Cotton Genomics and Genetics 2025, Vol.16, No.4, 184-191
http://cropscipublisher.com/index.php/cgg

Research Insight Open Access

# Study on Innate Immunity of Cotton to Biological Stress Based on Transcriptome Analysis

Zhen Li
Hainan Institute of Biotechnology, Haikou, 570206, Hainan, China
Corresponding email: zhen.li@hibio.org

Cotton Genomics and Genetics, 2025, Vol.16, No.4 doi: 10.5376/cgg.2025.16.0018
Received: 12 May, 2025
Accepted: 23 Jun., 2025
Published: 15 Jul., 2025



**Preferred citation for this article**:
Li Z., 2025, Study on innate immunity of cotton to biological stress based on transcriptome analysis, Cotton Genomics and Genetics, 16(4): 184-191 (doi: 10.5376/cgg.2025.16.0018)

**Abstract** Cotton (*Gossypium* spp.), as an important economic crop in the world, is often affected by biotic stresses such as pathogenic fungi, bacteria and pests, resulting in reduced yield and quality. Exploring its natural immune response mechanism is of great significance for improving disease and insect resistance and ensuring agricultural production safety. Based on transcriptome data, this study systematically analyzed the changes in gene expression of cotton when it was subjected to biotic stress, screened out key genes and signaling pathways closely related to defense response, including pathogen-related proteins (PRs), defensins, hormone regulatory factors, etc., and deeply explored the transcriptional regulatory mechanisms of two types of immune responses, PTI (PAMP-triggered immunity) and ETI (effector-triggered immunity). The relevant immune regulatory network was further constructed, and several resistance candidate genes with application potential were screened. This study provides a molecular basis for a deeper understanding of the natural immune mechanism of cotton, and provides theoretical references and gene resources for the breeding of highly resistant cotton varieties, hoping to promote the development of green prevention and control of cotton pests and diseases and molecular breeding.

**Keywords** Cotton; Biotic stress; Natural immunity; Transcriptome analysis; Resistance gene

## 1 Introduction

Biological stress, especially pathogens such as *Verticillium dahliae*, can seriously affect cotton yield and reduce fiber quality. Verticillium wilt is the most severe disease. Not only does it cause great economic losses, but most cotton varieties are not resistant to the disease, which is a headache for many growers (Xu et al., 2014; Wu et al., 2021).

Recent studies have found that cotton's immune system is actually very complex. When it is attacked by pathogens, it quickly produces reactive oxygen species (ROS) in the body, activates hormone signaling pathways such as salicylic acid and jasmonic acid, and also activates some defense genes and secondary metabolic pathways (Xu et al., 2014; Li et al., 2016, 2019; Chang et al., 2023). Through transcriptome analysis, researchers have found several key genes and regulatory proteins, such as WRKY transcription factors, calcium-dependent protein kinases, and antimicrobial proteins. These factors play an important role in the recognition of pathogens and the transmission of immune signals (Zhang et al., 2016; Wu et al., 2021; Xiao et al., 2023; Liu et al., 2024). However, the molecular mechanisms behind these responses are not yet fully understood, and there are relatively few disease resistance gene resources available, especially in commercial cotton varieties (Zhu et al., 2023).

This study used a transcriptome analysis system to explore the innate immune response of cotton to biotic stress, reviewed the effects of biotic stress, summarized the current knowledge about cotton innate immunity, and then proposed new transcriptomic insights, emphasizing their significance for future breeding and disease management strategies. This study identified and characterized key genes and pathways related to disease resistance, thereby comprehensively understanding the defense mechanism of cotton, hoping to provide valuable molecular targets for breeding disease-resistant cotton varieties, and ultimately help improve crop stress resistance and sustainable cotton production.

## 2 Applications of Transcriptomics in Plant Immunity Research

### 2.1 RNA-Seq technology and its advantages

RNA-Seq is a technology used to analyze RNA expression. It can measure the types and quantities of all RNA in a sample at one time. This technology is more sensitive than the older generation of methods (such as chips), can find new gene transcripts, and can more accurately calculate the expression level of each gene. When studying plant immune responses, RNA-Seq can help us understand which genes are activated and when, and which tissues are changing. This can reveal the details of plant immune changes, such as discovering immune channels or regulatory genes that were not noticed before, such as calcium channels or specific transcription factors (Moore et al., 2011; Bjornson et al., 2020; Zheng et al., 2024).

