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Regulatory Mechanisms of Protein Post-translational Modifications in Cotton Fiber Elongation and Maturation

Jinhua Cheng, Shanjun Zhu, Mengting Luo
Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, China
Corresponding email: mengting.luo@jicat.org

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Abstract Cotton (*Gossypium* spp.) fiber is an important natural textile raw material. Its development process mainly includes four stages: initiation, elongation, secondary wall thickening and maturity, which are finely regulated by complex molecular networks. In recent years, protein post-translational modifications (PTMs), as an important mechanism for regulating plant cell activities, play a key role in the development of cotton fibers. This study systematically sorted out the regulatory functions of currently known PTMs types (such as phosphorylation, ubiquitination, acetylation, methylation, etc.) in the process of fiber elongation and maturation, revealed its molecular mechanisms in signal transduction, cytoskeleton remodeling, cell wall synthesis, etc., summarized the key functional proteins closely related to PTMs and their regulatory pathways, and explored its application prospects in molecular breeding of high-quality cotton. This study provides new theoretical support and direction for improving fiber traits, and is expected to further promote the advancement of cotton molecular breeding technology and the upgrading of the cotton fiber industry.

Keywords Cotton; Fiber development; Protein post-translational modification; Phosphorylation; Molecular regulatory mechanism

1 Introduction

The development of cotton fiber is quite complex and goes through several different stages. It first grows, then slowly elongates, then the cell wall thickens, and finally matures. Each stage is different and affects the quality and yield of the fiber. Therefore, this process has become a special concern for agricultural production and the textile industry.

In these processes, a change called "post-translational modification (PTM) of proteins" is very important. It is actually the cells that process them after they are synthesized. For example, small molecules such as phosphate, acetyl, methyl or palmitoyl are added. These modifications affect the function of proteins, and may also cause them to change their location in the cell or change the connection between them. In cotton, scientists have found that these PTMs regulate many key links. For example, they affect whether mRNA is stable and whether it will be translated. They can also change the structure of chromatin and make some enzymes or structural proteins involved in fiber growth more active or more stable. These effects are particularly important for whether cotton fibers can be smoothly elongated and finally mature (Liu et al., 2016; Tao et al., 2016; Imran et al., 2019; Singh et al., 2020; Xing et al., 2023; Silaiyiman et al., 2024).

This study will comprehensively outline the regulatory mechanisms of protein post-translational modifications (PTMs) in the elongation and maturation of cotton fibers, and combine the latest advances in transcriptomics, proteomics, and functional genomics to explore how specific post-translational modifications (PTMs) affect fiber development, focusing on key regulatory proteins and pathways, and discussing their significance for cotton breeding and fiber quality improvement. This study lays the foundation for the development of new strategies for regulating PTM pathways, in order to improve fiber properties through precision breeding and molecular design, and promote the cultivation of high-quality and high-value-added cotton varieties.

2 Developmental Stages of Cotton Fiber Cells

2.1 Initiation and differentiation of fiber cells

Cotton fiber develops from a single cell on the seed epidermis, starting before or during flowering. This process is controlled by some important transcription factors, such as MYB25-like and HOX3. At the same time, plant hormones are also at work, such as auxin, gibberellins, brassinolide and ethylene. Through single-cell and spatial transcriptome technology, researchers have discovered some key genes and metabolites that are very important for the formation and early development of fiber cells. For example, genes such as DOX2, KCS19.4, BEE3, HOS3.7, SVB and SVBL, as well as substances such as linoleic acid, spermine and spermidine. At this step, the number of initial fiber cells will be determined, and their number will directly affect how many fibers can be grown in the end (Qin et al., 2022; Zhai et al., 2023; Bai and Scheffler, 2024; Sun et al., 2025; Zhang et al., 2025).

