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AN OVERVIEW OF GENETIC AND HORMONAL CONTROL OF COTTON FIBER DEVELOPMENT

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Abstract

Cotton being white gold for textile industry faces a severe problem of low fiber quality. Pakistan imports about 55,000 tons of long length cotton fiber for which 157 million USD is spent every year. Cotton fiber is a seed trichome that originates as an extension from epidermal layers of the seed coat and elongates to 2.5 – 3.0 cm in about 16 days post anthesis (DPA).Conventional approaches like breeding have not proven to be of much success in fulfilling the requirement of fiber quality. Current approach in molecular studies have helped to describe genes involved in fiber elongation such as *CEL, CelA1, CelA1, Exp1, ACT 1, BG, Pel, SuS1, LPT3, GhE6, pGhEX1, GhCESA1,* and *aquaporins* in addition to transcription factors like MYB, WRKY, AP2/EREBP, C_2H_2 and bHLH families, which might have vital role in fiber cell initiation.

Besides these different genes, phytohormones also have a progressive role in fiber development. Among other factors, the temperature is one of the limiting factors that directly influence cotton boll maturation and fiber elongation. The optimum temperature required for fiber elongation is slightly lower than that required for boll maturation. Cotton fiber is pure cellulose, a type of carbohydrates, which are influenced by inactivation of invertase enzyme at high temperature. Denaturation of Invertase results in poor fiber characteristics. Modern trends in molecular mechanisms that govern fiber development focus on elongation processes by regulating redox levels. Moreover *GAST1-like, Cop1/BONZAI* and *Pex1*, highly contribute to the regulation of fiber cell elongation by controlling H_2O_2 levels under cell stress. Over expression of one or multiple fiber-related traits through genetic modification could be an excellent strategy to overcome the problem of low fiber quality in cotton.

Key words: Genetic modification, Fiber elongation, Cotton, Temperature stress, Fiber related genes.

Introduction

Cotton is the world's largest textile fiber crop and has been used for producing garments, paper products, cottonseed oil and other purposes for many years. It is cultivated in more than 80 countries and has an annual production of 20 million tons. It belongs to genus *Gossypium* of *Malvaceae* family and includes about 50 species. Out of these 50, only four species are commercially cultivated which produce spinnable fiber; two of these *Gossypium arboreum*, *Gossypium herbaceum* are are diploid (AA) while *Gossypium hirsutum* and *Gossypium barbadanse* are tetraploid (AADD) (Khan *et al*., 2016). The former two are of Asiatic origin and later are of American origin. American cotton originated by polyploidization events of Asian *G. herbaceum*, an ancestor of diploid American species and resemble *G. raimondii* (DD). In the past century, classical breeding has significantly improved the yield and quality of cotton fiber. However, this approach has not been able to instigate excellence in fiber strength, length, water absorption, affinity for chemicals and dyes, thermal properties, resistance to crumple and shrinkage for clothing and textile purposes (Khan *et al*., 2015). The approach towards ameliorating such characteristics by traditional breeding is limited due to lack of compatibility between species and available traits. Biotechnology holds the potential to overcome such problems by incorporating desirable and targeted genes from different organisms or genes from synthetic origin into cotton and other enviable plants to overcome the drawbacks of conventional breeding (John & Keller, 1996; Iqbal *et al*., 2016).

Cotton staple length plays a key role in defining the quality of cotton fiber in the textile industry across the globe. Understanding the molecular mechanism and hormonal control of fiber initiation can be very useful for the improvement of fiber elongation and quality. A single cell type can be affected by multiple hormones, similarly, growth and differentiation of different tissues can be influenced by single hormone (Chow & McCourt, 2006). These signaling molecules have the ability to target specific transcriptional factors responsible for modulation of gene expression. Salih *et al.* (2016) identified different transcription factors like MYB, zinc finger, basic leucine zipper and reported their correlation with hormones like ACO and ABP in controlling the initiation of cotton fiber. Similarly, Islam *et al.* (2016) described the differential expression of genes involved in crystalline cellulose assembly controlled by ethylene and RLK signaling in developing fibers in different cotton lines.

Crop yield improvement remains the main goal of all cotton growing countries. One way to achieve this is to increase the number of fibers produced by each developing seeds quantitatively. According to Xiao *et al*. (2016), plant hormones play a vital role in cotton fiber growth and development. In their experiment, application of exogenous GA3 not only promoted fiber length but also increased the thickness of cell wall significantly. Long length cotton fibers with thicker cell wall and increased dry weight per unit cell length were obtained

after GA treatment. The results of these studies clearly demonstrate the role of hormonal pathways in the genetic control of fiber quality. Gathering all the information related to correlation of genetic control and hormonal control can prove to be beneficial for plant breeders and biotechnologist working in the field of cotton fiber improvement.

Cotton fiber is a single cell trichome or just an extension of epidermal cells that originates from outer integument of the ovule and undergoes fast and synchronous elongation during fiber expansion (Walford *et al*., 2011). Four distinct and overlaying stages of fiber development are; initiation, elongation (with primary cell wall synthesis), secondary cell wall synthesis and maturation (Basra & Malik, 1984; Patel *et al*., 2016). At early stages, about 30% of ovule epidermis cells (fiber initials) start to elongate and expand. Biologically a mature fiber is made up of cellulose with minute traces of proteins, water, hemicelluloses, pectins, wax, mineral substances, organic acids, sugars and pigments that give it outstanding durability as well as aesthetics (Bajwa *et al*., 2013). Based on accumulated knowledge of the biochemistry of fiber formation and development, several genes that are predominantly expressed in fiber have been isolated and characterized. The cell wall matrix of plant cell might be plastered with covalent bonds linking polysaccharides, lignins, and proteins. According to another school of thought, cell proteins form complex with cellulose microfibrils and such bonding might also exist in fiber cells. Thousands of genes are responsible for the development of cotton fiber which can be predicted by differential screening of cDNA libraries and used for the betterment of cotton fiber quality.

