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Research Insight **Open Access**

Research Insights into Hormonal Regulation of Cotton Fiber Elongation

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Abstract Cotton fiber elongation, a key factor in fiber quality and yield, is regulated by a complex network of phytohormones. Auxin, gibberellins (GAs), brassinosteroids (BRs), ethylene, and peptide hormones promote elongation, while cytokinin and abscisic acid (ABA) act as inhibitors. Key transcription factors such as GhMYB212, GhHOX3, and GhBES1.4 drive fiber growth through hormone signaling and sucrose transport regulation. Crosstalk between hormones, such as auxin-BR and GA-strigolactone interactions, further optimizes fiber elongation. Emerging insights into lipid metabolism (e.g., GhLTP4) and peptide hormones (e.g., GhPSK) reveal additional mechanisms enhancing fiber quality. Future efforts should focus on targeted genetic engineering, hormone pathway optimization, and integrating multi-omics approaches to develop high-quality, resilient cotton varieties, ensuring sustainable production for the textile industry.

Keywords Cotton fiber elongation; Plant hormonal regulation; Gibberellins (GAs); Brassinosteroids (BRs); Genetic engineering and breeding

1 Introduction

Cotton fiber grows from the epidermis of the ovule. It is actually a single cell that goes through four main stages during development: initiation, elongation, secondary cell wall formation, and the final maturation stage (Lee et al., 2007; Fang et al., 2018). Because these fiber cells grow very long and have many variations, they are often used to study how cells grow larger, how polyploidy forms, and how cell walls are synthesized (Xiao et al., 2019). Among them, the elongation step is the most important, which determines how long the fiber can grow in the end. And fiber length is a key quality indicator in textile production (Tuttle et al., 2015).

Whether the fiber can grow long directly affects the yield and quality of cotton. In textile mills, long fibers are more popular. They spin better yarn and higher quality fabrics (Sun et al., 2019; Wang et al., 2021). Fiber elongation is actually a process in which the cell itself becomes larger. This process is not simple and is regulated by both genes and hormones (Cao et al., 2020; Chen et al., 2023). Some hormones, such as auxin, gibberellin, brassinolide and ethylene, can help fibers grow longer. But some hormones, such as cytokinin and abscisic acid, make it difficult for fibers to elongate (Xiao et al., 2019). Understanding these regulatory mechanisms is very useful for us to improve the quality and yield of cotton. This information is important both from a genetic perspective and from an agricultural planting perspective (Li et al., 2020; Zhai et al., 2023).

This study aims to comprehensively explore the role of hormone regulation in cotton fiber elongation. We will integrate the latest findings in this field, with a particular focus on the effects of different plant hormones on fiber development. The study will also identify key genes related to hormone biosynthesis and signal transduction pathways, and explore the specific mechanisms of how these hormones regulate fiber elongation. By bringing together existing research results, this study hopes to provide valuable reference and guidance for the genetic improvement of cotton and the development of planting technology.

2 Hormonal Pathways in Plant Development

2.1 Role of hormones in cell elongation

Plant hormones are important for cell elongation. Cell elongation is the basis for plants to grow taller or larger. Many hormones can help cells grow longer, such as auxin, gibberellins, brassinolide, ethylene, jasmonic acid, and estrolactone. But some hormones prevent cell elongation, such as cytokinin and abscisic acid (Xiao et al., 2019; Jan et al., 2022). For example, brassinolide (BR) can affect the synthesis of a substance called "very long chain fatty acids" (VLCFAs). VLCFAs are critical for cell wall formation and elongation (Yang et al., 2023). In addition, there is a small peptide hormone called PSK-α, which can regulate potassium ion efflux and plant respiration, thereby helping cells elongate (Han et al., 2014).

2.2 Crosstalk between hormonal pathways

Cell elongation is not determined by just one hormone. It is the result of the combined action of multiple hormones. They cooperate with each other and sometimes affect each other's effects. For example, studies have found that glucose (Glc) can work with brassinolide (BR) to promote the growth of cotton fibers. Glucose activates some genes related to BR, making the fibers grow faster (Li et al., 2021). For another example, a protein called GhHOX3 and gibberellin (GA) signals also cooperate to enhance the expression of a protein in fiber cells that makes the cell wall "loosener", thereby helping the cells to grow longer (Shan et al., 2014). The "cooperation" of these hormones can enable plants to better cope with different environmental changes, and make cell lengthening more coordinated, which is beneficial to the development of the entire plant.