2.2 Cellular characteristics during elongation

After formation, fiber cells will grow rapidly, and some can even grow to several centimeters. This stage has several characteristics: the internal turgor pressure of the cell is very high, the cell wall will continue to loosen, and the cytoskeleton will also change, mainly the rearrangement of the actin and microtubule structures. At this time, the auxin signal becomes stronger, the enzymes related to cell wall relaxation are also very active, and lipid metabolism is also accelerated. These changes are conducive to cell expansion. Transcriptome and metabolome analysis found that the expression levels of many genes and metabolites have changed, among which aquaporins and regulatory factors related to gibberellins are particularly important. This stage mainly determines how long the fiber can grow, and the length of the fiber is a key criterion for evaluating fiber quality (Gou et al., 2007; Zhang et al., 2017; Prasad et al., 2022; Iqbal et al., 2023).

2.3 Secondary cell wall synthesis and maturation

When cotton fibers stop lengthening, they enter the next important phase: the synthesis of secondary cell walls. This phase generally occurs between 16 and 24 days after flowering, but may vary for different cotton varieties. At this point, fiber cells begin to synthesize cellulose in large quantities, while other metabolic activities gradually decrease, allowing the cells to focus on one thing: building a cell wall that is almost entirely made of cellulose. Proteins such as GhTCP4 and GhFIM2 control when this process begins and how fast it progresses. Studies of protein and gene expression have found that many genes related to carbohydrate metabolism, the cytoskeleton, and cellulose synthase become particularly active during this phase. Other genes involved in general metabolism decrease in expression. Next comes the maturation phase. The walls of fiber cells continue to thicken, and the cells themselves slowly move toward programmed cell death. This phase is like the final step in cotton fiber development, as the cells complete their mission and exit, leaving only mature fibers with complete structures. This whole set of processes together determines the final quality of cotton fiber (Abidi et al., 2010; Wang et al., 2010; Zhou et al., 2019; Cao et al., 2020; Jareczek et al., 2023; Grover et al., 2024; Meera et al., 2024).

3 Major Types of Post-Translational Modifications

3.1 Phosphorylation

Phosphorylation is a protein modification that can occur repeatedly. It is a process in which an enzyme called "kinase" adds a phosphate group to the protein. This action changes the function of the protein, such as increasing or decreasing its activity, and may also change its stability or affect the way it cooperates with other molecules. In plants, phosphorylation is very important. Especially in some signaling pathways such as MAPK, it can regulate cell differentiation and development. These processes are critical to the growth of cotton fibers. For example, phosphorylation can regulate the activity of certain enzymes and transcription factors, and also affect how plant hormones such as auxin transmit signals. And these changes will affect how the fiber elongates and when it matures (Aguilar-Hernández et al., 2020).

3.2 Ubiquitination

Ubiquitination is another common modification. It is to attach ubiquitin molecules to proteins. It's like marking a protein. With this mark, the protein may be degraded or its function may change. This process requires three enzymes to complete together, called E1, E2 and E3. In plants, ubiquitination is often combined with other modifications, such as phosphorylation and acetylation. Together, they regulate protein stability and help cells transmit signals. This type of regulation is very helpful for the rapid growth of fiber cells and allows cells to change their morphology in a timely manner (Cui et al., 2023; Zhang & Zeng, 2020; Lacoursiere et al., 2022).

3.3 Acetylation and methylation

Acetylation and methylation are two common modifications on proteins, especially at the lysine and arginine positions of histones or other proteins. They can change the structure of chromatin and affect the function of proteins (Li, 2024). Generally speaking, acetylation makes genes more likely to be expressed. Methylation is more complicated, sometimes promoting expression and sometimes inhibiting it. These two modifications are very critical in epigenetic regulation and can regulate genes related to cotton fiber elongation and maturation. In addition, these modifications often do not work alone. They work together with other modifications (such as phosphorylation or ubiquitination) to form a complex regulatory system that determines whether genes are active or silent during fiber development (Aguilar-Hernández et al., 2020).