Environmental factors such as low temperature also affect fiber properties. Low temperature slows down the rate of cellulose biogenesis in secondary cell wall formation. (Zheng *et al*., 2012). It also hinders axial growth rate of elongation during early stages (before 15 DPA) of fiber development (Qiu *et al*., 2007). In addition to environment, the activity of enzymes (like peroxidase) and proteins (like hydroxyproline-rich glycoproteins HRGP) of the cell wall, may also have a critical role in determining fiber properties. Peroxidases are thought to play a role in conferring rigidity to the cell wall and elongation of plant cells by the breaking intra and intermolecular cross-linkages of tyrosine residues to form isodotyrosine residues of HRGP that result in rigidification of cell wall (Francoz *et al*., 2015). Thus, alteration in expression of peroxidases and HRGPs may affect fiber characteristics. Attempt to reveal the function of phytohormones is an additional approach towards modification of fiber characteristics (Aleman *et al*., 2008). This review primarily focuses on recent progress towards identification of genes and transcription factors along with their potential functions at different stages of fiber development in cotton. Cross talk between plant hormones and genes presented here might provide a framework for further studies in this area.

Transcription factors and genes for fiber development and elongation: Studies on cotton fiber development have mainly focused on gene expression profiling throughout the event of elongation and secondary wall biosynthesis in fiber. Early findings revealed the significant role of transcription factors in cotton fiber development as well. A number of genes have been reported to be involved in cotton fiber cell development and their expression is being controlled by transcription factor machinery (Table 1). Some of these genes are also similar to the *Arabidopsis* trichome specific transcription factor proteins.

Table 1. Genes involved in fiber development and elongation.

Gene	Accession no.	Potential function	Reference
CEL	AY574906	Endo 1,4 beta glucanase, necessary for plant cellulose biosynthesis	Zhu *et al*., 2012
CelA1	GHU58283	Cellulose Synthase	Zhu *et al*., 2012
CelA1	AF150630	Cellulose Synthase catalytic subunit, cellulose biosynthesis in developing cotton fibers	Zhu *et al*., 2012
Exp1	DQ204495	Alpha expansin1, cell wall extension and effect on length and quality of fiber	Zhu *et al*., 2012
ACT 1	AY305723	Actin1, play major role in fiber elongation	Zhu *et al*., 2012
BG	DQ103699	Beta 1,4 glucanase, loosing of primary wall and promotion of secondary cell wall synthesis	Zhu *et al*., 2012
Pel	DQ073046	Pectatelyase, degradation of de-esterified pectin and help in normal fiber elongation	Zhu *et al*., 2012
SuS1	U73588	Sucrose synthase, play important role in cotton fiber initiation and elongation by influencing carbon partitioning to cellulose synthesis	Zhu *et al*., 2012
GhTUB1	AF487511	Play role in polar elongation of cotton fiber	Zhang *et al*., 2003
LTP3	AF228333	Lipid transfer protein gene, cutin synthesis during fiber primary cell wall synthesis stage	Zhu *et al*., 2012
GhE6	BM356398	Fiber protein E6, fiber elongation and secondary wall biosynthesis	John & Keller, (1996).
pGhEX1	AF043284	Abundant in cotton fiber cells and regulated during fiber elongation	Orford & Timmis, (1998)
GhCESA1	U58283	Up-regulated at onset of secondary wall synthesis	Pear *et al*. (1996)
GhGlcAT1	AY346330	Glycuronosyl transferase-like protein involved in synthesis of non cellulosic cell wall components during fiber elongation	Wu *et al*. (2006)

Initiation: Cotton fiber cell initiation is the preliminary extension of ovule epidermal cells in an isodiametric manner and this phase may last for one day or so for each fiber cell. As there might be numerous waves of fiber cell initiation on the surface of ovule so fiber initials can be found during first 5 to 6-day post anthesis at any time (Haigler *et al*., 2012; Xian *et al*., 2014). On the basis of expressed sequence tag data, it was found that proportion of transcription factors (MYB, WRKY, AP2/EREBP, C2H2, and bHLH) may play a vital role in fiber cell initiation process (Samuel-Yang *et al.*, 2006). Similarly, three important transcription factors including GhMYB25, GhMYB25-like, GhHD1 that regulate lint fiber initiation using cDNA microarray were reported by Wu *et al*. (2006). In cotton GhMYB25 silencing resulted in short length fibers, less number of trichomes on leaves, petioles, petals and delayed fiber initiation while its overexpression led to an addition in a number of both fiber initiation and trichomes (Machado *et al*., 2009). Inhibition of *Gossypium hirsutum* GhMYB25-like eliminated the fiber growth on seed surface similar to fibreless mutant, however, no effect was found on trichome development anywhere else (Walford *et al*., 2011). Delay of fiber initiation and retarded trichome formation was observed in the case of the decline in GhHD1 transcripts while its overexpression resulted in improved fiber initiation, however, no effect was found on leaf trichome (Walford *et al*., 2011). Besides these, some additional transcription factor genes like *G. arboreum* MYB2, HOX1, TCP (GaMYB2, GaHOX1, GaTCP), *G. hirsutum* MYB109 (GhMYB109) and *G. barbadense* ML1 (GbML1) are concerned with controlling initial stages of fiber development in cotton (Zheng *et al*., 2012; Ma *et al*., 2016). GhMYB25 gene overexpression increases leaf trichome branches in transgenic tobacco, representing a relationship between fiber and leaf trichome development in cotton (Wu *et al*., 2006).

