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Proteomics Analysis of Cotton's Response to Drought and Salt Stress

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Abstract Cotton is one of the most economically important fiber crops worldwide, yet its productivity is significantly hindered by abiotic stresses such as drought and salinity. In this study, we utilized proteomics approaches to explore the molecular mechanisms underlying cotton's response to drought and salt stress, providing a comprehensive overview of stress-induced protein expression profiles. We summarized the major types of abiotic stress affecting cotton, detailed current proteomics technologies, and highlighted key proteins involved in stress perception, antioxidant defense, ion transport, and signaling pathways. Comparative proteomic analyses revealed both common and stress-specific protein expression patterns, enhancing our understanding of cotton's adaptive responses. A case study involving *Gossypium hirsutum* under field-imposed conditions demonstrated how proteomic insights can inform breeding for stress tolerance. This study underscores the value of proteomics in dissecting cotton's complex responses to environmental stress and anticipates that future research integrating multi-omics and functional genomics will facilitate the development of stress-resilient cotton cultivars.

Keywords Cotton; Proteomics; Drought stress; Salt stress; Stress tolerance mechanisms

1 Introduction

When it comes to cotton (*Gossypium* spp.), most people first think of clothes and fabrics, but in fact, it supports the livelihoods of millions of farmers around the world. It is not just a fiber crop, but also an integral part of the economic system in many regions. Especially in some places where soil conditions are not good, such as saline-alkali land, cotton has become one of the few crops that can still grow well, which also gives it a special position in agricultural development (Xiao et al., 2020).

Of course, cotton is not "invincible". Abiotic stresses such as drought and excessive soil salinity often make it "unbearable". Yield decline and slow growth are not new problems. Scientists want to figure out how cotton copes with these stresses, so they turn their attention to the tool of proteomics. To put it bluntly, this set of technologies is to study when various proteins in plants "go online", what they do, and the relationship between them.

In recent years, some studies have revealed which proteins cotton activates when facing adversity. Some are involved in energy metabolism, some are responsible for anti-oxidation, and some are like signal "couriers" to transmit information everywhere (Deeba et al., 2012; Li et al., 2015; Zhang et al., 2016; Chen et al., 2020; Nagamalla et al., 2021; Yuan et al., 2023). Interestingly, different proteins behave differently at different stress stages, and this difference just provides us with clues to find key regulatory points. In the future, if this information can be used in breeding, maybe we can breed more drought-resistant and salt-tolerant cotton.

This study is mainly to systematically sort out these existing proteomics results. We will pick out some key findings to make it clear which proteins and pathways cotton activates under drought and salt stress. At the same time, we will also look at how to use these data with transcriptome information to further explore the "response strategy" of cotton. Although this work cannot be used directly in farming, we hope that it can pave the way for subsequent research and provide some practical reference for the development of stress-resistant cotton varieties.

2 Overview of Abiotic Stresses in Cotton

2.1 Drought stress in cotton

Many farmers know that cotton is afraid of drought. Once there is a lack of water, not only will the leaves wilt, but the yield will also decline and the fiber quality will also be affected. But cotton is not completely helpless. It will find ways to save itself - such as adjusting metabolism, changing physiological state, and even a series of changes will occur inside the cells. Some regulatory genes such as *GhMAP4K13*, *GhMAPKK5*, *GhABF3* and *GhMAPK3* will be activated at this time (Zeng et al., 2025). Once they come on the scene, the plant's antioxidant capacity is enhanced, hormone transmission is smoother, and it can retain water. The root system will be more developed and the survival rate will be higher, which is critical for whether cotton can survive the drought period (Figure 1) (Sadau et al., 2021). However, not all proteins are so "high-profile". For example, LEA protein, it is more of a silent protection of cell structure, making them less likely to be damaged by drought. GhLEA3 is a representative, which is considered a "stabilizer" of cotton (Shiraku et al., 2022).