### 2.2 Cotton transcriptome databases and resource integration

Integrating transcriptome data from different experiments is the key to studying plant immunity. There are many public databases that collect RNA data from different plants and different experimental conditions, which can be used for comparative analysis. These data help scientists find some common immune-related genes, such as antimicrobial peptides. With these resources, researchers can also develop some computational tools to discover new genes or regulatory sites (Shelenkov et al., 2020; De Jong and Bosco, 2021).

### 2.3 Bioinformatics methods and analytical pipeline

Bioinformatics plays a big role in analyzing RNA-Seq data. Generally speaking, the analysis process starts with a data quality check, then the reads are aligned to the genome, then which genes have changed in expression, and finally the functions of these genes are checked. Some new algorithms can find which genes work together, which regulatory modules are at work, and which pathways are involved in the immune response. This type of analysis helps us understand the activity of genes in different time and space, and can also predict some new immune-related genes or small peptides (Zhang et al., 2017; De Jong and Bosco, 2021; Liu et al., 2024). Now, researchers have also begun to combine batch sequencing and single-cell sequencing data, which can see more details and further understand the mechanisms behind plant immune responses (Stubbington et al., 2017).

## 3 Gene Expression Changes in Cotton under Biotic Stress

### 3.1 Transcriptional regulation under pathogen stress

When cotton encounters pathogen invasion, a complex transcriptional response mechanism is quickly activated. Transcription factors such as WRKY28, WRKY40, and WRKY53, as well as proteins such as ERF and bHLH, will rise rapidly in leaves. They can activate hormone signals (such as jasmonic acid, salicylic acid, and ethylene) and regulate the synthesis of some secondary metabolites to help cotton resist pathogens. Studies have found that transcription factors of the WRKY and ERF families can be activated under a variety of biotic stresses, indicating that they play a core role in defense (Liu et al., 2016; Bihani et al., 2024; Huang et al., 2024). There is also a gene called *GhJAZ2*, which can also regulate the jasmonic acid pathway, helping cotton find a balance in defense between pathogens and leaf-eating insects (Figure 1) (He et al., 2018).

### 3.2 Differential gene expression induced by insect infestation

Insects such as aphids, cotton bollworms, and whiteflies can cause a series of genetic changes in cotton. Some transcription factors, such as WRKY28, WRKY40, WRKY53, ERF4 and ERF5, are activated when different insects invade, which is a more "universal" response. But there are also some genes that are "specific for a certain insect", such as GH3.1, ACS1, CYP74A, TIFY10A, BHLH25, ABR1, ERF025, which are particularly active when cotton bollworm invades. These genes are responsible for regulating hormone responses, MAPK signaling pathways and the production of some defensive metabolites, allowing cotton to respond more accurately to different insects (Bihani et al., 2024).

### 3.3 Integration of immune pathways under multiple stresses

Sometimes, cotton may face attacks from pathogens and insects at the same time. At this time, it will activate multiple defense channels to work together. Some genes, such as GhWRKY28, are activated when encountering abiotic stresses such as diseases and drought, indicating that these defense signals can be combined with each

other. In this case, cotton will increase the expression of genes involved in hormone transmission, MAPK signaling, and secondary metabolite synthesis. This "multi-pathway" approach can enable cotton to respond more effectively to different threats and enhance its overall stress resistance (He et al., 2018; Bihani et al., 2024).