Elongation: This phase comprises the main expansion phase of fiber growth and may proceed for many days post anthesis (DPAs) depending on the genotype. The process of fiber cell elongation also involves turgor pressure and opening and closing of plasmodesmata. Plasmodesmata remain open from 0-9 DPA, and close from 10-15 DPA and then reopen at 16 DPA. Correlation between fiber length and duration of plasmodesmatal opening and closure in different cotton genotypes was observed by Ruan *et al*. (1997). Fiber accumulates thin flexible primary wall that consists of several polymers made up of different monosaccharides (Haigler *et al*., 2012). Cotton fiber cell shape is also determined by cytoskeleton assembly. A member of Rac/Rop GTPases family known as GhRac1 is well expressed during elongation stage of cotton fiber cell development. GhRac1 level decreases rapidly as fiber elongation rate decreases which indicates that GhRac1 GTPase may act as a probable controlling factor for fiber elongation by regulating components of cytoskeleton (Kim & Triplett, 2004). Li *et al*. (2005) investigated that in various cotton tissues GhACT genes show differential expression and are categorized into four groups. Out of the four groups, GhACT1 is expressed in fiber cells and has a vital role in fiber elongation (Fig. 1). Suppression of GhACT1 by RNAi resulted in a significant decline of mRNA and disrupted cytoskeleton network in fibers and, subsequent inhibition of fiber elongation. Aquaporins are special proteins present in the plasma membrane and tonoplast and have a critical role in cell expansion. Two important aquaporin genes GhPIP1-2 and GhTIP1 were reported to be highly expressed during cotton fiber cell elongation (Liu *et al*., 2000). GhHOX3 controls cotton fiber elongation. Silencing of this gene reduces fiber length up to 80% and overexpression of GhHOX3 results in lengthening of fiber (Shan *et al*., 2014). GhHOX3 binds to an HD-ZIP protein (GhHD1) resulting in increased transcriptional activity while gibberellic acid (GA) repressor DELLA interferes with this activity by competitive binding to GhHOX3. Elevated GA concentration breaks DELLA protein which indicates that GA plays a decisive role in fiber elongation (Chen, 2017). Recent investigations reported PIN gene family in *G. arboreum*, *G. raimondii* and *G. hirsutum* that played role in cotton fiber development especially at initiation and elongation stages (Zhang *et al*., 2017).

Some of the proteins are responsible for cold stress at the time of fiber elongation in cotton. A few of these proteins are related to low-temperature stress including phosphoenolpyruvate carboxylase (PEP-Case) (Crecelius *et al*., 2003), H^{+-}ATPase and sucrose synthase (Baud *et al*., 2004) which have also been identified in other plants through genetic studies (Zheng *et al.*, 2012). In addition to the above proteins, some act as general stress-inducible proteins, like molecular chaperones and superoxide dismutase (SOD). Three main groups of proteins were also reported to be involved in elongation and biosynthesis of fiber, and transportation of fiber cell wall components, fiber cell elongation mechanism and those related to interaction with the environment, defense, and signaling. The enzymes which increase synthesis and transport of cell wall components in cold stress include sucrose synthase (SuS), β-galactosidase and phenylcoumaranbenzylic ether reductase (PCBER).

Genes associated with fiber elongation are assumed to provide us with resources that can be explored for fiber quality improvement in cotton (Zhao *et al*., 2001). Fiber differentiation is controlled by various genes in multiple cotton species that were reportedly expressed in different phases of fiber development. However, only a small number of genes were found to be involved in the synthesis of various enzymes, polysaccharides, waxes, lignin's and many fibers specific structural proteins as reported by (Liu *et al*., 2000). Depending upon their expression in fiber cell, a few genes have been characterized for improvement of fiber length and micronaire value. Proteins like ethylene receptors, ethylene response factor 2, Dicer-like 1 protein (DCL1), heat shock proteins (HSPs) and benzoquinone reductase (BR), that help plant in environment interaction, signaling, and defense mechanism were found to be expressed under stress (Li *et al*., 2015).

Secondary wall biosynthesis and maturation: Elongation of fiber development is followed by secondary wall biosynthesis phase (Fig. 1). Contrary to normal cell secondary wall, the fiber cell secondary wall is extraordinary as it is made up of almost 100% cellulose that forms somewhat crystalline microfibrils (Haigler *et al.*, 2009). This stage lasts until boll opens i-e 50-60 DPA. During this phase cell wall becomes thick due to deposition of secondary wall cellulose inside primary wall and this leads to decrease in living protoplast content and the space engaged by large central vacuole is gradually occupied by cellulose deposition (Gokani & Thaker, 2002b). This

represents that phases of fiber elongation and secondary wall biosynthesis considerably overlap (Fig. 1). Hence, fibers undergo simultaneous elongation and secondary wall deposition process. The reversible interconversion of sucrose and UDP into fructose and UDP-glucose is catalyzed by sucrose synthase (SuS), which is directly involved in cellulose biosynthesis (Brill *et al*., 2011). Cellulose is then assembled in a specific pattern to form microfibrils. B-Galactosidase catalyzes the synthesis of galactose, which is one of the main components of pectin and pectin is linked with elongation of fiber (Vaughn & Turley, 1999). PCBR is concerned with the biosynthesis of lignin (Turley, 2008). Newly synthesized lignin and galactose are processed in Golgi apparatus of the cell and then moved through secretory vesicles towards cell wall by exocytosis (Staehelin & Moore, 1995). Actin filament of the cytoskeleton is very important for fiber elongation process as it helps in transport of secretory vesicles released from Golgi apparatus. The onset of cold stress results in decreased number of actin filaments that considerably reduces the number of cell organelles moving in fiber cell, hence eventually results in retardation of fiber elongation rate (Li *et al*., 2005).