4 Roles of PTMs in Cotton Fiber Elongation

4.1 Signal transduction and hormone response regulation

Post-translational modifications (PTMs) such as ubiquitination play an important role in cotton fiber elongation. They mainly affect the hormone signaling pathway. For example, the F-box type E3 enzyme GhMAX2 causes the transcriptional repressor GhS1FA to be ubiquitinated and degraded. This process can activate the signal of brassinolide, increase the synthesis of fatty acids, and thus help the fiber grow better (Sun et al., 2025). There is also a hormone called brassinolide, which also works through PTM. It can regulate genes related to the cytoskeleton. Transcription factors such as GhBES1 can activate the β-tubulin gene *GhTUB17*. This method connects hormone signals and cytoskeleton regulation together (Zhang et al., 2024).

4.2 Regulation of cell wall remodeling proteins

PTMs also affect the functions of some important proteins in the cell wall. Especially in the synthesis and remodeling of polysaccharides, they directly affect the elongation of fibers. Some genes, such as *GhMDHAR1* and *GhDHAR2*, regulate the redox state of cells. This regulation can improve antioxidant capacity and increase the supply of cell wall polysaccharides, thereby prolonging the rapid growth period of fibers (Tian et al., 2024). PTMs such as ubiquitination may regulate the number and activity of enzymes in these processes so that the cell wall can remain flexible and stable during rapid growth (Sun et al., 2025; Tian et al., 2024).

4.3 Cytoplasmic skeleton and cell polarity maintenance

The skeleton of fiber cells is mainly composed of microtubules and actin filaments. They help cells maintain polarity and support the special elongation of fibers. PTMs regulate the expression of some cytoskeleton-related proteins, such as GhMAP20L5 and GhTUB17. These proteins can control the arrangement of microtubules and affect the deposition mode of cellulose (Song et al., 2022; Wang et al., 2024; Zhang et al., 2024). Live cell imaging experiments have found that the arrangement of actin and microtubules in cotton fibers is very special, showing a diffuse growth pattern that is biased towards the tip. This pattern is finely controlled by PTM, which allows the cell direction to be stable and the fibers to grow forward all the time (Yu et al., 2019).

5 Roles of PTMs in Fiber Maturation

5.1 Regulation of cellulose and lignin accumulation

When cotton fibers enter the mature stage, they begin to synthesize cellulose and lignin in large quantities. At this time, post-translational modifications (PTMs) play a big role. It affects some key proteins, such as transcription factors that regulate genes, and enzymes involved in the synthesis process. Some NAC-like proteins work in pairs. They can regulate genes like *GhCesA*, which is related to cellulose synthesis. If this gene is expressed more, the fiber cell wall will become thicker (Chen et al., 2025). In addition, there is a transcription factor called GhMYB7, which can bind to a region in front of the *GhCesA* gene, so that it can control the synthesis rate of cellulose. Changes in PTMs will affect the start time and speed of this process (Figure 1) (Huang et al., 2021). Lignin synthesis is also regulated by PTMs. For example, the enzyme GhCAD37 plays a role in regulating lignin synthesis. If lignin increases, the strength and maturity of cotton fibers will also change (Li et al., 2024). However, the amount of lignin cannot be too much, otherwise it will hinder the synthesis of cellulose and ultimately deteriorate the quality of the fiber (Zheng et al., 2024).