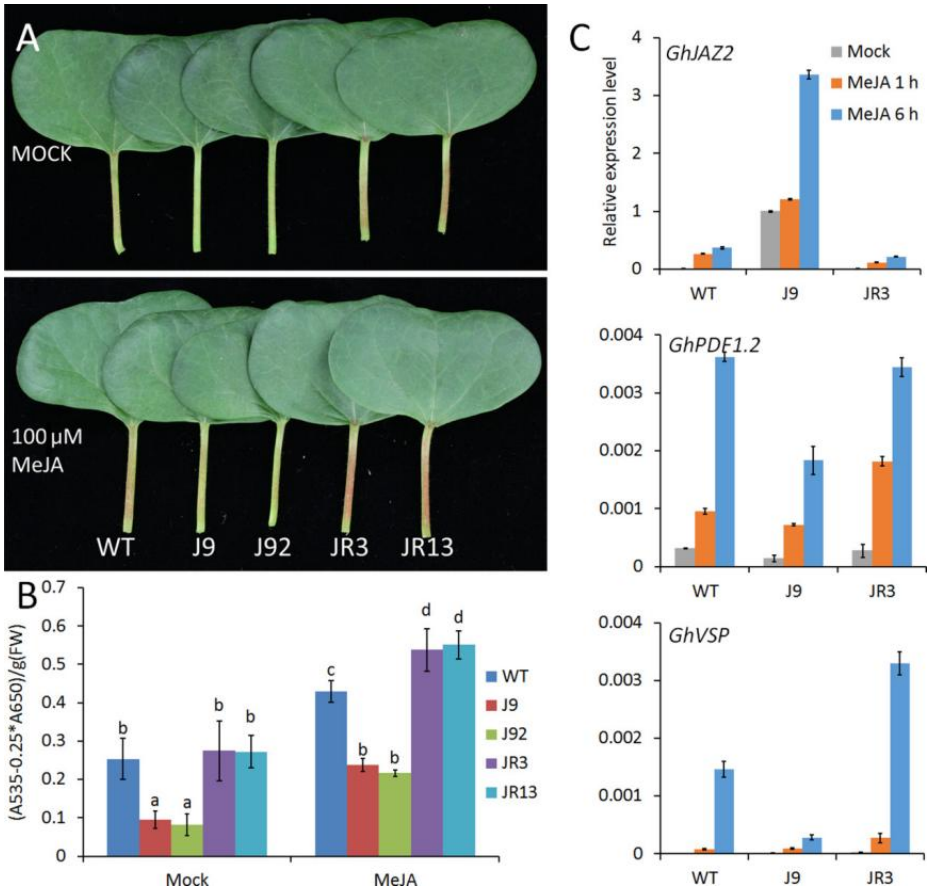


Figure 1 GhJAZ2 reduces methyl jasmonate (MeJA)-induced anthocyanin accumulation and the expression of jasmonate (JA)-responsive defence marker genes in cotton. (A) The cotyledon petioles of wild-type and *GhJAZ2* transgenic cotton seedlings were treated with or without (MOCK) MeJA for 3 days. (B) Anthocyanin content of the cotyledon petioles in (A). The data are the mean ± standard error (SE) of three independent biological replications, and different letters indicate significant differences at $P<0.05$ (Duncan's multiple range test). (C) Quantitative reverse transcription-polymerase chain reaction (qRT-PCR) analysis of *GhJAZ2*, *GhPDF1.2* and *GhVSP* in roots of wild-type and *GhJAZ2* transgenic cotton lines treated with or without MeJA. Total RNAs were extracted from roots of seedlings at the indicated time points after treatment. The *GhUBQ7* gene was used as the endogenous reference gene. The data represent the mean ± standard deviation (SD) of three technical replicates. WT, wild-type; J9 and J92, *GhJAZ2*-overexpressing cotton lines; JR3 and JR13, *GhJAZ2*-RNAi (RNA interference) cotton lines (Adopted from He et al., 2018)

## 4 Identification and Functional Annotation of Key Immune Genes

### 4.1 Expression patterns of resistance gene families

Part of cotton's disease resistance comes from some specific gene families, such as NBS-LRR resistance genes. These genes are activated when pathogens invade, especially in varieties with strong disease resistance, such as *Gossypium hirsutum* L. and *Gossypium barbadense* L. When cotton is infected with *Verticillium dahliae*, receptor kinase genes such as BAK1 and CERK1 are activated, and their splicing patterns change. One of the key proteins is called GauSR45a, which can regulate the splicing of these immune genes, making cotton's defense response more flexible and effective. Interestingly, these genes in disease-resistant varieties have more changes in splicing, while those in disease-prone varieties have fewer changes. This suggests that there may be a great relationship between the diversity of gene splicing and cotton's disease resistance (Liu et al., 2024).