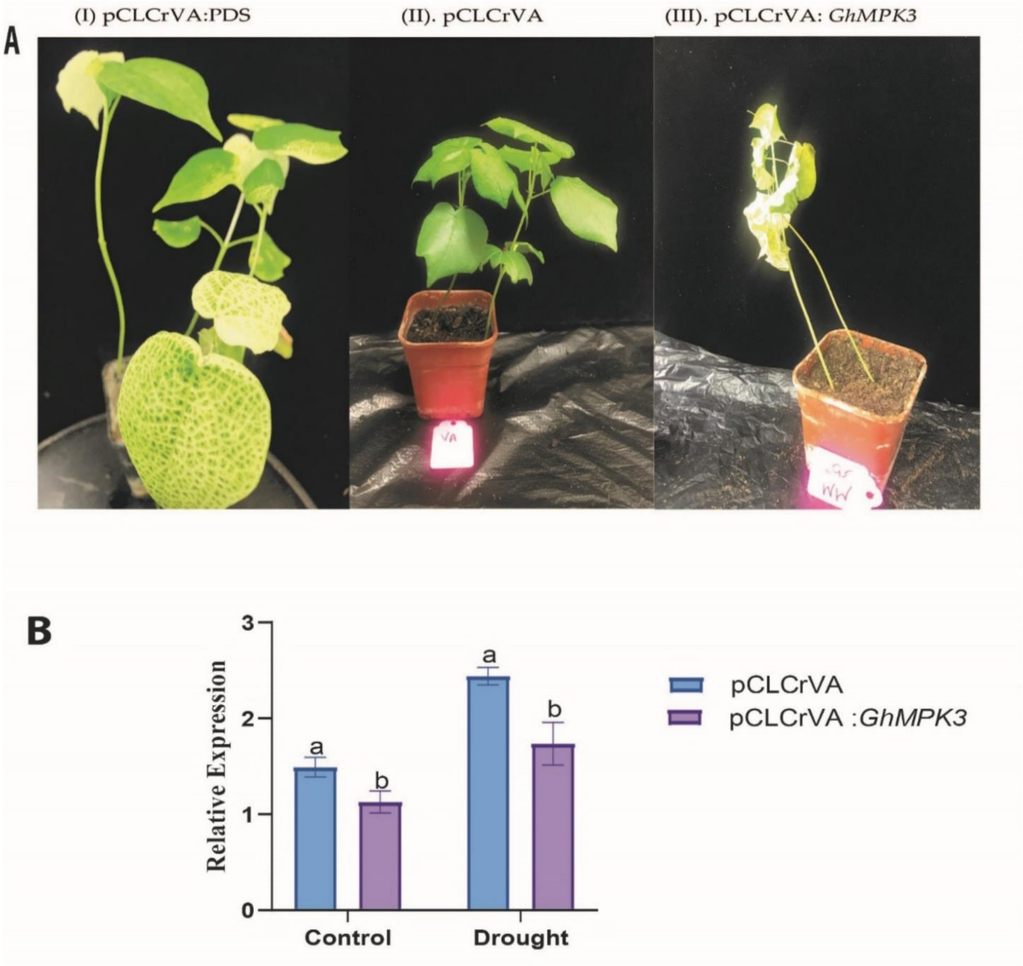

Figure 1 Phenotypic feature of *GhMPK3*-silenced plants (A) (I) pCLCrVA:PDS (II) pCLCrVA (III) pCLCrVA:*GhMPK3* (B). *GhMPK3's* expression level in empty control and *GhMPK3*-silenced plants. Each experiment was conducted three times. The error bar represents the three biological replicate's standard deviation. The significant differences between VA and *GhMPK3*-VIGS plants (ANOVA; $p < 0.05$) are indicated by different letters a/b (Adopted from Sadau et al., 2021)

2.2 Salt stress in cotton

Compared with drought, salt stress is slightly different, mainly occurring when the soil salt content is too high. Too much salt can also make cotton uncomfortable, as the root system cannot expand well and water absorption is also hindered. However, some genes will step up at this time, such as *GhMAP4K13*, *GhMAPKK5*, *GhABF3* and *GbTCP4*. They can help the root system stabilize its position, reduce cell damage, and increase antioxidant levels (Zhang et al., 2022; Ding et al., 2024). Many experiments have shown that after increasing the expression of these genes, cotton does behave differently-the germination rate is higher, the roots are longer, and the oxidative damage is less (Zhang et al., 2023). In addition to genes, proteins such as LEA are also present. They can stabilize the internal state of cells in a high-salt environment and can be regarded as the "balancer" of cotton.

