Cotton Genomics and Genetics 2025, Vol.16, No.6, 290-299
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Feature Review Open Access

Spatial Transcriptomics of Cotton Fibers During Elongation Stage

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Cotton Genomics and Genetics, 2025, Vol.16, No.6 doi: 10.5376/cgg.2025.16.0029
Received: 17 Oct., 2025
Accepted: 27 Nov., 2025
Published: 16 Dec., 2025

Preferred citation for this article:
Yang X.J., and Zhu Y.X., 2025, Spatial transcriptomics of cotton fibers during elongation stage, Cotton Genomics and Genetics, 16(6): 290-299 (doi: 10.5376/cgg.2025.16.0029)

Abstract Cotton fiber development plays a vital role in the global textile economy, and the elongation stage is crucial in determining fiber length and quality. In this study, we employed spatial transcriptomics to uncover the spatial organization of gene expression during the elongation phase of *Gossypium hirsutum* fibers. By integrating spatial barcoding and high-resolution transcriptomic mapping, we localized fiber-specific gene expression domains and identified elongation-zone-enriched transcripts. Our analysis revealed expression gradients of *GhEXPA1*, *GhRDL1*, and *GhMYB25*-like along fiber tips, highlighting region-specific transcriptional modules associated with cell wall remodeling, ROS scavenging, and energy metabolism. These findings provide functional insights into the spatial coordination of molecular pathways underlying fiber elongation. This study not only demonstrates the power of spatial transcriptomics in dissecting complex developmental processes but also lays a foundation for future applications in targeted breeding, genome editing, and molecular improvement of cotton fiber quality.

Keywords Cotton fiber elongation; Spatial transcriptomics; Gene expression mapping; *Gossypium hirsutum*; Fiber development

1 Introduction

Among the crops worldwide, cotton (*Gossypium* spp.) holds an irreplaceable position. It is not only a natural fiber but also an integral part of the economic lifeline of many countries. Especially in developing countries, the cotton industry is related to the livelihoods of millions of people and the stability of regional economies (Wang and Zhang,, 2024). Today, the global annual cotton output has exceeded 25 million tons, among which India, China, the United States and Pakistan are the major producers (Khan et al., 2020). From farmlands to textile workshops, this crop has brought in hundreds of billions of dollars in economic benefits.

The story of cotton fibers begins with the extension of those individual cells on the epidermis of the ovules. Its development is not achieved overnight but goes through stages such as initiation, elongation, formation of secondary cell walls and maturation. It is precisely these subtle processes that determine the final fiber quality and yield, and also determine whether cotton can become the raw material for high-quality textiles (Jan et al., 2022). In recent years, with the rapid progress of genomics, transcriptomics and molecular breeding techniques, people have begun to see more clearly the key genes and regulatory networks that control fibrous traits, which provides the possibility for the breeding of superior varieties.

However, among all the stages, the extension stage seems to be the most crucial. Approximately 20 days after flowering, fibroblasts will rapidly expand and can grow to about 30 millimeters. This elongation capacity not only has a distinct hereditary nature but is also closely related to the mechanical properties of the fibers, such as tensile strength and fracture resistance (Mathangadeera et al., 2020). If fibers can be better stretched, the quality of yarns is often higher and there are fewer defects in textiles. Therefore, "increasing elongation" has become one of the core goals of improvement work. Researchers have found that transcription factors, plant hormones and REDOX balance all play key roles in this process (Tian et al., 2024).

Meanwhile, an emerging technology, spatial transcriptomics, is quietly changing the perspective of plant molecular research. It is not merely about measuring gene expression, but rather being able to "see" the active locations of genes in the tissue space. This method enables people to track the differences in cell types and developmental trajectories in situ for the first time (Giacomello, 2021). Although the cell walls of plant tissues

complicate experiments, technological breakthroughs are gradually overcoming these obstacles. The latest research shows that this technology has demonstrated great potential in revealing the molecular regulation of key biological processes such as cotton fiber elongation, opening a new window for future crop improvement and basic research (Chen et al., 2023).