Fiber development genes are controlled by different transcription factors. Specific transcription factors are responsible for lint, fuzz and fibreless phenotypes. Overexpression or down regulation of these transcription factors may initiate or inhibit fiber or trichome development in different plant tissues. Understanding the role of different transcription factors that interact with genes at different phases of fiber development is necessary for the application of genetic manipulation mechanism in the improvement of fibers and trichomes in plants.

Hormonal control of fiber development and elongation: Plants use different types of hormones as signaling molecules to coordinate a broad range of functions that synchronize their growth and development. Studies on cotton fiber development have investigated the role of phytohormones as key regulators for the development of these economically important cells. Previous studies suggest that auxin, gibberellins, and brassinosteroids promote cotton fiber development *In vitro*. EST analysis from ovule exposed various presumed plant growth regulators which are associated with the majority of plant hormones gibberellic acids, auxins, brassinosteroids and abscisic acids. These growth regulators are abundant during different stages of fiber development (Fig. 1).

Auxins and gibberellins: The combination of auxin and gibberellins has been found to enhance fiber growth in in-vitro cultured ovules (Seagull *et al*., 2004), whereas unfertilized ovules need auxin and gibberellins application from exogenous source for fiber growth (Beasley & Ting, 1974). Gene expression studies also explored the role of gibberellins and auxin in fiber growth. In cDNA microarray, a cupin super family protein was found to be up-regulated in 10 DPA ovules (Ji *et al*., 2003).

A constructive relationship exists among fiber length as well as auxins (IAA). Gokani and Thaker (2002b) analyzed fibers of three cotton cultivars *Gossypium hirsutum* hybrid-4 (H-4), hybrid-8 (H-8) and *G. arboreum* G.Cot-15 which revealed the role of auxin in fiber elongation both in-vitro and in-vivo. Auxin's function in fiber cell elongation is related to the regulation of cell wall loosening and supply of wall materials (Chen *et al*., 2012). Auxin also plays a role in secondary cell wall deposition and stimulation of cellulose formation in this process (Hunsaker *et al*., 1994). During whole phases of growth, fibers were examined for conjugated and free indole acetic acid (IAA) and phenylacetic acid (PAA) constituents. Water contents increased during rapid cell elongation phase and declined when fiber passed through secondary thickening phase (18-42 DPA) in all of three cultivars. In an in-vivo study related to fiber growth, media supplemented with IAA considerably improved fiber length in case of short and middle staple cultivars, whereas PAA increases fiber length in short staple cultivars. While in another study GA3 contents remained low during elongation and increased after a decrease in the rate of fiber elongation in all three genotypes (Gokani & Thaker, 2002a).

Use of transgenic approach has enhanced the manipulation of hormone concentrations with respect to tissue sensitivity in plants to get improved crop yield and quality (Phillips, 2007; Zhang *et al*., 2011). For the betterment of fiber length and micronaire value, much effort has been made by scientists at the molecular level. By the overexpression of GhGA20ox1 a GA20-oxidase gene, an increase in the endogenous GA concentration in developing ovules as well as in fiber for increased lint percentage and elongation was observed (Xiao *et al*., 2010). In a similar study, targeted expression of an IAA biosynthetic gene, iaaM under floral binding protein promoter (FBP7), amplified the endogenous IAA levels at the fiber initiation stage (Zhang *et al*., 2011). Auxins also indirectly contribute to fiber development, for instance in the case of DELLA proteins which are critical components in GA (gibberellic acid) signal transduction and regulated by both ethylene and auxin. These DELLA genes are involved in the process of fiber cell initiation and elongation (Hu *et al*., 2011). The natural transporter of auxins are PIN-FORMED (PIN) proteins, which play a significant role in the distribution of auxin and also control various biological processes such as overexpression of GhPIN6_At, GhPIN1a_Dt, and GhPIN8-At, also act to promote the density and length of trichomes in *Arabidopsis*. Their putative effect on cotton fiber is still under investigation (Zhang *et al*., 2017).

Brassinosteroids (BR): Brassinosteroids are naturally occurring hormones with steroid chemistry and are found throughout the plant kingdom. They elicit growth stimulation at nanomolar concentrations. BR enhances cell elongation, affects cytoskeleton, and cell wall structure. Sun *et al*. (2005) revealed that adding a minute concentration of brassinosteroid brassinolide (BL) to cultured cotton ovules increased cotton fiber elongation while the use of Brassinazole 2001 (BRZ), which was the inhibitor of BR biosynthesis, retarded fiber length, and ovule size. Application of BR biosynthesis inhibitor (brassinazole2001) hindered fiber initiation probably due to alteration in the differentiation of ovule epidermal cells into fibers. Hence, application of exogenous BL increases fiber formation whereas use of BRZ reverses this effect (Shi *et al*., 2006).