2.3 Combined stress scenarios

The fields are not so simple. Drought is coming, and salinity may not be far behind. These two stresses often come together, doubling the pressure and causing more trouble to cotton. But cotton is not completely helpless. Studies have found that signaling pathways such as MAPK cascades (such as GhMAP4K13, GhMAPKK5, and GhMAPK3) are activated simultaneously under two stresses (Jian et al., 2024). This shows that they may follow the same "procedure" when responding to different stresses. Transcription factors GhABF3 and GbTCP4, as well as stress proteins such as LEA3, are actively expressed in both stress environments. They help cotton retain water and resist oxidation, and can also regulate many stress-related genes (Wang et al., 2022). Combining proteomic and transcriptomic data, scientists have found many key points that allow cotton to "shoot from both sides" (Bano et al., 2022; Ahmad et al., 2024). These achievements have also laid a lot of foundations for future breeding and genetic engineering.

3 Proteomics Approaches in Stress Response Studies

3.1 Techniques in proteomic analysis

There are two common methods for studying protein changes in plants under stress: gel-based and non-gel-based methods. Two-dimensional electrophoresis (2-DE) and two-dimensional difference gel electrophoresis (2D-DIGE) are commonly used in gel-based methods, which separate proteins based on their isoelectric point and molecular weight. There are more non-gel-based methods, such as isotope-coded affinity tags (ICAT), isotope tag quantification (iTRAQ), and various mass spectrometry platforms, such as liquid chromatography-mass spectrometry (LC-MS) and matrix-assisted laser desorption ionization mass spectrometry (MALDI-MS). These techniques can quickly analyze many proteins with high sensitivity and quantification (Jan et al., 2022). These techniques help us more easily find proteins whose expression changes under drought or salt stress, and can also more accurately analyze their quantity (Choudhary et al., 2025).

3.2 Protein identification and bioinformatics

After protein separation and detection, researchers generally use mass spectrometry to determine the type of protein. After that, bioinformatics tools are used to analyze the data. Through functional network and pathway analysis, differently expressed proteins can be classified into categories, and their roles in plant adaptation to adversity can be clarified, such as participating in photosynthesis, sugar metabolism, signal transduction, and defense processes (Alaiya et al., 2024). Bioinformatics tools can also integrate proteomic data with other omics data, so that we can better understand the overall response of plants to stress (Guo et al., 2021).

3.3 Challenges and limitations

Although proteomics has achieved a lot of results in plant stress research, there are still many challenges. First of all, the protein database of many crops is still incomplete, and there are many genetic differences between varieties, and the types of proteins are also very complex, which makes it difficult to fully identify and analyze proteins (Nesatyy and Suter, 2007). In addition, some technical problems are also common, such as insufficient efficiency of protein extraction, large differences in protein content, and unstable experimental results, which will affect the reliability of research results (Hossain et al., 2013). Another important issue is that in order to accurately explain the changes in proteins under stress, very rigorous experiments need to be designed and subsequent verification needs to be done (Kosová et al., 2011). In order to truly apply the results of proteomics to crop improvement, these problems must be solved step by step.

4 Key Proteomic Findings in Drought Stress Response

4.1 Stress perception and signal transduction

When drought strikes, cotton does not "give up" all at once. It will first sense changes in the environment and then slowly respond. However, this "perception" process is not simple at all. Some proteins, such as signal receptors distributed on the cell membrane and some proteins called molecular chaperones, will be the first to "perceive" the signal of drought (Wang et al., 2016). These proteins are like "sensors" that go out in the first place. However, not all reactions occur at the same time. For example, in the roots, when drought just begins, the proteins involved in the synthesis of cutin, suberin, and wax have begun to increase in expression (Xiao et al., 2020). Their role is more like building a line of defense to help cells stabilize their structure while sending the signal that "we are short of water." Looking further down, some proteins are specifically responsible for "messaging" and "regulation." For example, some proteins involved in phosphorylation and post-translational modification are activated during drought and regulate the intensity and direction of signal transduction pathways (Koh et al., 2015; Ghatak et al., 2017). Simply put, this entire reaction chain, from "discovering problems" to "mobilizing responses", is linked together by these proteins.