2.3 Significance in cotton fiber growth

Cotton fibers are very special. They are the result of a single cell being elongated. Studying this cell elongation is very helpful in understanding how plants grow. Many hormones contribute to the growth of cotton fibers. For example, auxin, gibberellin and brassinolide (Xiao et al., 2019; Jan et al., 2022). Studies have found that a key gene in the BR signaling pathway is called *GhBES1.4*. When its expression is increased, it will regulate the genes that control VLCFA synthesis, thereby making the fibers grow longer (Liu et al., 2022; Yang et al., 2023). There is also a small peptide hormone called PSK-α, which can also help fibers elongate by regulating potassium ion outflow and reactive oxygen (Han et al., 2014). These studies show that hormone regulation is very important for the development of cotton fibers. Understanding these processes will help us improve the quality and yield of cotton.

3 Auxin-Mediated Regulation

3.1 Mechanisms of auxin signaling in fiber cells

Auxin is particularly important in making cotton fiber cells grow longer. It works through a series of signals. There is a transcription factor called GhTCP14, which is a key regulator discovered in the study. It can affect the expression of auxin-related genes, such as *AUX1* and *PIN2*. These genes determine how auxin is distributed and how it works in the cell (Wang et al., 2013). There is also an auxin response factor called GhARF18, which directly binds to the promoters of gibberellin-related genes, such as GhGA3OX4D and GhGA20OX1D-2. This increases the synthesis of gibberellins and makes the fibers grow faster (Zhu et al., 2021). In addition, GhERF108 interacts with GhARF7-1 and GhARF7-2. This effect connects the signals of ethylene and auxin, which is critical for the formation of cell walls in the later stages of fiber (Wang et al., 2023).

3.2 Auxin transport and distribution in cotton

Auxin does not run around randomly. Its transport and distribution in cotton fibers are accomplished by PIN proteins. GhPIN3a is a special auxin transporter that can transport auxin outward and control its concentration in fiber cells. If these GhPIN genes are inhibited, cotton fibers will not easily begin to develop and their length will also be affected (Zhang et al., 2016). There is also a GTPase called GhROP6, which can control the location and degradation of GhPIN3a, thereby concentrating auxin in cells. This is very important for cell elongation (Xi et al., 2022). In addition, the study also found that most auxin is transported, not synthesized by fiber cells themselves, which also shows that the role of transport proteins is particularly large (Zhang et al., 2016).

3.3 Genetic evidence of auxin’s role in elongation

Many genetic experiments have shown that auxin can indeed make cotton fibers longer. For example, if *GhARF18* is expressed more, the fibers will become longer; and if *GhARF16* is knocked out, the fibers will become shorter. This shows that they are indeed regulating fiber length (Figure 1) (Zhu et al., 2021).