### 4.2 Regulatory roles of transcription factors

Transcription factors are a class of regulatory proteins that can "switch" many genes, and the WRKY family is particularly important in this regard. For example, the factor GhWRKY41 can be quickly activated after pathogen

infection, especially in disease-resistant varieties. It can also stimulate its own continuous expression, forming a positive feedback. This factor controls many important defense-related genes, such as those involved in phenylpropanoid metabolism, lignin synthesis, and flavonoid synthesis. These metabolites can strengthen the "body defense line" of cotton. In addition, a class of WRKY factors called IId also improves cotton's resistance to *Fusarium oxysporum* through the MAPK signaling pathway (Wang et al., 2022; Xiao et al., 2023). These findings all indicate that transcription factors play a critical role in disease resistance.

### 4.3 Annotation and validation of core genes in signaling pathways

Through functional analysis and experiments, researchers have found some signaling pathways that are particularly important in the disease resistance process, such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET). Many immune genes undergo different changes after pathogen invasion or hormone treatment. For example, a study found that 24 genes responded to both *Verticillium dahliae* and methyl jasmonate. This suggests that these genes are related to jasmonic acid and may be directly involved in the defense response. Subsequent experiments also verified their role in producing reactive oxygen species and transmitting hormone signals, which are important for improving disease resistance (Xu et al., 2014).

## 5 Integrated Models of Immune Pathways and Defense Mechanisms

### 5.1 Pattern recognition receptors (PRRs) and early signaling events

The immune system of cotton starts with recognition. It first uses some "sensors" to identify the enemy. These sensors are called pattern recognition receptors, such as receptor-like kinases and extracellular proteins. They can recognize certain molecular signals of pathogens. For example, kinases like GbEIR5A/D will trigger the accumulation of reactive oxygen species (ROS) and cell death when they recognize fungi, thereby initiating two immune responses: one is PAMP-triggered (PTI) and the other is effector-triggered (ETI) (Sun et al., 2024). There are also some proteins, such as CRR1, which can protect defense enzymes from being destroyed by pathogen enzymes. Enzymes like chitinase 28, under the protection of CRR1, can better work outside the cell and block pathogens (Han et al., 2019). These reactions occur quickly and can start subsequent immune responses in time.

### 5.2 Hormonal signaling networks and immune coordination

Once cotton recognizes pathogens, it will regulate defense through several hormones in the plant body. The most common are salicylic acid (SA), jasmonic acid (JA) and ethylene (ET). Like a command system, they mobilize various parts of the plant to resist diseases. For example, some beneficial bacteria (such as *Bacillus subtilis* NCD-2) will activate these hormone pathways in cotton, which can increase the expression of defense genes such as *NPR1*, *ICS1*, *COI1* and *LOX1* in cotton. If any of these pathways is "turned off", cotton's disease resistance will also decrease, indicating that these pathways are indispensable (Mo et al., 2025). In addition, some proteins, such as GhJAZ2, can bind to transcription factors to control JA signals, helping cotton find a balance between "growing" and "preventing diseases" (He et al., 2018). There is also a membrane protein such as GhSYP121, which can regulate SA signals, indicating that hormones and cell transport systems work together (Gao et al., 2024).

### 5.3 Systematic integration of resistance-induced pathways and regulatory networks

The disease resistance mechanism of cotton is not just a single route, it integrates many signal pathways. Transcription factors such as WRKY will form a "positive feedback" circle. Once activated, they will continuously activate many defense genes, such as genes that control phenylpropanoid metabolism and lignin synthesis (Hu et al., 2021; Xiao et al., 2023). There is also a signal "amplifier" called MAPK in cotton, which can amplify early pathogen recognition signals and transmit them to downstream genes. For example, GhMPK9 and GhWRKY40a are such a link. They work together to help cotton deal with different types of pathogens at the same time (Wang et al., 2022; Mi et al., 2024). Some studies have also used proteomic and transcriptomic methods to find that these regulatory systems are very flexible and also involve reactive oxygen metabolism, secondary metabolite production and epigenetic control. These reactions are intertwined, allowing cotton to form a comprehensive and rapid immune system (Zhang et al., 2017; Liu et al., 2024).