4.2 Antioxidant and defense proteins

Drought can easily cause plants to produce a large amount of reactive oxygen species (ROS), which can damage cells. In order to reduce damage, plants increase the content of some antioxidant and defense proteins. These proteins include various antioxidant enzymes, heat shock proteins, and some enzymes that can participate in detoxification (Wang et al., 2016). In drought-resistant cotton varieties, the content of these proteins is usually higher, which helps to enhance stress resistance (Yahoueian et al., 2021). The increased activity of these proteins is related to root growth, water retention, and survival rate under drought conditions (Zeng et al., 2019).

4.3 Metabolism and structural proteins

Not all proteins are silent during drought. Some metabolic and structural proteins become more active, but this "activity" varies in different cotton varieties. Proteins related to sugar, energy, fatty acid, and amino acid metabolism are often regulated under drought conditions. Plants do this to save energy and to regulate water balance in their bodies (Michaletti et al., 2018). However, not all cotton copes so well. Drought-sensitive varieties often have decreased sugar metabolism and nitrogen metabolism-related proteins, and photosynthesis is also slowed down. In contrast, drought-tolerant varieties are more "stable", and the expression of many key proteins has not only not decreased, but sometimes even increased, which allows them to continue to grow (Subramani et al., 2024). In addition, structural proteins cannot be ignored. In particular, proteins involved in cell wall construction and adjustment will also change significantly during drought (Ren et al., 2022). They are a bit like "scaffolds", which stabilize cell morphology on the one hand and prevent rapid water loss on the other. In the final analysis, these proteins are actually helping plants "save water".

5 Key Proteomic Findings in Salt Stress Response

5.1 Ion transport and homeostasis proteins

When there is too much salt, the first thing plants feel is often not "salty", but that the ions inside and outside the cells are not right. In the study of cotton, a special type of protein frequently "goes online", such as TIPs on the vacuole membrane and PIPs on the plasma membrane, which become more active (Li et al., 2015). These proteins help water and ions to transport back and forth between cell membranes, just like valves that regulate flow, maintaining electrolyte balance in cells. However, the flow of water and ions alone is not enough. Cotton also needs some proteins that can regulate the sodium-potassium ratio - especially those involved in the calcium signaling pathway, which are often involved. This type of protein can isolate or expel excess sodium ions, which can be regarded as a "clearance mechanism" for cells to fight salt poisoning (Passamani et al., 2017). After all, these seemingly inconspicuous membrane transport proteins are the key role in plants "keeping their ground" under salt stress.

5.2 Osmoprotectant biosynthesis enzymes

If cells want to avoid "dehydration" in a high-salt environment, it is not enough to control ions alone. They will also synthesize some "talismans" by themselves - osmotic protectants. These small molecules are not large, but they play a significant role. They can protect protein structures from deformation and stabilize cell membranes (Yan et al., 2005). Studies have found that when cotton faces salt stress, some enzymes related to carbohydrate and amino acid metabolism begin to express more strongly. These enzymes help synthesize small molecules such as proline and soluble sugars. They do not directly "fight salt", but can regulate the turgor pressure of cells so that cells are not "drained". Of course, not every cotton plant can respond quickly. Some varieties may synthesize slowly, resulting in faster water loss and more susceptible cells to damage. In those varieties that are more responsive, these metabolic regulation mechanisms are particularly important (Kausar and Komatsu, 2022).

5.3 Stress signaling and transcription factors

Proteomic studies have also found that salt stress can upregulate some signal-related proteins and transcription factors. Among them, leucine-rich repeat receptor kinases (LRR-RLKs), 14-3-3 proteins and other signaling molecules can recognize the signals of salt stress and then activate a series of defense responses (Ji et al., 2016). Some transcription factors and stress response proteins, such as universal stress proteins (USPs) and dirigent-like proteins, are also activated under salt stress. They can regulate the expression of some genes related to antioxidant, defense, cell wall remodeling and metabolism (Athar et al., 2022). These proteins play an important coordinating role in regulating the adaptation of plants to salt environments and can help maintain the stable operation of the entire response mechanism.