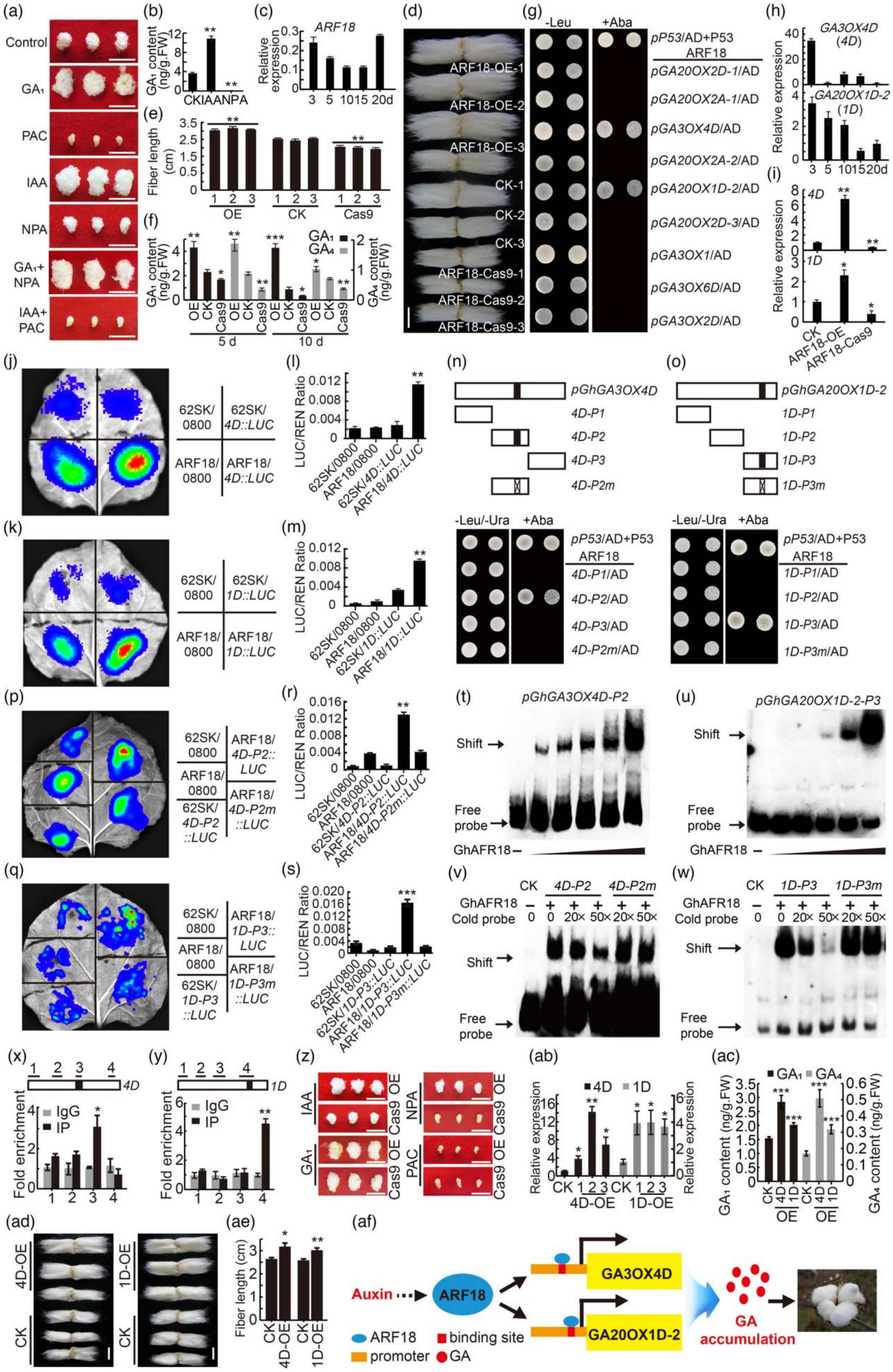

Figure 1 Auxin promotes fiber elongation by enhancing GA biosynthesis (Adopted from Zhu et al., 2021)

There is also a gene called *GhLTP4*, which is related to both lipid transport and auxin response. If its expression is upregulated, the fibers will be longer; if it is downregulated, the fibers will be shorter (Duan et al., 2023). In addition, GhMYB212 is a transcription factor that can regulate the process of sucrose transport into cells, which is critical for elongation. If the expression of this gene is reduced, the fibers will become shorter and sucrose will also be reduced (Sun et al., 2019). This also shows that auxin not only acts directly, but also helps the fibers to lengthen by affecting sucrose transport.

4 Gibberellins and Fiber Growth

4.1. Role of gibberellins in cell expansion

Gibberellins (GA) can make cells larger, which is important for the elongation of cotton fibers. There is a gene called *GhGA20ox1* that is involved in the synthesis of GA. If it is expressed more, the GA in the cotton body, especially GA_4 , will increase, resulting in longer fibers and more fibers growing on the ovules (Xiao et al., 2010). GA can also increase the expression of some cell wall-related genes, such as CesA (cellulose synthase), which help the cell wall grow so that the cell can continue to elongate (Xiao et al., 2015). In addition, GA will work with some transcription factors (such as GhHOX3) to transmit GA signals to genes that regulate cell wall loosening, thereby promoting the continued elongation of fiber cells (Xiao et al., 2015).