## 6 Case Studies: Innate Immune Responses in Specific Cotton Varieties

### 6.1 Transcriptomic features of resistant hybrids

Disease-resistant cotton hybrids exhibit rapid and robust induction of immune-related gene expression after pathogen infection. For example, in disease-resistant varieties, transcription factors such as WRKY41 are generally and rapidly upregulated after inoculation with *Verticillium dahliae*. Overexpression of GhWRKY41 enhances resistance by activating phenylpropanoid metabolism and upregulating genes involved in lignin and flavonoid biosynthesis, while knockdown increases susceptibility. Whole-genome analysis showed that a large proportion of WRKY41 target genes were upregulated during infection, including receptor kinases and other disease resistance proteins, which emphasizes the importance of transcriptional reprogramming in disease-resistant hybrids (Figure 2) (Xiao et al., 2023).

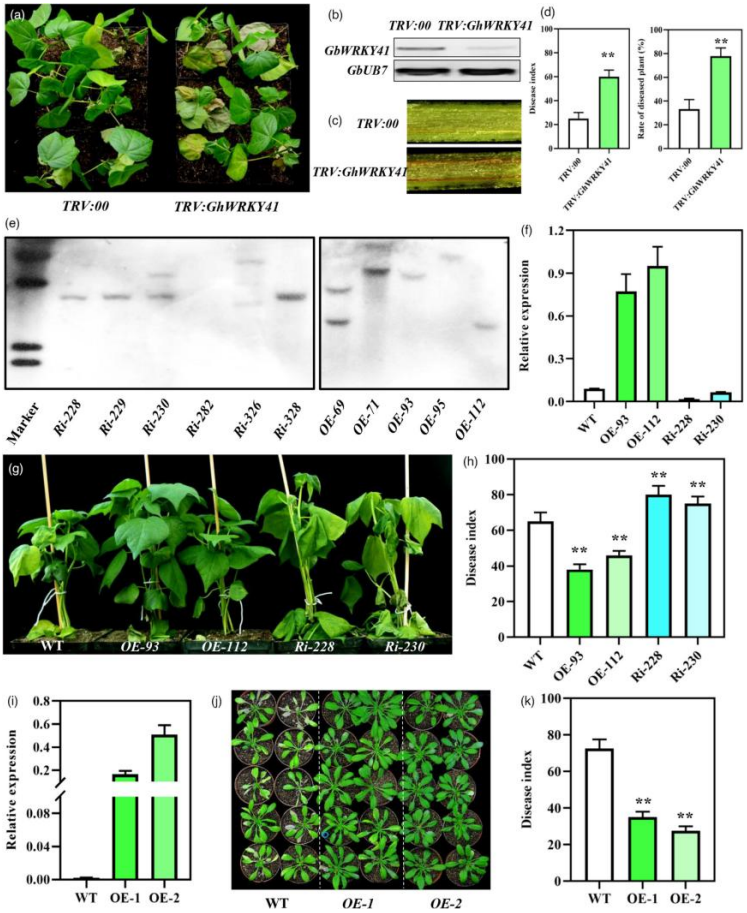


Figure 2 GhWRKY41 is a positive regulator of cotton resistance to *Verticillium dahliae*. (a) Disease symptoms of cotton seedlings (*G. barbadense cv.* 7124) after inoculation for 20 days. Seedlings of *TRV:00* and *TRV:GhWRKY41* were inoculated with *V. dahliae* and re-planted in soil with at least 25 plants. (b) Reverse transcription PCR analysis to examine the expression of GbWRKY41 in TRV:00 and *TRV:GhWRKY41* plants. The *GbUB7* gene was used as a control for expression. (c) *V. dahliae* hyphal accumulation of in TRV:00 and *TRV:GhWRKY41* plant stems. (d) Disease index and rate of diseased plants of *TRV:00* and *TRV:GhWRKY41* plants after inoculation for 20 days. Values represent means ± SD; n=3. (e-f) Southern blotting (e) and reverse transcription-quantitative PCR (RT-qPCR) analysis (f) to examine the copy number and expression respectively of *GhWRKY41* in *GhWRKY41*-transgenic cotton lines. The *GhUB7* gene was used as the endogenous reference gene. Values represent means ± SD; n=3. (g) Disease symptoms in wild type (WT), overexpression (OE) and RNAi (Ri) cotton plants after inoculation for 11 days. Seedlings of WT and transgenic lines were inoculated with *V. dahliae* and re-planted in soil with at least 25 plants for each line. (h) Disease index of WT and transgenic plants at 5 days after the plants beginning to present disease symptoms. Values represent means ± SD; n=3. (i) RT-qPCR analysis of *GhWRKY41* in WT and transgenic *Arabidopsis* lines. The *AtACTIN* gene was used as the endogenous reference gene. The values are the means ± SD; n=3. (j) Disease symptoms in WT and overexpressing *Arabidopsis* lines at 3 weeks after inoculation with *V. dahliae*. (k) Disease index statistics in WT and transgenic *Arabidopsis* lines after inoculation with *V. dahliae* for 3 weeks. Values are the means ± SD; n=3. All statistical analyses were performed using Student's t test: **, $P < 0.01$. All assays were repeated three times with similar results (Adopted from Xiao et al., 2023)