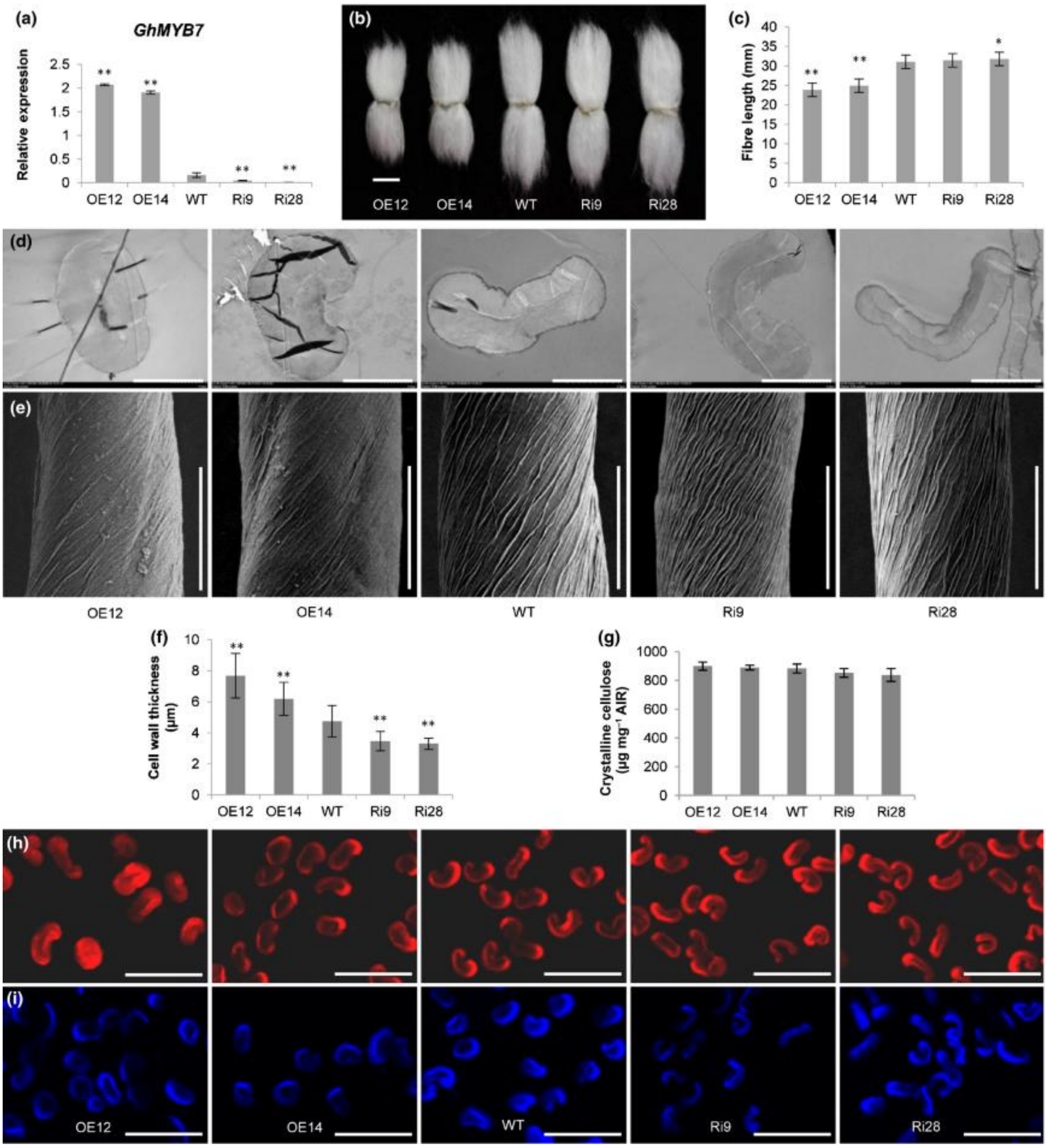

Figure 1 Phenotypic analysis of fibres of GhMYB7 overexpression and RNA interference (RNAi)-silenced transgenic cotton plants. (a) Quantitative PCR analysis of GhMYB7 transcript levels in 18 d post anthesis (DPA) fibres of wild-type, GhMYB7 overexpression and RNAi-silenced transgenic lines from T3 generation. Cotton ubiquitin gene (*GhUBI1*) was used as an internal control for normalisation. Values represent mean ± SD of three biological replicates. OE12 and OE14, two independent lines from GhMYB7 overexpression plants; WT, wild-type; Ri9 and Ri28, two GhMYB7-RNAi-silenced transgenic cotton plants. Student's t-tests demonstrated significant differences (*, P<0.05; **, P<0.01) between transcript levels of the transgenic lines and the wild-type. (b) Image of mature fibres from transgenic cotton lines and WT. Bar, 10 mm. (c) Statistical analysis of average mature fibre length of WT and transgenic lines. Values represent mean ± SD (n≥60). *, P < 0.05; **, P<0.01. (d) Transmission electron microscopy analysis of the cell wall thickness of mature fibres of WT and transgenic lines. Bars, 10 μm. (e) Scanning electron microscopy images of the cellulose microfibrils arrangement on the surface of mature fibre in WT and transgenic lines. Bars, 10 μm. (f) Comparison of the median cell wall thickness of mature fibres from WT and transgenic lines shown in (d). Values represent mean ± SD (n≥10). *, P<0.05; **, P<0.01. (g) Crystalline cellulose content comparison of mature fibres between wild-type and transgenic lines. Values represent mean ± SD of three biological replicates. Student's t-tests demonstrated that there were significant differences (*, P<0.05; **, P<0.01) between the transgenic lines and the wild-type. (h, i) Cross-sections of paraffin-embedded mature cotton fibres were stained with Pontamine Fast Scarlet 4B (S4B) and Calcofluor White to show cellulose distribution and abundance. Bars, 50 μm (Adopted from Huang et al., 2021)