2 Cotton Fiber Elongation: Developmental and Molecular Features

2.1 Cellular mechanisms of fiber elongation: turgor-driven expansion and cytoskeletal dynamics

Cotton fibers are actually cells that can grow by themselves. It can be continuously elongated, even reaching several centimeters in length, and this ability is quite impressive. Its driving force comes from inflationary pressure, but inflationary pressure does not emerge out of thin air. Sucrose and potassium ions play a crucial role here. Transport proteins carry them into the cells, and water enters along with them, thereby maintaining internal pressure. Meanwhile, the intercellular filaments act like "gates" that can open and close to regulate these flow processes.

However, inflation pressure alone is not enough. The directionality and shape maintenance of fibers rely on the cytoskeleton, especially actin filaments and microtubules. In vivo imaging shows that these structures are not static but are constantly rearranged. The growth of fibers is not uniform and advancing from the top, but rather follows a slightly topical and somewhat diffused stretching pattern (Figure 1). It is precisely this flexible and dynamic skeletal organization that enables individual cells to complete elongation at an extremely high speed.

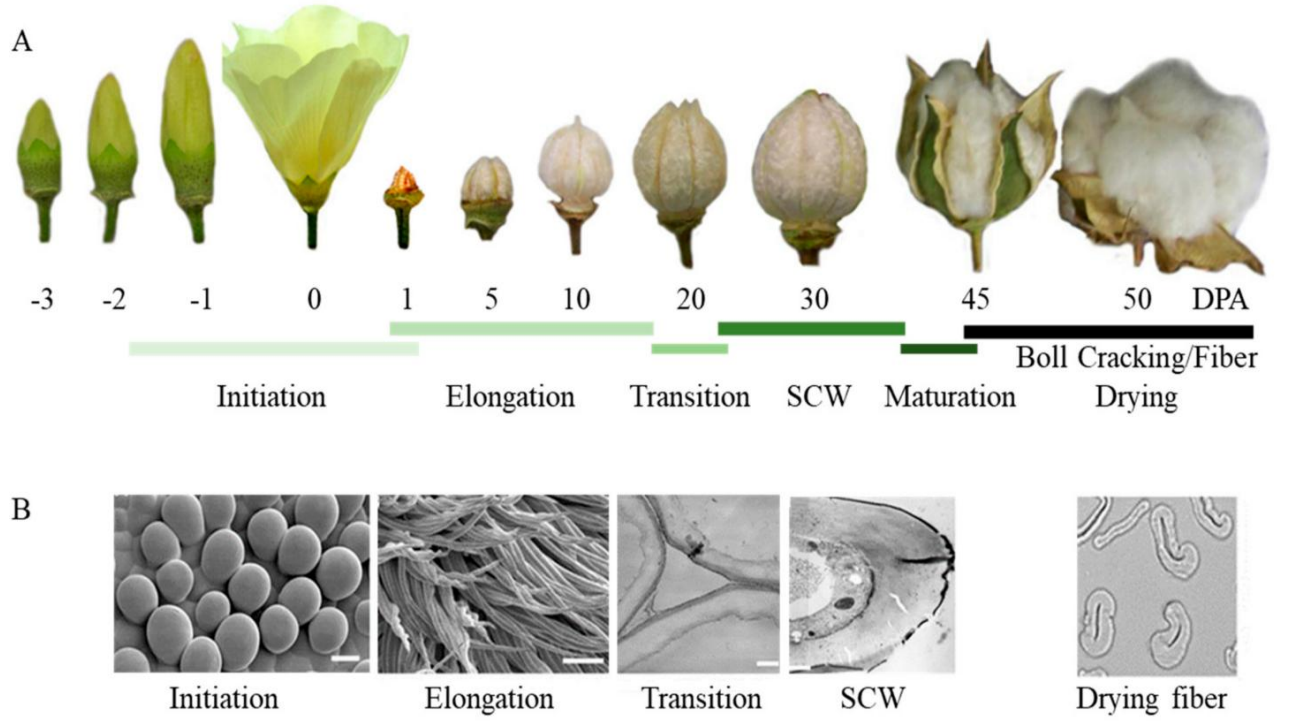

Figure 1 Cotton fiber development. (A) Progression of cotton flower and boll development. Fiber developments are classified into five stages, including initiation, elongation, transition, secondary cell wall (SCW) biosynthesis, and maturation. DPA, days post-anthesis. (B) Images of fibers at progressive developmental stages: SEM of fiber initials (bar = 10 μm) and fibers during early elongation (bar = 100 μm); TEM of the first stage of fiber thickening during the transition stage (three adjacent fibers are shown; bar = 300 nm) and near the end of secondary cell wall synthesis (bar = 1 μm); and light micrograph of cross-sectioned mature, dried, fibers (Adapted from Bai and Scheffler, 2024)

2.2 Key hormonal regulators and gene networks involved in fiber cell elongation

There is not just one "behind-the-scenes commander" regulating the elongation of cotton fibers. Plant hormones are like several commanders with distinct personalities. Auxin, gibberellin (GA), brassinosterol (BRs), and ethylene drive cells to continue growing, while abscisic acid (ABA) and cytokinin often hit the brakes.