BR signal transduction plays role in determining cotton fiber length. Transgenic plants with altered brassinosteroid Insensitive 1 (BRI1) expression produce fibers similar in length to wild-type plants. The plants that overexpress BRI1 produced fibers with the thicker secondary wall. Antisense suppression of BRI1 expression reduced secondary cell wall deposition. These changes in fiber cell growth correlated with alterations in expression of cellulose synthase gene in fiber development. This indicates that the BR signaling pathway promotes the expansion of fiber cell in plants by the accumulation of cellulose (Sun *et al*., 2015). BR deficiency led to the impairment and decrease in fiber elongation. previous studies isolated a dwarf mutant *pag1*with small, dark green leaves, short fibers. It was found that dwarfism was caused by BR deficiency as exhibited by *pag1* characteristics. Exogenous application of BL rescued *pag1*but no significant affect was observed on wild-type (Yang *et al*., 2014). Experiments using cDNA microarray revealed that transcript level of BL biosynthesis genes SMT1 and DET2 are associated with fiber growth (Shi *et al.,* 2006). The expression level of SMT1 and DET2 mRNA in cotton ovule increased from the day of anthesis to 10 days post anthesis and then decreased at 20 DPA ovules of fibreless fl mutant in comparison with wild-type (Shi *et al*., 2006).Genes involved in BR biosynthesis and inactivation are regulated by a feedback mechanism. BRs may act as a master integrator of fiber elongation by altering ethylene, and cadmium signaling, and cell wall and cytoskeleton-related gene expression. Detailed molecular mechanism of BR controlled fiber elongation needs to be explored yet.

Ethylene: Ethylene biosynthesis is the most important pathway that is up-regulated during cotton fiber cell elongation in accordance with recent physiology and gene expression analysis (Shi *et al*., 2006). Experiments on gene expression profile depicted that 1-Aminocyclopropane-1-Carboxylic Acid Oxidase1-3 (ACO1-3) genes involved in ethylene production were found to be at a high level during 10-15 DPA of fiber elongation. Exogenous application of ethylene increased fiber cell expansion and ethylene inhibitor 2-aminoethoxyvinyl glycine (AVG) inhibited fiber growth (Shi *et al*., 2006).The results suggest that this hormone has a significant role in supporting cotton fiber growth and elongation. Additionally, ethylene might enhance cell elongation by escalating the expression of tubulin, sucrose synthase and expansin genes (Shi *et al*., 2006). Detection of ethylene in fibers proved that it affects fiber elongation. Ethylene biosynthesis genes (ACO1-3) are expressed at fiber elongation stage. Studies have investigated that it may interact with BR and ROS signaling pathway. Experiments on cultured ovules with exogenous application of ethylene ameliorate the problem of fiber elongation caused due to BR biosynthesis inhibition. However, application of both ethylene and BR on cultured ovules triggered the expression of genes for biosynthesis of other phytohormones. This cross-talk between hormones and genes may regulate fiber development in both negative and positive perspective (Shi *et al*., 2006; Stiff and Haigler, 2012).

Treatment of ovule culture with H_2O_2 enhanced fiber length and APX activity in addition to ethylene production, while ethylene treatment stimulated the production level of H_2O_2 and promoted fiber length (Qin *et al*., 2008). Ethylene level in cotton fiber is also affected by very long chain fatty acids (VLCFA). Addition of VLCFA to cultured ovules elicits the expression of ethylene biosynthesis genes that lead to fiber elongation (Qin *et al*., 2007a). Future studies to explain the interaction of VLCFA, ethylene, BR and ROS can help in understanding composite signaling set-up coordinating the fiber development.

Abscisic acid: Abscisic acid (ABA) plays an inhibitory role in fiber development. Use of ABA to unfertilized cultured ovules results in a decline of fiber growth (Haigler *et al*., 2012).The inhibitory function of ABA is somewhat balanced in the presence of cytokinins, which inhibits fiber development in the absence of ABA.

ABA concentration in fruit is low at the time of anthesis and decreases during next two days. It then increases up to 15 fold between the 2nd and 10th day of development. The amount of ABA decreases and is undetectable up to 30 DPA. From 30 to 50 DPA the level of ABA increased again (Haigler *et al*., 2012). In another study, it was investigated that ABA level was higher in mature cotton fruits as compared to young healthy fruits (Gokani *et al*., 1998). It was concluded that internal ABA level exhibited a reverse correlation with the rate of fiber elongation. High internal ABA contents result in shorter fiber among different cotton cultivars. A reverse relationship exists between ABA contents and fiber length. Dasani & Thaker (2006) analyzed fiber of three cotton cultivars *G. hirsutum* hybrid-4 (H-4), hybrid-8 (H-8) and *G. arboreum* G.Cot-15 to reveal the function of ABA in fiber elongation in both *In vitro* and in-vivo situations. Significant inhibition in length of fiber was seen when media supplemented with ABA was applied to the in-vitro grown fiber. The inhibitory effect of ABA on fiber length was reduced due to the addition of growth promoters like NAA and GA along with ABA. From the results of *In vivo* and *In vitro* experiments, it can be concluded that ABA may be playing an inhibitory role in fiber elongation and is a positive indicator of the onset of cell wall thickening.