5.2 Protein degradation and energy metabolism

As the fiber gradually matures, some proteins and enzymes are no longer needed. At this time, they must be degraded, and ubiquitination, a post-translational modification, can do this. The advantage of doing this is that the fiber cells can smoothly transition from the "elongation" state to the "maturity" stage. It can also save energy and use this energy in more important places, such as making cellulose and lignin (Hammarén et al., 2022). Therefore, PTMs not only help clean up old proteins, but also make metabolic activities in cells more organized. This is critical for maintaining normal cell function and supporting cotton fiber maturation.

5.3 PTM regulation of senescence-related processes

As fibers gradually mature, some aging-related processes also begin to occur, such as programmed cell death and the slow cessation of metabolic activity. PTMs also play a role at this time. They regulate proteins related to aging signals to ensure that these proteins play a role at the right time. In this way, fiber cells can complete their development step by step and eventually become mature fibers with good structure and stable performance.

6 Application of Omics Data in PTM Studies

6.1 Joint analysis of transcriptome and proteome

To understand how cotton fiber develops and matures, it is not enough to look at genes or proteins alone. Analyzing the two together can give us a more comprehensive view. Transcriptome studies gene expression, while proteome looks at changes in proteins. If we compare the gene expression data with the protein modification, we can know which genes may regulate which proteins. This method is more reliable than analyzing one omics alone, and can also discover associations that were not noticed before (Manzoni et al., 2016; Misra et al., 2019; Rajczewski et al., 2022). This joint analysis can also help us understand what kind of post-translational modification will occur to the protein generated after a gene is expressed. This is particularly helpful for understanding how cotton fiber develops step by step.

6.2 PTMs identification technology and database

To find out which modifications have occurred on proteins, mass spectrometry (MS) technology is the most commonly used. It can quickly detect the modification of many proteins and can also quantitatively analyze these changes (Rajczewski et al., 2022). Mass spectrometry technology is becoming more and more advanced. Whether it is analyzing the entire protein or just one segment, it can give accurate results. There are also many professional databases that include a lot of PTMs information in cotton or other plants. Researchers can directly refer to these data, which is more reproducible and more convenient for collaboration (Misra et al., 2019; Lu et al., 2023).

6.3 Bioinformatics prediction and network construction

It would be slow to analyze these complex data experimentally alone, so bioinformatics tools are particularly useful. These tools can help us predict where modifications may occur in proteins. They can also help us draw a diagram of the relationship between proteins, that is, the regulatory network (Yin, 2023; Sanches et al., 2024). With the help of network analysis and machine learning, researchers can find proteins that play a key role in fiber development more quickly. These predictions can also help us design subsequent experiments, avoid detours, and save time (Vlachavas et al., 2021; O'Connor et al., 2023).

7 Case Studies

7.1 Functional analysis of GhPIN phosphorylation in fiber polarity

The study found that phosphorylation, a post-translational modification (PTM), is very important in the development of cotton fibers. For example, GhMPK3-1 adds a phosphate group to the transcription factor GhWRKY16, which is particularly critical to its function. In this way, GhWRKY16 can normally regulate some genes related to fiber initiation and elongation. This shows that whether it is GhWRKY16 or GhPIN, their phosphorylation state may determine how the cell expands. By regulating the activity of these proteins, cotton fibers can establish the correct growth direction (Figure 2) (Wang et al., 2021).