4.2 GA synthesis and sensitivity in cotton

In cotton, the synthesis of GA and the plant's response to it are both controlled by specific genes. For example, *GhGA20ox1*, *GhGA20ox2* and *GhGA20ox3* are all involved in the synthesis of GA. Among them, *GhGA20ox1* is mainly expressed in elongated fibers, while the other two are more active in ovules (Xiao et al., 2010). This different expression pattern shows that the production of GA is "regionally regulated" so that the fibers can be elongated in the right place. Another point is that GA response elements (called GARE) can be found in the promoters of many genes involved in cell wall synthesis, such as KCS and CesA. This means that these genes can directly receive GA signals and then regulate fiber growth and cell wall thickness (Xiao et al., 2015).

4.3. Interaction with Other Hormones

GA does not "work alone". It often cooperates with other hormones to regulate fiber growth. For example, trimethylolate (SL) works after the GA signal. It can promote the synthesis of some very long chain fatty acids (VLCFAs) and cellulose, which is important for cell elongation and cell wall thickening (Zhang et al., 2022a). Studies have also found that GA can activate a transcription factor called GhGRF4, which in turn promotes the expression of SL-related genes, so that the amount of SL in fiber cells increases (Figure 2) (Zhang et al., 2022b). GA also cooperates with jasmonic acid (JA) to promote the initiation and elongation of fibers. Proteins such as GhJAZ3 and GhSLR1 are responsible for "messaging" between them (Xia et al., 2018). These complex hormone combinations indicate that the development of cotton fiber is not accomplished by a single hormone, but by multiple hormones working together.

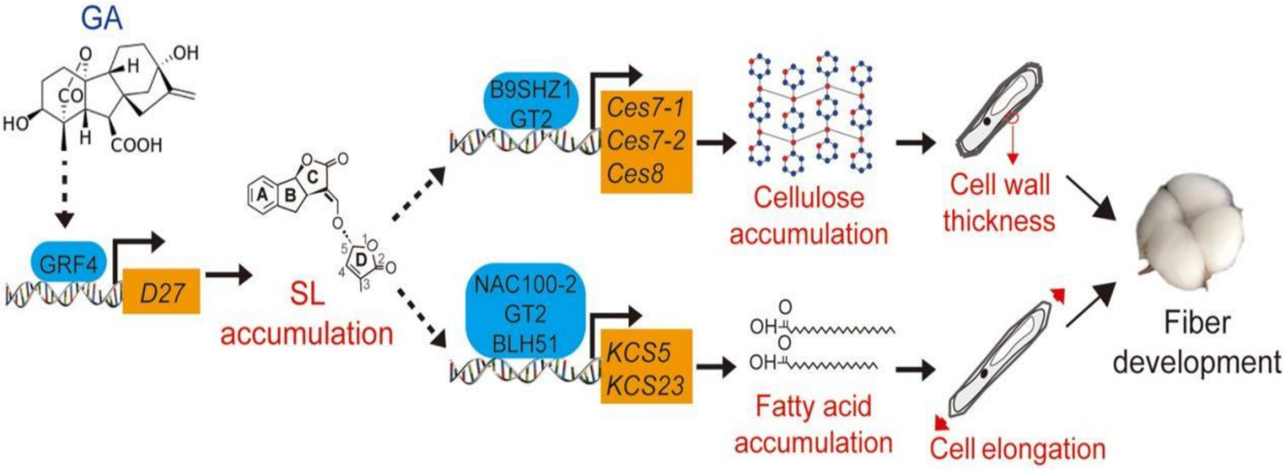

Figure 2 Schematic diagram depicting the mechanistic framework of SL-GA crosstalk signaling in the regulation of cotton fiber cell elongation and cell wall thickness (Adopted from Zhang et al., 2022b)

5 Ethylene Signaling in Fiber Elongation

5.1 Ethylene's contribution to fiber cell wall softening

Ethylene can make cotton fiber cell walls softer, which is a key step in cell elongation. It promotes the production of reactive oxygen species (such as hydrogen peroxide H_2O_2), which affect the activity of some enzymes, such as ascorbate peroxidase (APX). This enzyme helps stabilize the level of reactive oxygen, thereby loosening the cell wall and making the cell larger (Qin et al., 2008). In addition, ethylene can also increase the expression of some cell wall-related genes, such as expansin. This protein can directly soften the cell wall and make the fiber elongate more smoothly (Shi et al., 2006).