## 7 Concluding Remarks

Recent studies have found that cotton's natural immune system is actually quite complex. It has several layers of defense mechanisms. Some disease-resistant genes react very quickly, such as a transcription factor called WRKY41, which can regulate phenylpropanoid metabolism and drive subsequent defense steps to help cotton resist pathogens such as *Verticillium dahliae*. Studies have also found that cotton's immune sensors work with the immune response triggered by pathogens, and some special receptor kinases, such as GbEIR5A/D, can enhance this defense response. In addition, proteins such as SR45a can cause different splicing versions of the same gene, which can also affect cotton's immunity, with some varieties performing well and others not so well. Plant hormones (such as salicylic acid, jasmonic acid, and ethylene) also participate in regulating immunity, and cotton must find a balance between "growing fast" and "strong disease resistance."

Despite these advances, there are still some challenges. We still don't understand the disease resistance mechanisms of some cotton varieties, and there are not many disease-resistant genes that can really be used for breeding. In addition, cotton is polyploid, and its genome itself is quite complex, with many variations and splicing methods, which makes research more difficult. To transfer the disease resistance of wild cotton to cultivated cotton, genetic barriers or unwanted traits are often encountered. In addition, many experiments are done under laboratory conditions, and they have to be tried repeatedly in real fields to see if the results are reliable.

In the future, more large-scale genome association analysis can be done to find more disease-resistant genes. Wild cotton resources can also be used to find new useful traits. If high-throughput phenotypic analysis, gene editing technology (such as CRISPR/Cas9) and large-scale genetic research can be combined, varieties with strong disease resistance can be bred more quickly. At the same time, we must continue to study how gene expression is regulated, especially complex mechanisms such as alternative splicing. This will allow us to have a more comprehensive understanding of the cotton immune system and make it easier to breed good varieties that can adapt to different diseases and have more stable resistance.

### Acknowledgments

I am grateful to Dr. Z. Xu for his assistance with the serious reading and helpful discussions during the course of this work.