Cytokinins: Cytokinins are a group of plant hormones that take part in cell division and also various physiological and developmental processes of plants (Werner & Schmülling, 2009). Cytokinins have a vital function in seed and root development, however, they retard fiber elongation at elevated concentration in ovule culture (Pear *et al*., 1996). Cotton fiber and seed yield were improved by slightly raising the level of endogenous cytokinin and suppressing cytokinin dehydrogenase (GhCKX) expression (Zhao *et al*., 2015).

Plant hormones play a decisive role during interaction with physiological and developmental 'switches' involved in fiber growth. Auxins help in cell elongation by loosening the cell wall and supply of

structural materials. Auxins also play a role in secondary cell wall deposition and stimulation of cellulose formation during this process. Ethylene increases the expression of some fiber development-related genes. The antagonistic effect of some hormones may act as a limiting factor for fiber cell development. However, the exogenous application of plant growth regulators at a particular time may be helpful for the appropriate cell development. Little is known about the fact that how some of the cells are differentiated into lint (long fibers) and others into fuzz (short fibers) from the same ovule/ epidermis. The possible reason could be the selective utilization of nutrients for elongation of long fibers. Another reason might be the fact that when a number of cells differentiate into fiber some substances from ovule epidermal cells are transferred into to fuzz which the effect of other cells to develop into full-length fibers. The mechanism is yet unknown and needs to be explored.

Effect of temperature on fiber elongation: Cotton (*Gossypium* spp.) fruit quality, particularly fiber quality, is the consequence of interface among genetic (Mansoor & Paterson, 2012), environmental (Zheng *et al*., 2012) and management factors. Both fiber length and dry weight are influenced by the interaction of the environment and genotype. The difference in fiber quality is due to meteorological alterations, especially temperature which is the limiting factor in fiber maturation and secondary cell wall thickening. The optimal temperature required for the process of fiber elongation is somehow less than the optimal temperature for boll maturation (Pettigrew, 2001). High temperature (above 35°C) is common throughout cotton-growing regions of the world which profoundly affects its growth and yield. In Pakistan, Cotton is cultivated in warm areas. High temperature affects both vegetative and reproductive growth of plants and ultimately influences fiber quality (Farooq *et al*., 2009). High temperature (35-40°C) result in infertility and boll retention as well as cell membrane thermos-stability issue (Reddy *et al*., 1999).Wang *et al*. (2014) reported that in Xinjiang at the beginning of a cotton growing season when the temperature is relatively low, delay in sowing date affects fiber quality as the low temperature can stop boll maturation at the end of growing period. This effect is also prominent in achieving optimal fiber length.

The fiber of shorter length is the result of low temperature (Zheng *et al*., 2012). Cool average temperature and low night temperature below 22.0°C hinders fiber elongation by diminishing the rate of axial growth of fibers in early stages of elongation prior to 15 DPA (Qiu *et al*., 2007). Under low-temperature stress, fiber quality is considerably deteriorated and fiber development is affected adversely (Liakatas *et al*., 1998). Hence, more information about the mechanism of low-temperature adaptation or low-temperature resistance with respect to cotton fiber elongation is essential for cotton agriculture (Fig. 2).

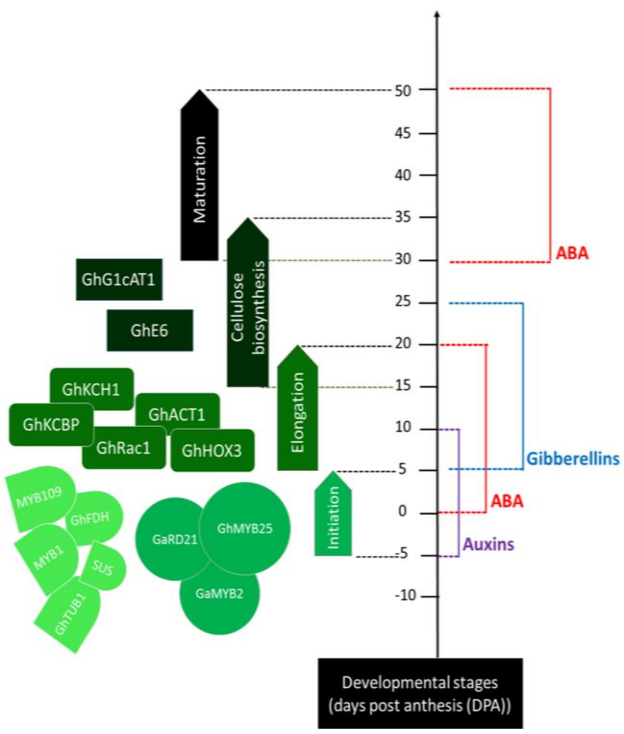

Fig. 1. A representation of stages of fiber development (time scale in black indicates partially overlapping stages of fiber cell including initiation, elongation, cellulose biosynthesis and maturation) with duration of each stage in days post anthesis (DPA), genes and hormones expressed at each stage are also shown. The direction of arrows shows sequence from initiation to maturation.