6 Comparative Analysis of Drought vs. Salt Stress Proteomes

6.1 Shared proteomic responses

Although drought and salt stress are different, they both cause similar changes in the proteome of plants. For example, plants accumulate small molecules that can regulate osmotic pressure and increase the expression of proteins related to antioxidants. At the same time, plant photosynthesis and energy metabolism will also be adjusted. Under these two stresses, some common signaling pathways will be activated, such as calcium ion (Ca^{2+}) signaling, G protein signaling, 14-3-3 protein and phosphorylation cascade. Among them, some proteins, such as calcium-binding EF-hand family proteins, play a role in both stresses and are the "connection points" between them (Luo et al., 2015). There are also some enzymes related to sugar metabolism and energy production that increase in both drought and salt stress, which shows that plants use similar methods to maintain the homeostasis of cells (Ma et al., 2017).

6.2 Stress-specific protein expression

Although there are similarities, drought and salt stress also have their own characteristics. Each stress causes some protein changes that only appear under that condition. Generally speaking, drought has a greater impact on plants, so the number of differentially expressed proteins (DEPs) that are exclusive to drought is also greater. For example, STN7 and BSL are phosphorylated signaling proteins that are activated only under drought conditions; while CDPK21, TPR, and CTR1 are unique to salt stress. In addition, some metabolic enzymes and photosynthesis-related proteins (such as transketolase, RubisCO fragments) respond differently in the two stresses, and some are only expressed under drought or salt stress (Rabey et al., 2015; Rabey et al., 2016).

6.3 Insights into stress tolerance mechanisms

By comparing protein changes under different stresses, the study found that although many defense and metabolic pathways are activated, the expression strength and specificity of each protein determines the tolerance of the plant. Some protein families develop different functions according to different adversities, which allows plants to adjust their responses more flexibly. Some "tandem" proteins are involved in regulation in both stresses, and they are potential targets for improving the multi-stress resistance of plants (Du et al., 2020). Combining proteomic and transcriptomic data for analysis can better understand these regulatory networks. This will be of great help to future stress-resistant breeding and genetic engineering, and also provide direction for the development of more drought- and salt-tolerant crop varieties.

7 Case Study: Proteomics of *Gossypium hirsutum* under Field-Imposed Stress Conditions

7.1 Experimental setup and stress treatments

Not all experiments are done in the lab. To understand how field crops like cotton respond to drought and salinity in real environments, we need to move the research to a more realistic scenario. So the researchers designed a set of proteomics experiments to observe the response of upland cotton (*Gossypium hirsutum*) under simulated drought and salt stress conditions. How to simulate drought? They reduced the relative moisture content of one group of soils to 40%-45%, while maintaining the relative moisture content of another group at 70%-75% as a control (Xiao et al., 2020). The response of cotton is not visible all at once, so the sampling time points are also set more dispersed, with both early responses and long-term adaptation observations. Salt stress is handled slightly differently. Instead of treating the entire plant, it focuses on the roots of the seedlings. The researchers directly treated the roots with a solution containing NaCl and then quickly collected samples because protein changes caused by this type of stress usually occur quickly. To figure out which proteins in the roots and leaves change, they also used technologies such as TMT and iTRAQ. These methods can help them perform quantitative analysis on a high-throughput basis with high efficiency and high precision. Compared with traditional methods, this combination of methods is obviously more suitable for processing complex samples under field conditions.

7.2 Major findings

Proteomic analysis under drought stress conditions revealed that many proteins related to metabolism, stress defense, ion transport and hormone signaling were changed in expression (Wang et al., 2024). The study found that at the beginning of drought, proteins related to cutin, suberin and wax synthesis were upregulated in cotton fine roots. If the drought lasted for a long time, there would be extensive changes in carbohydrate, energy, fatty acid and amino acid metabolism (Figure 2). Under salt stress conditions, some important differentially expressed proteins (DEPs) were found, which were involved in carbohydrate and energy metabolism, cell wall structure, cytoskeleton formation, membrane transport (such as TIPs and PIPs) and signal transduction (such as LRR-RLKs) (Li et al., 2015). In addition, the levels of antioxidant enzymes such as superoxide dismutase and peroxidase increased, indicating that they are related to improving stress tolerance. Some key genes confirmed by joint proteomic and transcriptomic analysis were also shown to play an important role in salt tolerance. If these genes are turned off, plants will become more susceptible to salt stress and more reactive oxygen will accumulate.