7.2 Acetylation of GhXTHs and its impact on cell wall extensibility

Researchers have found that protein post-translational modification (PTM) affects the function of cell wall-related enzymes. Modifications such as acetylation will change the activity and stability of a protein called XTH. XTH is used for cell wall modification, which can make the cell wall looser and softer, which is conducive to stretching. In this way, the cell wall can be more easily stretched, which is important for the rapid growth of cotton fibers. If XTH is acetylated, its activity will change, thereby affecting the structure of the cell wall. The whole process can help the fiber grow longer and stronger (Cao et al., 2020; Zhang et al., 2018).

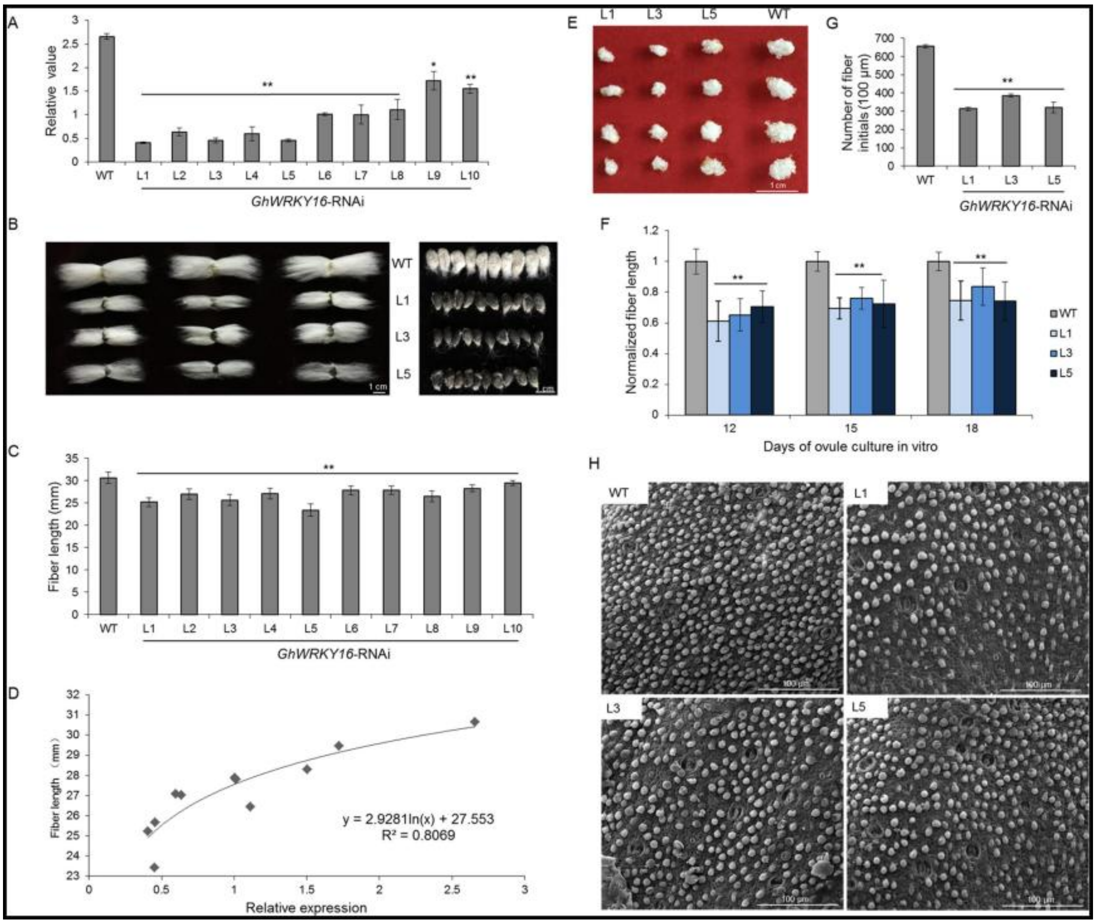

Figure 2 Silencing GhWRKY16 by RNA interference in cotton hinders fiber initiation and elongation. A, RT-qPCR analysis of GhWRKY16 (Gh_D06G0175) expression in 9 DPA fibers of the wild-type and GhWRKY16-RNAi lines. The cotton polyubiquitin gene *GhUBI1* (EU604080) was used as reference; GhWRKY16 transcript levels in the wild-type were set to 1. B, Comparison of mature fiber length and seed phenotype with or without fuzz between GhWRKY16-RNAi lines (T2 generation) and the wild-type. C, Mean mature fiber length in GhWRKY16-RNAi lines and the wild-type. D, Fiber length and relative GhWRKY16 expression is positively correlated in the RNAi lines. E, In vitro cotton ovule culture. 1 DPA ovules of GhWRKY16-RNAi lines and the wild-type were cultured in liquid Beasley-Ting medium for 12 days. F, Mean fiber length of the cultured ovules (12-18 days) from GhWRKY16-RNAi lines and the wild-type (n > 30 ovules per line). Fiber length of wild-type ovules was set to 1. G, Mean number of fiber initials counted from the middle of 0 DPA ovules. H, Scanning electronic micrographs of ovule surface from GhWRKY16-RNAi lines and the wild-type. Error bars represent standard deviation (sd) of three biological replicates. $**P < 0.01$ by Dunnett t test between the wild-type and GhWRKY16-RNAi lines. WT, wild-type; L1 - L10, GhWRKY16-RNAi cotton lines. Scale bars: 1 cm (B, E), 100 μm (H) (Adopted from Wang et al., 2021)

7.3 Correlation between E2 ubiquitin ligases and fiber length