Take BR as an example. It regulates the synthesis of very long chain fatty acids (VLCFA) and the modification of cell walls through transcription factors such as GhBES1.4, thereby affecting fiber length (Yang et al., 2023). Gibberellin has a different pathway. It activates genes related to wall dilation by degrading DELLA proteins and releasing inhibited transcription factors (He et al., 2024). Furthermore, transcription factors such as MYB, WRKY, HD-ZIP and bHLH jointly weave a vast signaling network, integrating hormone and developmental stage information (Bai and Scheffler, 2024).

Interestingly, this regulation also has a division of labor among different subgenomes. For instance, the GhWRKY28-GhTOL9 module can participate in regulation through the ESCRT pathway, further refining the elongation response. The complexity of fiber growth largely stems from this interwoven signal dialogue layer upon layer.

2.3 Role of cell wall modification enzymes and their spatial expression patterns

If turgor pressure provides the driving force, the cell wall is the bottleneck that determines whether it can be stretched open. Modifying enzymes such as dilator proteins, XTHs, pectin lyase and β -galactosyltransferase play a role of "unbinding" in it. They make the nascent cell walls more elastic, thereby cooperating with the turgor pressure to achieve cell extension.

However, these enzymes are not always active. They are expressed at the highest level in the early stage of rapid fiber elongation, but their activity significantly decreases once they enter the secondary wall synthesis stage (Lu et al., 2022). This indicates that the plasticity of the cell wall is a process precisely controlled by time and space.

Studies have found that the transcription factor GhMYB201 can directly activate the expression of these enzymes, thereby linking hormone signaling with wall remodeling (Suo et al., 2024). In addition, the interaction between the REDOX state within cells and polysaccharide synthesis is also believed to regulate the ductility of the cell wall, which may explain why fibers can continue to grow without losing their stability.

3 Spatial Transcriptomics: Tools and Techniques

3.1 Overview of mainstream spatial transcriptomics technologies and workflows

The emergence of spatial transcriptomics has enabled us to observe gene expression on the "geographical coordinates" of tissues, and there is more than one way to achieve this. Techniques such as microdissection, in situ sequencing (ISS), single-molecule fluorescence in situ hybridization (smFISH), spatial barcoding (such as Visium, Slide-seq), and selection for specific regions have each developed unique paths. Their differences often lie in how mRNA is captured and located. Some pursue high resolution, while others emphasize flux or coverage.

Typically, research begins with tissue sections, followed by the capture or labeling of transcripts, then proceeds to the sequencing or imaging stage, and finally reconstructs the spatial expression map through computational means. With the advancement of analytical processes and algorithms, these methods are no longer confined to medium and low resolutions but are gradually moving towards the study of the entire transcriptome and even single-cell and subcellular levels (Asp et al., 2020; Robles-Remacho et al., 2023). The combination of different technologies also enables spatial information to be analyzed at a higher dimension.

3.2 Technical advantages in resolving spatial gene activity over conventional transcriptomics

Compared with traditional RNA sequencing, the most distinctive feature of spatial transcriptomics is that it does not "disrupt" the positions of genes. In other words, it not only tells you what the gene is expressing, but also where it is expressed. This "where" often conceals the key to biology.

Therefore, researchers were able to identify genes with significant spatial differences, map the distribution of tissue structure, and observe cell interactions and local microenvironments that would otherwise be concealed in homogeneous samples (Rao et al., 2021; Williams et al., 2022). This method can not only help to propose hypotheses but also be used to verify them. In the construction of large-scale tissue maps and the integration with multi-omics data, it offers a level of detail that is difficult for traditional sequencing to reach. It can be said that it is more like a "microscope with coordinates", placing the complex molecular activities back into their original spatial context.