5.2. Regulatory genes involved in ethylene synthesis

Ethylene synthesis does not occur randomly. It is controlled by some enzymes, especially ACS (1-aminocyclopropane-1-carboxylic acid synthase) and ACO (1-aminocyclopropane-1-carboxylic acid oxidase). For example, genes such as ACO1-3 are activated in large quantities when the fiber is elongated, indicating that they are directly related to the increase of ethylene (Shi et al., 2006). There is also an E3 ubiquitin ligase called GhXB38D, which inhibits the synthesis of ethylene. It marks ACS4 and ACO1 for degradation, thereby reducing the amount of ethylene and affecting the elongation of the fiber (Song et al., 2023).

5.3. Temporal dynamics of ethylene in fiber development

The role of ethylene is also different at different time stages. Studies have found that the level of ethylene is the highest during the stage of rapid fiber elongation. At this time, ethylene can help the cell swell and is also conducive to its continued elongation (Shi et al., 2006). The production of ethylene is also regulated by the reactive oxygen species (ROS) feedback mechanism. Simply put, ethylene promotes the production of H_2O_2, and H_2O_2 can in turn stimulate the synthesis of more ethylene. In this way, the level of ethylene can be continuously maintained at a state that is conducive to growth (Qin et al., 2008). In addition, during this rapid growth period, some genes related to ethylene response, such as *GhVTC1*, will also be activated. It is involved in the synthesis of ascorbic acid, which also shows that the role of ethylene in this stage is very critical (Song et al., 2019).

6 Cytokinin and Abscisic Acid (ABA) Interplay

6.1 Impact of cytokinin on fiber development

Cytokinins are important for plants, as they help cells divide and differentiate. However, they behave differently in cotton fiber development. Studies have found that cytokinins actually inhibit fiber growth. For example, after external addition of cytokinins, the initiation and elongation of cotton fibers are weakened (Xiao et al., 2019; Wu, 2024). This inhibitory effect may be because it changes the expression of some genes related to cell wall synthesis. And the cell wall is very important for fiber elongation.

6.2 ABA's role in stress response and elongation

Abscisic acid (ABA) is the main hormone used by plants to cope with stress such as drought and salt. Its "main job" is to cope with stress, but in cotton fiber development, it also plays a certain inhibitory role. Studies have shown that when ABA levels increase, cotton fibers tend to become shorter. This shows that ABA is not conducive to fiber elongation (Xiao et al., 2019). This may be because ABA affects the expression of some genes related to elongation and stress. In this way, plants will shift resources from "growth" to "self-protection".

6.3 Balance between cytokinin and aba for fiber growth

Both cytokinin and ABA hormones inhibit the elongation of cotton fibers. However, there is a "degree" to their interaction. If the two can maintain a balance, it will help the fiber grow normally. If one of them is too strong, it will easily break the balance and make the fiber development worse. Therefore, plants need to precisely regulate the levels of these two hormones. On the one hand, the fiber can continue to elongate, and on the other hand, it must be prepared to deal with external pressure (Xiao et al., 2019). Understanding how they interact will help us use hormone regulation methods to improve cotton fiber quality and yield.

7 Emerging Roles of Brassinosteroids

7.1 Brassinosteroid pathways in fiber elongation

Brassinosteroids (BR) are a plant hormone that is particularly important for cotton fiber elongation. It can help fiber growth by regulating some metabolic pathways. One of the key pathways is the synthesis of very long chain fatty acids (VLCFA). For example, when cotton lacks BR, the expression of GhKCSs (3-ketoacyl-CoA synthase) required for VLCFA synthesis will decrease, which will affect fiber elongation (Yang et al., 2023). In addition, BR also cooperates with the glucose signaling pathway. Glucose can increase the synthesis of BR and enhance the signaling function of BR, further helping fiber elongation (Li et al., 2021). The BR signaling process is not simple. It includes a series of "phosphorus addition" and "phosphorus removal" processes. GSK3 kinase is one of the "brake molecules" that inhibits BR signals (Wang et al., 2020).