Studies have found that some E3 ubiquitin ligases, such as GhMAX2 and GhATL68b, play a big role in cotton fiber development. GhMAX2 will "tag" a protein called GhS1FA, so that the protein will be degraded. GhS1FA is an inhibitory protein that affects fatty acid synthesis. If it is gone, fatty acids can be synthesized normally, which helps fiber growth (Sun et al., 2025). GhATL68b is also related to fatty acid metabolism. Experiments have found that without GhATL68b, cotton fibers will become shorter and the quality will deteriorate. But if some specific fatty acids are added to it, the situation will improve (Li et al., 2024). This shows that the ubiquitination process is critical. It allows some unnecessary proteins to be removed in time, ensuring that the fibers can grow smoothly, become longer and stronger.

8 Concluding Remarks

During the growth of cotton fiber, protein post-translational modification (PTM) plays a big role. It affects how cells elongate, how cell walls are built, and how plants respond to hormones and external stress. PTM regulates the activity and stability of some key proteins and transcription factors, allowing them to function normally at different stages. These modifications are needed to coordinate the entire fiber from the beginning to the gradual maturity. PTM can also integrate hormones, metabolism and environmental signals together to affect the final quality and yield of cotton.

However, there are still many unclear points in this regard. PTM changes quickly and is reversible, which makes research more difficult. In addition, the cotton genome itself is very complex and not easy to fully analyze. We are not able to fully draw a map of all PTM changes, nor can we understand how they specifically affect the fiber. In order to better study, we need to obtain high-quality omics data at different developmental stages. At the same time, the current PTM detection tools are not strong enough and need to be improved. In addition, different PTMs may affect each other, and they work together to affect the properties of the fiber. However, this relationship is not very clear yet, and many potential important genes and regulatory pathways have not been verified in vivo.

Future research can combine different omics methods, such as analyzing the genome, transcriptome, proteome and metabolome together. In this way, we can have a more comprehensive understanding of the role of PTM in fiber growth. If a more complete PTM database can be established, coupled with the advancement of gene editing and molecular breeding technology, we may be able to improve cotton varieties with good fiber quality, high yield and strong stress resistance. This can also promote the green and sustainable development of the cotton industry.

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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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