3.3 Challenges in tissue sectioning, resolution limits, and data integration

Of course, spatial transcriptomics is not without cost. The first difficulties encountered often come from the samples themselves. The cell walls of plant tissues are hard, making sectioning and segmentation a delicate and fragile process (Giacomello & Lundeberg, 2018; Yin et al., 2023). Even if the slicing is successful, the differences in resolution and sensitivity among different techniques are still inevitable, and sometimes trade-offs must be made between details and coverage.

What is more complicated is data integration. Results from different organizations, experimental batches or platforms do not always align directly, which requires powerful computational algorithms to standardize and interpret high-dimensional data. Cell overlap in thick sections, batch effects, and the combination with multi-omics information all make subsequent analysis more challenging (Du et al., 2023; Yin et al., 2023). In other words, technology has come a long way, but there is still a long way to go before achieving "perfect analysis".

4 Applications in Cotton Fiber Research

4.1 Use of spatial transcriptomics to localize fiber-specific gene expression domains

The formation of cotton fibers is not an isolated process. By combining spatial transcriptomics with single-cell RNA sequencing, researchers can now "see" how genes are distributed and active in ovules and fibrous tissues. In the past, it was only possible to guess which genes were at work, but now they can be directly located.

In this way, a number of marker gene clusters and regulatory factors closely related to fiber development have been identified, such as SVB and SVBL, which are mainly active in the initiation and early elongation stages. Spatial resolution data make these processes three-dimensional and also allow us to re-understand the metabolic priorities in early fiber growth: sucrose synthesis and lipid metabolism. These familiar faces seem to be more crucial than previously thought. Such a map is not merely an accumulation of information; it is more of a "molecular map" that sketches out the spatiotemporal outline of fiber growth.

4.2 Identification of tissue-specific and elongation-zone-enriched transcripts

The genetic activities of fibers in different tissues are not the same. High-resolution transcriptome analysis indicated that the number of differentially expressed genes (DEGs) between fibrous tissue and non-fibrous tissue far exceeded expectations (Yang et al., 2021). During the rapid elongation phase, such as 10 to 20 days after flowering, certain transcripts will be concentrated. Genes specific to these stages are often closely related to the elongation rate.

It is worth noting that not only coding genes play a role, but also long non-coding Rnas (lncrnas) and small open reading frames (sORFs) show tissue and stage-specific expression (Qanmber et al., 2023). They are not as conspicuous as the main characters, but their regulatory effects often occur at key nodes. This information provides a direction for the next step of screening candidate genes to improve fiber quality, and also reminds us that the formation of fibers is not a single process but the result of coordinated regulation at multiple levels.

4.3 Integration with developmental time-course data to infer spatial-temporal dynamics

If spatial data allows us to see "where" is being expressed, then the integration of time series answers "when" changes occur. By combining spatial transcriptomics with time series transcriptomics and metabolomics data, taking samples daily and analyzing them step by step, researchers were able to reconstruct the spatiotemporal trajectory of fiber development.

In this continuous observation, the synergistic changes of different gene modules gradually emerge, and their turning points often correspond to important stages of development, such as the moment when the secondary wall begins to form (Grover et al., 2024; Swaminathan et al., 2024). These dynamic data not only present trends, but also help researchers identify the key regulatory networks that drive fiber growth and quality changes (You et al., 2023). It can be said that this integrated analysis makes "time" another dimension for understanding fiber growth and also provides a solid basis for future functional research and variety improvement.

5 Case Study: Spatial Gene Expression in *Gossypium hirsutum*

5.1 Sampling design: dissecting elongation zones and applying spatial barcoding methods

To truly understand the "elongation map" of cotton fibers on land, researchers often have to start from the most minute details. Recent studies have utilized spatial barcode technology in combination with high-resolution sampling to conduct analyses on different parts of fibers. Not all fibers are the same. The tip, middle and base each have different active genes. By dissecting these regions at specific developmental stages, researchers were able to map out the local transcriptome distribution.

Furthermore, genetic materials such as chromosome fragment replacement lines (CSSL) and gene infiltration populations have also played significant roles in the research (Qi et al., 2024). They can reveal the differences under different genetic backgrounds, making it possible to compare gene expression in various regions. This design not only showcases spatial differences but also helps clarify the genetic basis behind fiber elongation.