7.2 Functional studies in cotton

Many experiments have shown that BR is indeed critical to the growth of cotton fibers. For example, researchers expressed GhBES1.4, a BR-related transcription factor, more in cotton and found that the fibers became significantly longer; but if this gene was "turned off", the fibers became shorter (Liu et al., 2022; Yang et al., 2023) (Figure 3). For another example, adding external BR (such as brassinolide BL) to cotton will also make the fibers longer. On the contrary, if a drug called Brz is used to inhibit the synthesis of BR, the fibers will not grow (Sun et al., 2005). There is also a BR-deficient cotton mutant called pagda1 (or pag1), whose fibers cannot grow. But if BL is added to it, the fibers can resume growth. This also shows that BR is necessary for the development of cotton fibers (Yang et al., 2014).

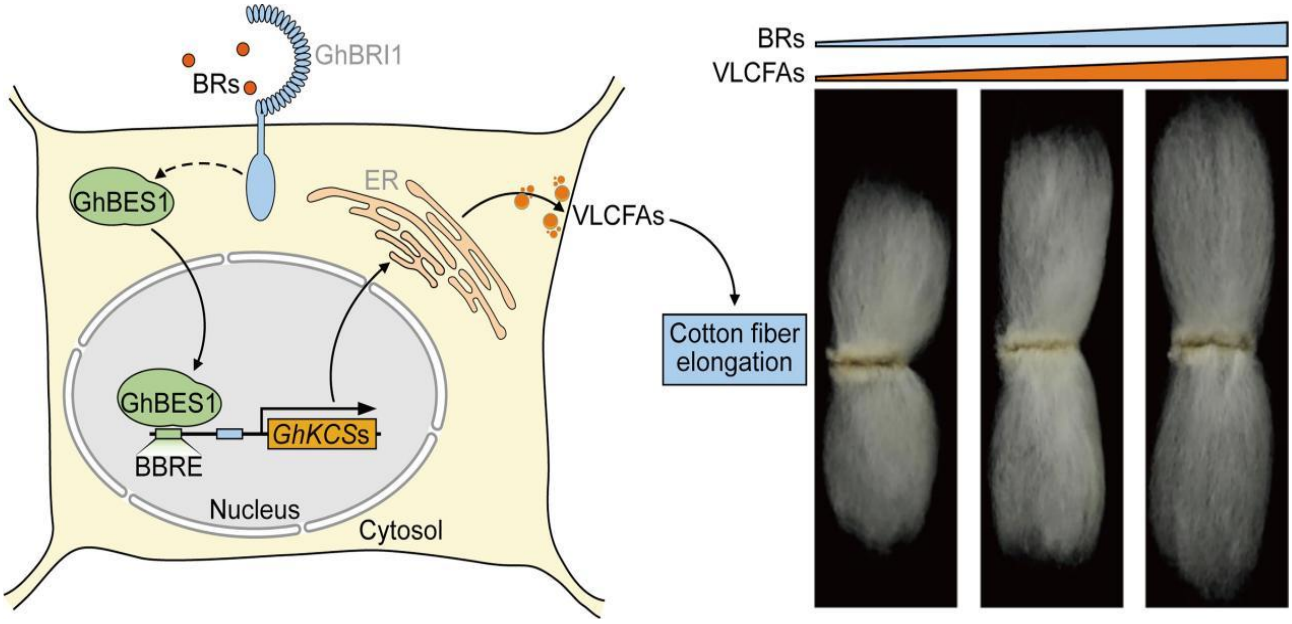

Figure 3 A model for the regulation of cotton fiber elongation through the crosstalk between BR and VLCFA. In the presence of BR, the key TF in the BR signaling pathway, GhBES1, moves to the nucleus and directly binds to the BRRE of *GhKCSs* to activate its expression. High expression of *GhKCSs*, encoding the rate-limiting enzyme of VLCFA biosynthesis, increases endogenous VLCFAs contents, which promotes fiber elongation (Adopted from Yang et al., 2023)

7.3 Interaction with auxin and gibberellins

BR does not work alone. It often cooperates with auxin and gibberellins to affect fiber elongation. For example, some studies have added auxin and gibberellin to cultured cotton ovules and found that they can promote the initial development and elongation of fibers, which is very similar to the effect of BR (Sun et al., 2005). The relationship between these hormones is very complex. Studies have found that BR can enhance the expression of some genes in the auxin and gibberellin pathways, that is, it "amplifies" their effects (Xiao et al., 2019). In addition, BR and gibberellin can also regulate some of the same target genes together, which shows that they actually have a "cooperative mechanism" when regulating fiber elongation (Xiao et al., 2010).