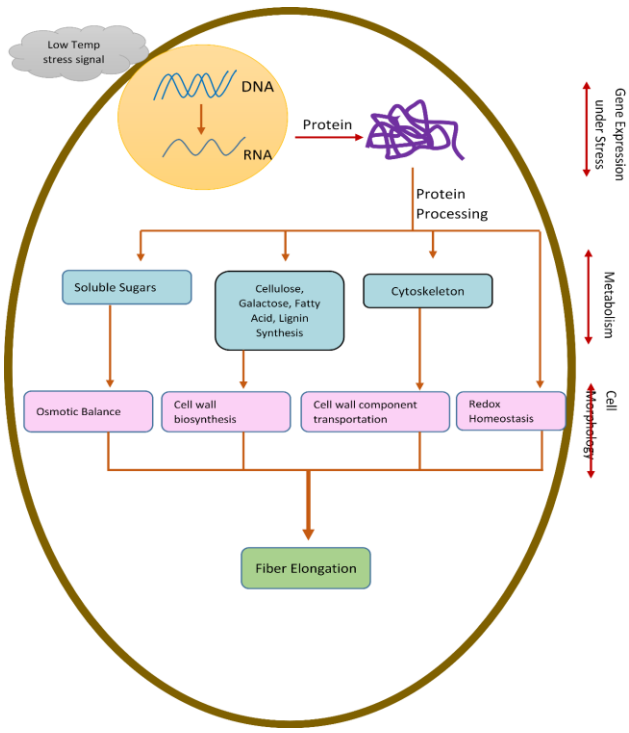

Fig. 2. A schematic model showing low temperature stress response in cotton fibers. On exposure to low temperature stress cotton fibers perceive stress signals and transmit into cellular machinery to control gene expression. Amount of proteins involved in synthesis of sugars, polymers and cytoskeleton in fiber cells can change that results in regulation of redox homeostasis, transportation of cell wall components, cell wall synthesis and osmotic balance to develop low temperature of cotton fiber.

Mechanism of fiber cell elongation under low temperature: High turgor pressure and expandable primary walls result in quick fiber elongation (Ruan *et al*., 2004).Organic solutes with malate and soluble sugars are main factors for increasing turgor while expansin and endoxyloglucantransferase (EXGT) genes are concerned with cell wall expansion (Cosgrove, 2000). Phosphoenolpyruvate carboxylase (PEPCase) and two R1 proteins are engaged in the metabolism of malate sugar (Smart *et al*., 1998). Transketolase and transaldolase are part of pentose phosphate pathway that generates C3 to C7 sugar phosphates. On exposure to cold stress, these proteins are increased quickly at 10 and 15 DPA in low temperature tolerant but decreased in low-temperature sensitive cotton cultivars. One PEPCase that might act as a proton-translocating pump, transports malate and soluble sugars towards cell vacuoles and is found to increase under low-temperature stimulus in the cold tolerant cultivar. The aforesaid proteins change rapidly at 10 to15 DPA rather than 20 DPA, as fiber elongation is fast between 10 –to 15 DPA and at this stage metabolism is high (Ruan *et al*., 1997). Therefore, the early fiber elongation (10 to 15 DPA) may be more susceptible to low-temperature stress.Using microarray and quantitative real-time PCR Liu *et al*. (2000) compared the transcriptome of two cotton cultivars, a short fiber mutant Ligon lintless-1and normal wild-type TM-1.The results revealed that only a few genes expressed from 0 to 3 DPA fiber whereas most of the transcripts which were differentially expressed were in 6 DPA fiber. This indicates that 6 DPA is perhaps a key phase in determining fiber elongation.

Endoxyloglucantransferase (EXGT) helps in the breakdown and molecular grafting of xyloglucan polymers, reorganization, and formation of cellulose and xyloglucan complex of cell wall after cell elongation. Expansin weakens the non-covalent binding between wall polysaccharides, allowing turgor-driven polymer creep. The activity of these two enzymes is in acidic pH. The acidic environment is provided by H+-ATPase that translocates protons outside the cytosol to apoplast (Rayle & Cleland, 1992). Zheng *et al*. (2012) reported that expansin was upregulated in cold tolerant (Kemian 1), but down-regulated in low temperature sensitive (Sumian 15) cultivar under cold stress. These consequences represent that expansion of fibers under low-temperature stress was easier in Kemian 1 as compared to Sumian 15. EXGT and H+-ATPase increased in both cotton cultivars on exposure to low temperature.

High temperature and cotton fiber development: Cotton yield is mainly determined by the number of seeds per boll which is determined by the number of locules in each boll and number of ovules in each locule. It has been observed that seed development is negatively affected by high temperature. A slight rise in temperature (1°C) under field conditions although, not enough to decrease seed weight but is sufficient to cause a substantial decrease in seed number per boll (Pettigrew, 2001). The reason for this decline may be the negative effects of high temperatures on ovule fertilization (Snider *et al*., 2009).

High atmospheric temperature drastically affects the growth and development of plants (Ekinc *et al*., 2017). The heat stress caused by such high temperatures can increase the evaporation rates of the plants resulting in osmotic stress that affects different growth stages of crops. The optimum temperature for cotton has been reported to be from 20-30°C (Reddy *et al*., 1991), but cotton can also be grown at temperatures exceeding 40°C in Indo-Pak subcontinent yet their yield can be affected at extremely high temperatures (Oosterhuis, 1999).

Metabolic processes within plant cells are influenced by variation in temperature, higher the temperature faster the metabolic processes, lest it should become so high that the cells start to deteriorate and enzymes start to degrade. This boost up reaction is favorable during day time but when high temperature continues through the night then respiration rates are increased and plants tend to use up the stored energy for their survival.