5.2 Findings: expression gradients of *GhEXPA1*, *GhRDL1*, and *GhMYB25*-like along fiber tips

Research has found that some key genes controlling fiber elongation, such as *GhEXPA1* (expansion protein), *GhRDL1* (cell wall modifier related), and *GhMYB25*-like protein (MYB transcription factor), are not evenly distributed but form clear expression gradients along the fiber axis. Their activity is highest in the tip and early elongation regions. This "local overheating" pattern suggests that they are closely related to the relaxation of the cell wall and the rapid expansion of the cell.

When upstream regulatory factors (such as GhHDZ76) are disrupted, the expression levels of these genes decrease significantly and the fibers become shorter accordingly (Figure 2) (Wu et al., 2024). This kind of phenomenon makes people realize that elongation is not the task of a single gene, but a process maintained by multiple layers of regulation. Further co-expression network analysis revealed that *GhEXPA1*, *GhRDL1* and *GhMYB25*-like proteins would also form interactive networks with other factors (such as GhHOX3), jointly participating in the coordination of fiber growth.

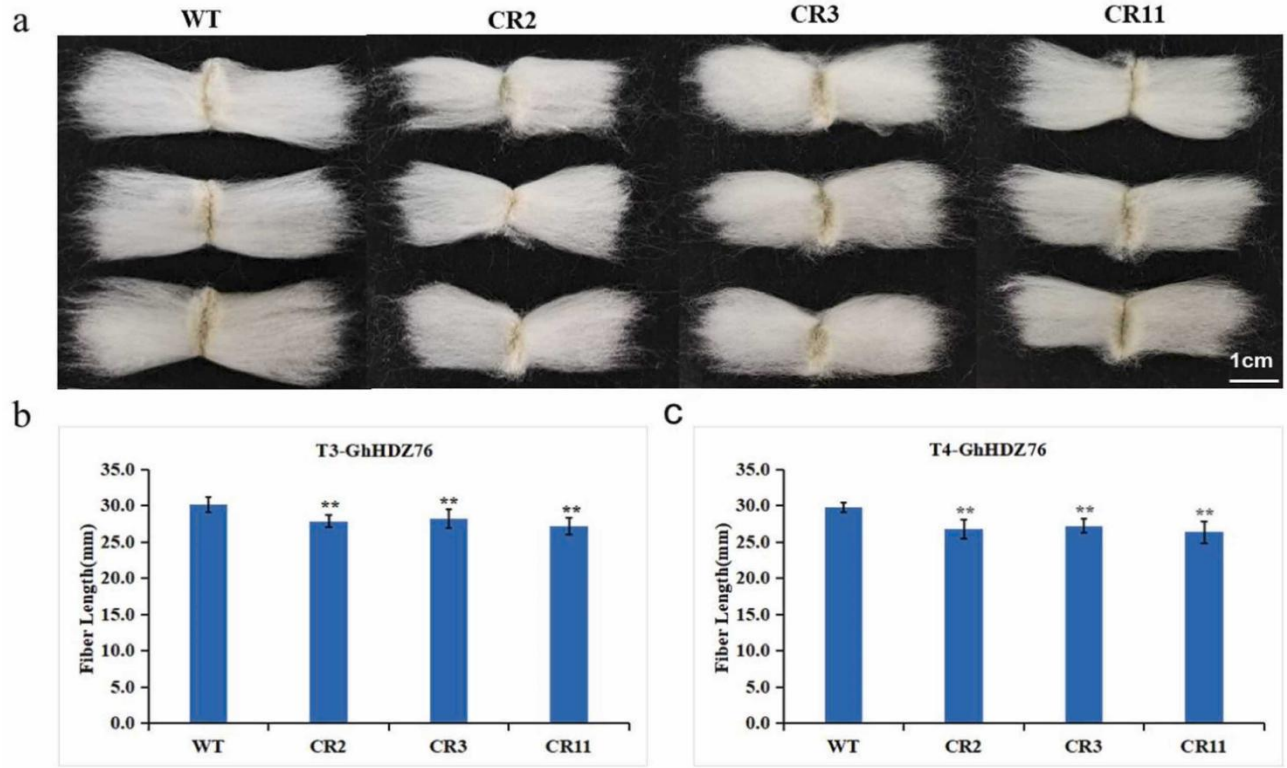

Figure 2 The fiber length measurements of *GhHDZ76* knockout lines in T_3 and T_4 generations. (a) Comparison of mature fiber length between *GhHDZ76* knockout lines and WT. Bar =1 cm. (b) Measurement of fiber length in *GhHDZ76* knockout lines and WT in T_3 generation. (c) Measurement of fiber length in *GhHDZ76* knockout lines and WT in T_4 generation. Data represent the mean ± SD. WT: WT; CR2, CR3, CR11: *GhHDZ76* knockout line by CRISPR/Cas9 (Adopted from Wu et al., 2024)