8 Case Study: Hormonal Interventions in Elite Cotton Varieties

8.1 Overview of selected case study

This case study focuses on how hormones can be used to improve the fiber quality of high-quality cotton. Cotton fiber develops from the epidermis of the ovule and is a very important raw material for the global textile industry. Recently, studies have found that many plant hormones are related to the development of cotton fiber, especially in the process of fiber lengthening and improvement (Shan et al., 2014; Xiao et al., 2019; Jan et al., 2022).

8.2 Hormonal manipulations to improve fiber quality

Researchers have tried several hormone intervention methods to improve cotton fiber quality: Auxin and gibberellin can make fibers longer. Auxin can loosen the cell wall, thereby allowing the cell to elongate. Gibberellin cooperates with some transcription factors to promote fiber elongation (Shan et al., 2014; Xiao et al., 2019). Brassinolide (BR) is very important for cotton fiber elongation. It can regulate the synthesis of a kind of VLCFA (very long chain fatty acid). VLCFAs are critical for cell membrane stability and cell elongation. Studies have found that if the BR-related gene *GhBES1.4* is expressed more, the fibers can become longer (Liu et al., 2022; Yang et al., 2023). The peptide hormone (GhPSK) can promote fiber growth by regulating potassium ion efflux and the cell respiratory chain. Overexpression of GhPSK makes cotton fibers thin and long (Han et al., 2014). Glucose is not only a nutrient, it can also be used as a "signal". It interacts with BR and promotes fiber elongation together. Studies have found that when the glucose concentration is low, the fiber grows better; too high a concentration will inhibit growth. This shows that glucose signaling is also important in fiber development (Li et al., 2021).

8.3 Lessons learned and implications for breeding programs

Through these hormone intervention methods, researchers have summarized some experiences that can help future breeding work: Precisely target hormone pathways: Figuring out which hormone pathways control fiber quality and how they affect each other is the key to improvement strategies. For example, the coordination between glucose and BR indicates that hormones should be used in “appropriate amounts” and not one-sidedly (Li et al., 2021). Use genetic engineering to regulate key genes: Some genes, such as *GhBES1.4* and *GhPSK*, are directly involved in hormone synthesis or signal transduction. If the expression of these genes is increased or decreased, the length and fineness of the fiber can be affected. Experimental results show that this regulation method is effective (Han et al., 2014; Liu et al., 2022). Use a combination hormone strategy: Different hormones sometimes cooperate with each other, and sometimes "fight" with each other. For example, auxin, gibberellin and BR have positive effects; but cytokinin and ABA have negative effects. Therefore, when using these hormones together, it is necessary to consider the ratio and balance to best promote fiber development (Xiao et al., 2019; Jan et al., 2022).

9 Technological Advances in Hormonal Studies

9.1 Transcriptomic approaches to decipher hormonal pathways

Now we have more advanced transcriptomics technology, which allows us to understand the role of hormones in cotton fiber growth more clearly. For example, a study found that if GhBES1.4, a transcription factor related to brassinolide (BR), is expressed more, the fiber will become longer; if it is "turned off", the fiber will become shorter. This was analyzed by combining DAP-seq and RNA-seq technologies. Scientists have found 1531 target genes regulated by this gene, which also allows us to better understand how it regulates cotton fiber development (Liu et al., 2022). In addition, scientists used digital gene expression analysis to compare the fiber transcriptomes of different cotton varieties and found that some genes related to sugars, fatty acids and secondary metabolism are more expressed in varieties with longer fibers. These genes are also likely to be related to fiber elongation (Fang et al., 2014).