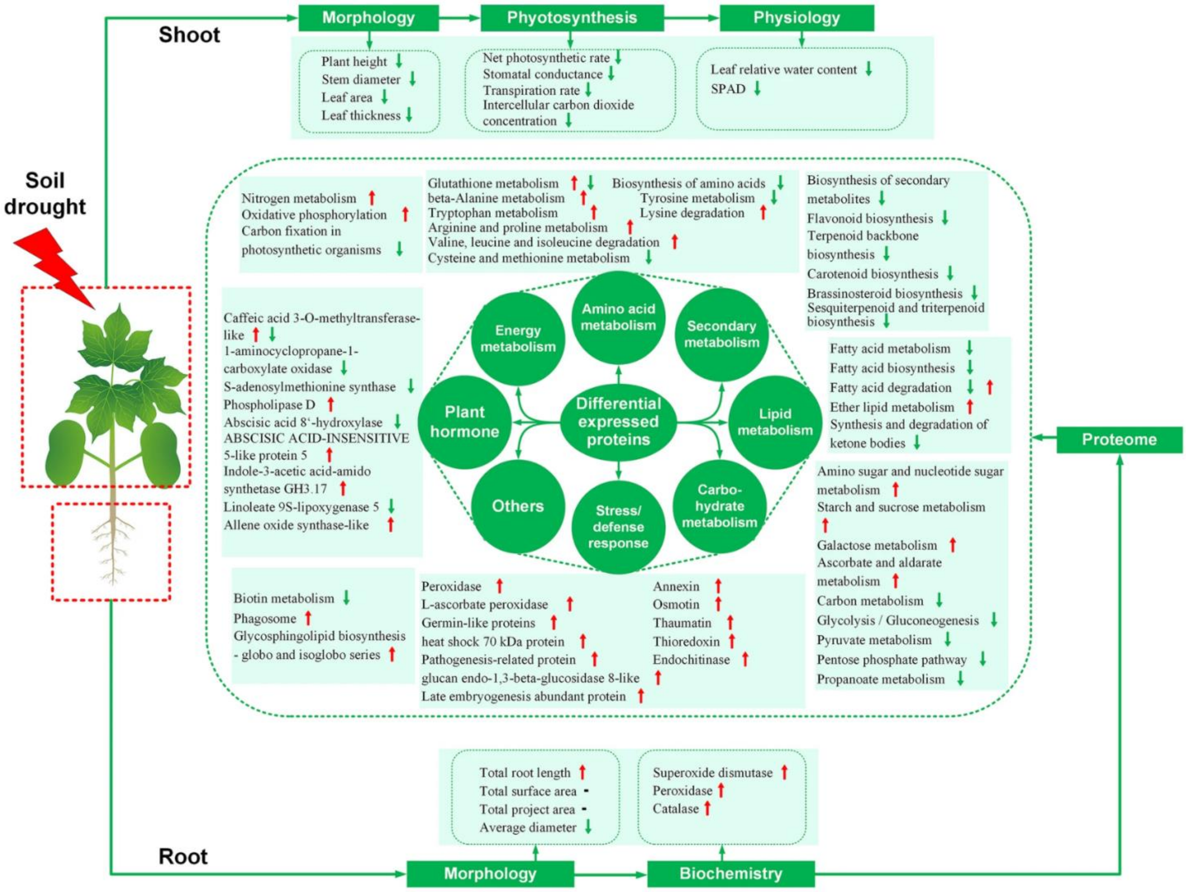

Figure 2 Model showing the responses of the fine roots of cotton plants (Adopted from Xiao et al., 2020)

7.3 Implications for breeding and biotechnology

Not all proteins can become the "new favorites" of breeding, but those related to drought and salt stress have indeed given researchers a lot of inspiration. Some proteins are involved in defense responses, some involve hormone signals, and some specialize in membrane transport. These are considered to be more reliable candidate targets, especially when doing genetic engineering and molecular marker-assisted breeding (Sun et al., 2023). Of course, it is not just the protein itself that can "rise to the top". Some key genes that can regulate the removal of reactive oxygen species and maintain ion balance have also been functionally verified in subsequent studies. These genes have one thing in common - they are very stable in improving cotton's ability to resist stress, both in the laboratory and in the field. Having said that, using the results of proteomics in actual breeding is still a little way from "direct transformation". But these basic studies have slowly built bridges - allowing molecular-level information to truly serve cotton variety improvement. Especially in places where climate change is frequent and water and salt pressure is high, these results may bring some real changes.