### 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.

### References

Bihani D., Khuman A., and Chaudhary B., 2024, Comparative Transcriptomics reveals novel spatial gene expression profiles in cotton (*Gossypium hirsutum* L.) under herbivory and drought stress, Journal of Plant Growth Regulation, 43(11): 4018-4037.
https://doi.org/10.1007/s00344-024-11362-3

Bjornson M., Pimprikar P., Nürnberger T., and Zipfel C., 2020, The transcriptional landscape of *Arabidopsis thaliana* pattern-triggered immunity, Nature Plants, 7(5): 579-586.
https://doi.org/10.1038/s41477-021-00874-5

Bu B., Qiu D., Zeng H., Guo L., Yuan J., and Yang X., 2014, A fungal protein elicitor PevD1 induces Verticillium wilt resistance in cotton, Plant Cell Reports, 33(3): 461-470.
https://doi.org/10.1007/s00299-013-1546-7

Chang B., Zhao L., Feng Z., Wei F., Zhang Y., Zhang Y., Huo P., Cheng Y., Zhou J., and Feng H., 2023, Galactosyltransferase GhRFS6 interacting with GhOPR9 involved in defense against Verticillium wilt in cotton, Plant Science, 328: 111582.
https://doi.org/10.1016/j.plantsci.2022.111582

De Jong E., and Bosco A., 2021, Unlocking immune-mediated disease mechanisms with transcriptomics, Biochemical Society Transactions, 49(2): 705-714.
https://doi.org/10.1042/BST20200652

Gao L., Pei Y., Wang P., Cen Y., Yan X., and Hou Y., 2024, Cotton SNARE complex component GhSYP121 regulates salicylic acid signaling during defense against *Verticillium dahliae*, Journal of Cellular Physiology, 239(11): e31329.
https://doi.org/10.1002/jcp.31329

Han L., Li Y., Wang F., Wang W., Liu J., Wu J., Zhong N., Wu S., Jiao G., Wang H., and Xia G., 2019, The cotton apoplastic protein CRR1 stabilizes chitinase 28 to facilitate defense against the fungal pathogen *Verticillium dahliae*, The Plant Cell, 31(2): 520-536.
https://doi.org/10.1105/tpc.18.00390

He X., Zhu L., Wassan G., Wang Y., Miao Y., Shaban M., Hu H., Sun H., and Zhang X., 2018, GhJAZ2 attenuates cotton resistance to biotic stresses via the inhibition of the transcriptional activity of GhbHLH171, Molecular Plant Pathology, 19(4): 896-908.
https://doi.org/10.1111/mpp.12575

Hu Q., Xiao S., Wang X., Ao C., Zhang X., and Zhu L., 2021, GhWRKY1-like enhances cotton resistance to *Verticillium dahliae* via an increase in defense-induced lignification and S monolignol content, Plant Science, 305: 110833.
https://doi.org/10.1016/j.plantsci.2021.110833

Huang F., Du X.Y., Zou S.K., Wang L., and Han Y.L., 2024, Advancements in wheat hybridization: overcoming biological barriers, Bioscience Evidence, 14(5): 195-205.
https://doi.org/10.5376/be.2024.14.0021

Li C., He Q., Zhang F., Yu J., Li C., Zhao T., Zhang Y., Xie Q., Su B., Mei L., Zhu S., and Chen J., 2019, Melatonin enhances cotton immunity to *Verticillium* wilt via manipulating lignin and gossypol biosynthesis, The Plant Journal, 100(4): 784-800.
https://doi.org/10.1111/tpj.14477

Li Y., Han L., Wang H., Zhang J., Sun S., Feng D., Yang C., Sun Y., Zhong N., and Xia G., 2016, The thioredoxin GbNRX1 plays a crucial role in homeostasis of apoplastic reactive oxygen species in response to *Verticillium dahliae* infection in cotton, Plant Physiology, 170(4): 2392-2406.
https://doi.org/10.1104/pp.15.01930

Lin J.F., and Zhu Y.X., 2024, Alternaria leaf spot in cotton: identification and control, Molecular Microbiology Research, 14(4): 181-187.
https://doi.org/10.5376/mmr.2024.14.0020

Liu F., Cai S., Dai L., Ai N., Feng G., Wang N., Zhang W., Liu K., and Zhou B., 2024, SR45a plays a key role in enhancing cotton resistance to *Verticillium dahliae* by alternative splicing of immunity genes, The Plant Journal, 119(1): 137-152.
https://doi.org/10.1111/tpj.16750