9.2 CRISPR/Cas9 and functional genomics in cotton

CRISPR/Cas9 and other genomic tools are now being used to study the functions of key genes in cotton. For example, GhHOX3 is a transcription factor involved in fiber elongation. If we reduce its expression, the fibers will become shorter; but if we increase its expression, the fibers will become longer. Transcriptome and biochemical analyses further demonstrated how this gene controls cell wall relaxation, allowing fibers to elongate (Shan et al., 2014). In addition, a regulatory module called miR396b-GRF5 was also found to be important for fiber development. After inhibiting miR396b through virus-induced gene silencing (VIGS), cotton fibers became longer, indicating that this module can also be used to improve fiber quality (Zhang et al., 2022a).

9.3 Integrative omics for hormonal regulation insights

Researchers are now also using a combination of "multi-omics" methods to fully understand how hormones affect cotton fiber growth. For example, a study used GWAS, RNA-seq, and DAP-seq together to find seven genes related to fiber elongation. These genes are all regulated by GhBES1.4 in the BR pathway (Liu et al., 2022). Another study comparing phosphorylated proteomes found the role of GhSK13 in the BR signaling pathway. This gene is related to the organization of the microtubule skeleton, energy metabolism, etc., and has a great influence. This study found a total of 900 protein substrates that may be regulated, deepening our understanding of BR signaling (Wang et al., 2020). Another gene, *GhLTP4*, is also very important. It can increase the content of ceramide and activate auxin signaling. These two effects combined can make cotton fiber cells grow faster (Duan et al., 2023).

10 Conclusions and Future Perspectives

Research on how hormones regulate cotton fiber elongation has led to a number of important discoveries. For example, GhMYB212 is a key transcription factor that regulates the *GhSWEET12* gene, thereby controlling the entry of sucrose into the elongating fiber cells. In this way, it can affect the length and quality of cotton fibers. Studies have also found that a variety of hormones are involved in regulating fiber development. Some hormones have a promoting effect, such as auxin, gibberellins, brassinolide, ethylene, jasmonic acid and estrolactone; there are also hormones that inhibit fiber growth, such as cytokinins and abscisic acid. In addition, two transcription factors called GhFP2 and GhACE1, one promoting growth and the other inhibiting growth, play an "antagonistic" regulatory role.

There is also GhHOX3, which is a homeodomain protein that can work with other proteins and gibberellins signals to control the fiber elongation process. Glucose is not just a nutrient, it can also act as a signaling substance, synergistically with brassinolide to regulate fiber lengthening. The study also found that the peptide hormone GhPSK can promote fiber growth and improve quality. The Ca^{2+}-dependent protein kinases GhCPK84 and GhCPK93 phosphorylate GhSUS2 (sucrose synthase). Phosphorylated GhSUS2 inhibits fiber elongation. Finally, there is a gene called *GhLTP4*, which regulates lipid metabolism, increases ceramide content, and activates auxin signaling, thereby promoting continued elongation of fiber cells.

Although we have made many discoveries, there are still many unresolved problems in this field. For example, the relationship between hormones is very complex, and they will affect each other and even interfere with each other. Although we know which hormones are involved in regulation, it is not clear how they "cooperate" or "fight" specifically. In addition, transcription factors with opposite functions such as GhFP2 and GhACE1 also make research more difficult to analyze. Another problem is that it is not easy to turn discoveries in the laboratory into technologies that can be used in the field. Genes like *GhPSK*, which seem to have potential, work well in experiments, but will they have side effects in real field environments? We don't know yet. In addition, external environments such as weather, soil, and climate can also affect the effects of hormones, which adds another layer of difficulty to the research.

However, the research also brings a lot of hope. It provides us with many new directions for improving cotton in the future. For example, regulating GhMYB212 and GhSWEET12 can improve the transport of sucrose and make the fibers longer. We can also adjust the hormone pathway: while strengthening the effects of "good hormones" such as auxin and gibberellin, while reducing the negative effects of cytokinin and abscisic acid, it is more likely that cotton will grow high-quality fibers. Peptide hormones such as GhPSK also provide new ideas for us to try biotechnology intervention.

There are also lipid metabolism pathways, such as the role of GhLTP4, which can also be used as a regulatory target to further improve the length and quality of fibers. In general, these new discoveries and technical means are expected to help us cultivate better quality, higher yield, and more resistant to environmental changes in cotton varieties, providing new opportunities for the sustainable development of cotton planting.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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