8 Future Directions and Research Gaps

8.1 Integration with multi-omics approaches

Proteomics can provide a lot of clues, but it is unrealistic to say that "it can help us understand how cotton resists stress". After all, information from one dimension is never enough. Now more and more studies tend to integrate "omics puzzle" - genome, transcriptome, metabolome, and even phenotypic data must be pulled together. Not every study can be well integrated at the beginning, especially in the early days of proteomics, most of which were single-line analysis. But now it is different, especially the development of single-cell proteomics technology, which gives us a "magnifying glass" to observe the responses of different cells under adversity, which is much more detailed and specific (Bawa et al., 2022). These different omics are put together not just for show. It does give us the opportunity to see how more key molecules work together, especially when cotton copes with drought or salt stress. Some studies have also begun to use these integrated ideas to screen varieties with stronger stress resistance. Although it is still in progress, the direction is clear (Ijaz et al., 2024; Choudhary et al., 2025).

8.2 Functional characterization of key proteins

Although many stress-related proteins have been found, many of them are still unclear about how they work. We still need more genetic and biochemical experiments to further verify the true functions of these proteins (Xiao et al., 2020). Methods such as gene editing, overexpression or gene silencing, if combined with phenotypic analysis and physiological tests, can more clearly show whether these proteins can help cotton resist drought or salt (Li et al., 2015). In addition, functional studies are also very important to understand how proteins interact with each other and how post-translational modifications are regulated (Hu et al., 2015; Liu et al., 2019).

8.3 Translational potential in stress-resilient cotton

The ultimate goal of proteomics research is to apply these molecular-level discoveries to actual cotton improvement. Now some stress-related proteins and pathways have been found, which can be used as molecular markers for breeding and as targets for transgenics (Perveen et al., 2025). But the problem is that the results in the laboratory must be verified in different environments and different cotton varieties before they can be truly transformed into the field (Zhou et al., 2014). Therefore, in the future, we must continue to integrate proteomic, transcriptomic and functional genomic data and combine them with modern breeding technology, so that we can select good varieties that are truly drought-resistant and salt-resistant and adapt to future climates.

9 Concluding Remarks

Proteomics studies have given us a clearer understanding of how cotton responds to drought and salt stress. These studies have found that in stress-resistant cotton varieties, many proteins involved in photosynthesis, antioxidants, defense, metabolic regulation, and stress signaling are expressed more. In varieties that are more susceptible to stress, protein expression in these pathways tends to decrease. Whether it is drought or salt stress, energy metabolism, ion transport, hormone signaling, and detoxification mechanisms in plants will change. Although some reactions are common, each stress also has its own unique proteins and reaction pathways. It is not objective to say that proteomics has not brought us anything new in recent years. It has indeed helped us find a number of key proteins and candidate genes related to stress resistance. This information is a valuable resource for breeding or genetic engineering, especially in issues such as "who to choose and who not to choose", the targets are much clearer.

Of course, proteomics data alone is not enough. Looking at it alone is always like seeing only half of a picture. So later everyone began to try to piece it together with the transcriptome. What was the result? Some key regulatory nodes and signal pathways have gradually surfaced. These clues have indeed played a guiding role in subsequent variety improvement. Not to mention that some new technologies have emerged, such as proteomic analysis at the single-cell level, and more sophisticated quantitative methods, which allow us to "see smaller" and "see more accurately". Although these methods are still under development, the trend is already clear - in the future, cotton stress-resistant breeding may rely more on these molecular-level "micro-operations".

Integrating proteomics and other omics methods, coupled with functional verification of key proteins, is the key to turning experimental results into practical applications. In the future, continued research in this area will accelerate the pace of breeding stress-resistant cotton, and will also help cotton maintain stable yields and sustainable development in the face of increasingly severe natural environments.

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Conflict of Interest Disclosure

The author affirms 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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