Growth stage that is most prone to high temperature is the reproductive stage of cotton. The deposition of carbohydrates is inadequate leading to deformed or smaller bolls or even boll shedding and also less lint production giving lower yields (Reddy *et al*., 1995; Reddy *et al*., 1996; Reddy *et al*., 1999; Oosterhuis, 2002; Zhao *et al*., 2005). Increase in temperature from 30 to 40°C, also increases the number of fruiting sites but boll retention is decreased abruptly (Hodges *et al*., 1993). When the rise in temperature is persistent throughout the growing season then every 1°Crise in temperature can result in 17% decline in crop yield on average (Lobell *et al*., 2003). Lokhande & Reddy (2014) found out that fiber length was maximum at the optimum temperature of 22°C and with the rise in temperature fiber length was decreased but the strength increased. Fiber strength and micronaire are affected by temperature changes during cellulose deposition in secondary cell wall development (Ruan, 2007). At high temperatures, fibers formed showed high strength due to the enhanced secondary cell wall thickening. Fiber maturity and finesse are determined by micronaire values that also depend on secondary cell wall thickness. Fiber micronaire and uniformity were optimum at 25°C and showed quadratic tendencies with respect to temperature.

Previous studies reported that high-temperature stress leads to alleviated ethylene levels in cotton, therefore plant growth regulators that can block the overproduction and action of ethylene can prove to be a good strategy to produce thermo-tolerant varieties of cotton. One of such growth regulators is the 1-MCP (1-Methylcyclopropene) which has been reported to improve cotton yield (Storch, 2010). A set of miRNAs (miR2118, miR828, miR869, miR1030, miR159, miR165, miR170, miR319, miR529, and miR1884) has been reported to be upregulated in cotton during high-temperature stress. Overexpression of these miRNAs can be used to develop heat-tolerant cotton varieties (Zahid *et al*., 2016). According to Burke & Chen (2015), Heat Shock Proteins (HSPs) were synthesized in great number and accumulated in lab-grown cotton when exposed to high-temperature range from 38 to 41°C. These proteins are involved in thermos-tolerance, prevent protein denaturation, sustain cell integrity and aid in photosynthesis, but the realization of heat tolerance by overexpression of HSPs in plants have not been yet achieved.

Fiber improvement through genetic engineering an alternative to breeding: Cotton fiber growth is influenced by low-temperature stress due to reduced activity of enzymes involved in cellulose synthesis and sucrose metabolism. To ameliorate the harmful effect of low-temperature, alternative strategies are required such as overexpression of sucrose phosphatase synthase (SPS) and sucrose synthase (SuS) into cotton may be helpful in raising low-temperature tolerant cotton cultivars (Shu *et al*., 2009). The introduction of the antioxidative enzyme may reduce the extent of injury to low temperature (Zheng *et al*., 2012). Genes encoding the enzymes, β-ketothiolase (phaA), Acetyle-CoA reductase (phaB) and polyhydroxyalkanoate synthase (phaC) catalyze the production of aliphatic polyester poly-D-(2)-3-hydroxybutyrate (PHB) from acetyl-CoA. PHB can alter fiber characteristics when it is produced in cotton as it is the thermoplastic polymer. Cotton fibers exhibit endogenous phaA activity and cotton transformed with phaB and phaC genes along with GUS expression confirms the existence of phaB and phaC genes in fiber cells. Transgenic fibers with PHB exhibited considerable changes in thermal characteristics as these fibers showed improved insulation properties. The transgenic cotton fibers showed higher heat capacity due to the slow rate of heat uptake and cooling. These facts demonstrate that fiber properties can be improved by integrating novel traits into cotton from other genetic resources through metabolic pathway engineering. The successful use of this strategy will directly influence the output of textile industry by producing new generation fibers (John & Keller, 1996). Transformation of bacterial cellulose synthesis acsA and acsB genes into cotton played a significant role in the improvement of fiber length and strength. Up to 15%, transformants showed a significant difference in cellulose contents as compared to non-transformed control (Li *et al*., 2004). Genetic transformation of cotton with fiber-related genes from other plants with better fiber quality traits may also help to improve fiber elongation. In cotton, integration, and expression of *Calotropis procera*, CpEXPA3 gene increased the fiber strength as compared to the control plant (Akhtar *et al*., 2013; Bajwa *et al*., 2013).

Genetic transformation of cotton with fiber-related genes taken from other plants can be useful to improve the staple length of the cotton fiber. The manipulation of genes related to fiber growth promoting hormones such as auxin, BR, and gibberellins can play a significant role not only in the improvement of staple length but also in an overall yield of cotton. Overexpression of Invertase, SuS and SPS genes can play their role in the improvement of fiber maturity and increase plant biomass together with preparing the plant for temperature stress through the provision of substrates for cellulose synthesis, which is important for fiber maturity and temperature stresses tolerance.

Conclusion

Cotton fiber elongation is the key to success of cotton textile industry relying on the efforts of breeders and biotechnologists working for its improvement. Scattered information of physiology and molecular control have previously resulted in the loss of these efforts. The huge gap between plant geneticist and plant physiologist resulted in the scarcity of information needed for sound efforts for the improvement of fiber quality. The examples of different case studies and research outcomes from physiology and molecular characterization of fiber development presented here will prove beneficial for improvement of cotton fiber in future. Comprehensive understanding at the molecular and physiological level will enable the biologists to combine the two approaches together for maximum output in the form of increased staple length and micronaire value. It is important to understand more about the functional and metabolic pathways important for fiber development. Moreover, the people working on a genetic modification for fiber improvement can use this information for genetic manipulation of any fiber related trait in cotton. This kind of comparative study will help the scientific community to have an in-depth understanding of genetic improvement of fiber quality and yield traits.

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Declaration

Authors declare that there is no conflict of interest while publishing this article.

Compliance with ethics guidelines

The manuscript is a review article and does not involve any research protocol. So approval by institutional board or ethics committee is not required.

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