5.3 Interpretation: implications for targeted breeding and molecular interventions in elongation control

These spatially resolved data are not merely "academic refinances"; they actually provide available targets for breeding. Those genes that are highly expressed at the tips or elongation regions of fibers, such as *GhEXPA1*, *GhRDL1* and *GhMYB25*-like genes, are precisely the most worthy of attention in molecular improvement. They can provide direct references for genetic engineering or molecular marker-assisted selection, thereby enhancing fiber length and quality.

More importantly, understanding the regulatory networks and spatial dynamics of these genes means that researchers can intervene more specifically (Ma et al., 2024). Whether by adjusting the expression intensity or optimizing the signal pathway, these findings have paved the way for creating higher-quality and more economically valuable cotton varieties.

6 Functional Insights from Spatial Gene Expression Data

6.1 Discovery of region-specific transcriptional modules regulating elongation

In the growth of cotton fibers, control is not concentrated in a few genes but is dispersed in multiple region-specific regulatory modules. Through the reconstruction and analysis of large-scale spatial transcriptomes, researchers have depicted a complex map of gene regulatory networks.

The roles of some modules are particularly prominent. For example, the GhWRKY28-GhTOL9 module and its related ESCRT pathway are considered to play a key role in the initiation and elongation of fibers (Yang et al., 2024). Interestingly, such modules are often closely associated with expression quantitative trait loci (EQtls) between subgenomes, such as "regulatory hotspot 456", which can indirectly affect the expression of genes like KCS1, and KCS1 happens to be a key node that determines whether cells can elongate normally.

This also indicates that the development of fibers is not dominated by a single regulatory mechanism. Different regions and different developmental time Windows may each activate independent regulatory modules, like an orderly yet decentralized collaboration rather than a centralized command system.

6.2 Spatial distribution of oxidative stress genes and ros scavenging pathways

Rapidly growing fibers are a high-energy-consuming activity, and oxidative stress is inevitable. To maintain balance, plants seem to have "zoned out" their antioxidant systems. Studies have found that genes involved in the ascorbic acid-glutathione cycle, especially members of the MDHAR family, are expressed most strongly in the region with the fastest elongation (Zhou et al., 2021; Hou et al., 2022). These regions simultaneously exhibit higher ascorbic acid content and antioxidant activity, suggesting that the cells here must respond more actively to the stress brought by reactive oxygen species.

What's more interesting is that when some key elongation regulatory factors are silenced, the expression of genes related to oxidoreductases also decreases accordingly. In other words, the oxidation equilibrium is not maintained independently but is intertwined with the mechanism of fiber elongation. Through such spatial distribution regulation, plants not only elongate their fibers but also quietly prevent "self-oxidation".

6.3 Functional roles of sugar transporters and energy metabolism genes in elongation zones

For fibers to be elongated, they must first have "energy". The transport efficiency of sugar almost determines whether cells can expand smoothly. Studies have shown that the transcription factor GhMYB212 can directly activate the sucrose transporter gene *GhSWEET12*, helping sucrose continuously enter elongated cells (Liu et al., 2022; Duan et al., 2024).

Once the functions of *GhMYB212* or *GhSWEET12* are lost, the accumulation of sucrose is significantly reduced, and the length of the fibers also decreases significantly. Conversely, *GhMYB4* can also inhibit *GhSWEET12*, but this inhibition is not absolute. bHLH and other MYB factors will intervene in the opposite direction, thereby forming a delicate balance between sugar and lipid metabolism.

This regulatory network is like a dynamic energy supply system, not only maintaining energy supply but also participating in the growth rhythm of fibers. It can be said that the "vitality" of the elongation zone largely depends on the fine regulation of the sugar transport system.

