964
- Sawan Z.M. 2017. Cotton production and climatic factors: Studying the nature of its relationship by different statistical methods. *Current biology* 3:1292882
- Sawant, S. V., Singh, S. K., Singh, B., & Bhattacharya, P. 2018. A novel formulation for improving the yield and quality of fibre in cotton plants: Google Patents.
- Saxena, I.M., Kudlica, K. and Brown, R. M. Jr. 1994. Characterization of genes in the cellulose-synthesizing operon (acs operon) of *Acetobacterxylinum*: implications for cellulose crystallization. *J. Bacteriol*, 176:5735-5752.
- Schrader, S.M., R.R. Wise, W.F. Wacholtz, D.R. Ort, and T.D. Sharkey. 2004. Thylakoid membrane responses to moderately high leaf temperature in Pima cotton. *Plant, Cell Environ*. 27: 725-735.
- Seagull, R. W., & Giavalis, S. 2004. Pre-and post-anthesis application of exogenous hormones alters fibre production in *Gossypium hirsutum* L. cultivar Maxxa GTO. *Journal of cotton science*.
- Shan, C.M., Shangguan, X.X., Zhao, B., Zhang, X.F., Chao, L.M., Yang, C.Q., Guo, W.Z. 2014. Control of cotton fibre elongation by a homeodomain transcription factor GhHOX3. *Nature communications*, 5.
- Shi, Y.H., S.W. Zhu, X.Z. Mao, J.X. Feng, Y.M. Qin, L. Zhang, J. Cheng, L.P. Wei, Z.Y. Wang and Y.X. Zhu. 2006. Transcriptome profiling, molecular biological, and physiological studies reveal a major role for ethylene in cotton fibre cell elongation. *Plant Cell*, 18(3): 651-664.
- Shua, H., Zhou, Z., Xu, N., Wang, Y., Zheng, M., 2009. Sucrose metabolism in cotton (*Gossypium hirsutum* L.) fibre under low temperature during fibre development. *European Journal of Agronomy* 31: 61-68.
- Tan, L., Showalter, A.M., Egelund, J., Hernandez-Sanchez, A., Doblin M.S., and Bacic, A. 2012. Arabinogalactan-proteins and the research challenges for these enigmatic plant cell surface proteoglycans. *Front. Plant Sci*. 3: 140.
- Thomas, C., Moreau, F., Dieterle, M., Hoffmann, C., Gatti, S., Hoffmann, C., ... & Steinmetz, A. 2007. The LIM domains of WLIM1 define a new class of actin bundling modules. *Journal of Biological Chemistry*, 282(46), 33599-33608.
- Wang, R., Gao, M., Ji, S., Wang, S.S., Meng, Y.L., Zhou, Z.G., 2016. Carbon allocation, osmotic adjustment, antioxidant capacity and growth in cotton under long-term soil drought during flowering and boll-forming period. *Plant Physiol. Biochem*. 107, 137-146.
- Wong, H. C., Fear, A. L., Calhoon, R. D., Eidhinger, G. H., Mayer, R., Amikam, D., Benziman, M., Gelfand, D. H., Meade, J. H., Emerick, A. W., Bruner, R., Ben-Basat, B. A. and Aal, R. 1990. Genetic organization of the cellulose synthase operon in *Acetobacterxylinum*. *Proc Natl Acad Sci USA*, 87:8130-8134.
- Xiao, G.H., K. Wang, G. Huang and Y.X. Zhu. 2016. Genomescale analysis of the cotton KCS gene family revealed a binary mode of action for gibberellin A regulated fibre growth. *J. Integr. Plant Biol*, 58: 577-589.
- Yamada, Y., Hoshino, K. and Ishikawa, T. 1997. The phylogeny of acetic acid bacteria based on the partial sequences of 16S ribosomal RNA: the elevation of the subgenus *Gluconoacetobacter* to the generic level. *Bioscience Biotechnology and Biochemistry*, 61:1244-1251.
- Zhang, Z. *et al.* 2011. QTL alleles for improved fibre quality from a wild Hawaiian cotton, *Gossypium tomentosum*. *Theor. Appl. Genet*. 123,1075-1088.
- Zheng, M., Y. Wang, K. Liu, H. Shu and Z. Zhou. 2012. Protein expression changes during cotton fibre elongation in response to low temperature stress. *J. Plant Physiol*, 169(4): 399-409.