7 Limitations, Challenges, and Future Directions

7.1 Spatial resolution trade-offs and difficulties in long fiber cell profiling

The advantages of spatial transcriptomics are obvious, but truly "seeing clearly" long fibroblasts remains a challenge. Most platforms struggle to strike a balance between spatial resolution and transcriptome coverage. To see more details, one has to sacrifice some coverage. Especially for structures like cotton fibers that are slender in shape and have hard cell walls, once the section thickness is slightly thick, the expression gradient is prone to be blurred (Qin et al., 2022).

Researchers often find that the differences that should have been present at the single-cell level are "averaged" after section analysis. The size limitation of the spots also makes it difficult to restore the details at the subcellular level. Moreover, the fiber length far exceeds that of ordinary plant cells, making it almost a challenging task to obtain complete transcriptome information along the axis. It can be said that the analysis of fine spatial patterns often relies more on ingenious experimental design and computational compensation rather than merely on equipment improvement.

7.2 Integration of spatial transcriptomics with single-cell and epigenomic data

Theoretically, if spatial transcriptomics can be integrated with single-cell RNA sequencing (scRNA-seq) and epigenomic data, the depth and level of research will be greatly enhanced. In this way, not only can cell type mixtures be distinguished more accurately, but also the connection between gene expression and epigenetic modifications can be revealed (Wan et al., 2023).

But there are quite a few problems in practice. The formats, resolutions and even analysis logics of different omics data vary. How to compare, standardize and integrate them within the same framework remains a difficult problem (Fang et al., 2022). Algorithms are being updated rapidly, but standardized processes lag behind. In plant research, this issue is more prominent. Incomplete cell type markers and complex tissue structures make control matching even more challenging. The potential for integration is undoubtedly huge, but it is still in the exploration stage at present.

7.3 Future potential in genome editing, synthetic biology, and cotton improvement programs

Although there are still many limitations, the prospects of spatial transcriptomics in cotton improvement remain promising. It can depict high-resolution spatial maps, identify those candidate genes and regulatory networks that are most worthy of "action", and provide precise targets for gene editing (such as CRISPR/Cas9) and synthetic biology (Wen et al., 2023).

The future direction is becoming increasingly clear: If spatial data can be further integrated with single-cell and epigenomic information, new regulatory elements and pathways may be revealed (Khalilisamani et al., 2024). These achievements will directly promote the breeding process of high-yield and high-quality fiber varieties. Of course, all of this is inseparable from technological innovation and interdisciplinary cooperation. The spatial biology of cotton remains a field with huge potential, but this path requires patience and continuous investment.

8 Concluding Remarks

The emergence of spatial transcriptomics has led people to re-examine the growth process of cotton fibers. In the past, we could only see the result of fibers "growing up", but nowadays, researchers can "see" how they form step by step at the molecular level. By combining spatial transcriptomics with single-cell RNA sequencing, time series analysis and other means, the developmental map of cotton fibers has been reconstructed with unprecedented clarity.

Among these spectra, some familiar metabolic processes, such as sucrose synthesis and lipid metabolism, have been redefined in terms of position and significance. Specific transcription factors and regulatory modules have

also been found to have distinct spatial distribution characteristics. Especially those regions closely related to fiber initiation and elongation express genes, which provide a more intuitive understanding of the cellular differences and developmental rhythms behind fiber quality and yield.

These data are not merely breakthroughs at the scientific research level; they are quietly transforming the way cotton is bred. Through gene expression maps with higher spatial resolution, researchers can identify those candidate genes, superior alleles and core regulatory networks that are highly expressed in the elongation region. Whether it is marker-assisted selection, genome editing, or more complex molecular breeding strategies, there is now a clearer "steering wheel". In other words, spatial information is becoming the navigation system for cotton improvement, making the enhancement of key properties such as length, strength and toughness more controllable and precise. Of course, the research is far from over. The existing spatial data mainly focus on a few varieties and specific developmental stages, while the influence of environmental differences and genotype diversity on fiber formation still needs to be further explored. To make these achievements truly serve production, more extensive data accumulation and cross-level integration are still needed.

In the future, if spatial transcriptomics can be combined with information from epigenomics, proteomics and metabolomics, we may be able to understand the developmental logic of fibers more comprehensively. Meanwhile, higher-resolution technologies, more flexible computing models, and interdisciplinary collaborations will also determine how far this field can go. The complexity of cotton improvement will not decrease, but the tools are becoming increasingly sharp.

Acknowledgments

We are grateful to Dr. Wang and Dr. Long for their assistance with the data analysis and helpful discussions during the course of this research.

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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