Liu X., Song Y., Xing F., Wang N., Wen F., and Zhu C., 2016, *GhWRKY25*, a group I *WRKY* gene from cotton, confers differential tolerance to abiotic and biotic stresses in transgenic *Nicotiana benthamiana*, Protoplasma, 253(5): 1265-1281.
https://doi.org/10.1007/s00709-015-0885-3

Mi X., Li W., Chen C., Xu H., Wang G., Jin X., Zhang D., and Guo W., 2024, GhMPK9‐GhRAF39_1‐GhWRKY40a Regulates the GhERF1b‐ and GhABF2‐Mediated pathways to increase cotton disease resistance, Advanced Science, 11(29): 2404400.
https://doi.org/10.1002/advs.202404400

Mo S., Zhao W., Wei Y., Su Z., Li S., Lu X., Zhang X., Qu Y., Wang P., Dong L., Zhang J., Guo Q., and Ma P., 2025, Defense responses stimulated by *Bacillus subtilis* NCD-2 through salicylate- and jasmonate-dependent signaling pathways protect cotton against Verticillium wilt, International Journal of Molecular Sciences, 26(7): 2987.
https://doi.org/10.3390/ijms26072987

Moore J., Loake G., and Spoel S., 2011, Transcription dynamics in plant immunity, The Plant Cell, 23(8): 2809-2820.
https://doi.org/10.1105/tpc.111.087346

Shelenkov A., Slavokhotova A., and Odintsova T., 2020, Predicting antimicrobial and other cysteine-rich peptides in 1267 plant transcriptomes, Antibiotics, 9(2): 60.
https://doi.org/10.3390/antibiotics9020060

Stubbington M., Rozenblatt-Rosen O., Regev A., and Teichmann S., 2017, Single-cell transcriptomics to explore the immune system in health and disease, Science, 358(6359): 58-63.
https://doi.org/10.1126/science.aan6828

Sun L., Li X., Zhong J., Wang Y., Li B., Ye Z., and Zhang J., 2024, Recognition of a fungal effector potentiates pathogen‐associated molecular pattern‐triggered immunity in cotton, Advanced Science, 12(1): 2407787.
https://doi.org/10.1002/advs.202407787

Wang L., Guo D., Zhao G., Wang J., Zhang S., Wang C., and Guo X., 2022, Group IIc WRKY transcription factors regulate cotton resistance to *Fusarium oxysporum* by promoting GhMKK2-mediated flavonoid biosynthesis, New Phytologist, 236(1): 249-265.
https://doi.org/10.1111/nph.18329

Wu Y., Zhang L., Zhou J., Zhang X., Feng Z., Wei F., Zhao L., Zhang Y., Feng H., and Zhu H., 2021, Calcium-dependent protein kinase GhCDPK28 was dentified and involved in Verticillium wilt resistance in cotton, Frontiers in Plant Science, 12: 772649.
https://doi.org/10.3389/fpls.2021.772649

Xiao S., Ming Y., Hu Q., Ye Z., Si H., Liu S., Zhang X., Wang W., Yu Y., Kong J., Klosterman S., Lindsey K., Zhang X., Aierxi A., and Zhu L., 2023, GhWRKY41 forms a positive feedback regulation loop and increases cotton defence response against *Verticillium dahliae* by regulating phenylpropanoid metabolism, Plant Biotechnology Journal, 21(5): 961-978.
https://doi.org/10.1111/pbi.14008

Xu L., Zhang W., He X., Liu M., Zhang K., Shaban M., Sun L., Zhu J., Luo Y., Yuan D., Zhang X., and Zhu L., 2014, Functional characterization of cotton genes responsive to *Verticillium dahliae* through bioinformatics and reverse genetics strategies, Journal of Experimental Botany, 65(22): 6679-6692.
https://doi.org/10.1093/jxb/eru393

Yan Z., Wang X., Wei R., Jun Y., and Ma Z., 2016, Island cotton enhanced disease susceptibility 1 gene encoding a lipase-like protein plays a crucial role in response to *Verticillium dahliae* by regulating the SA level and $H_2O_2$ accumulation, Frontiers in Plant Science, 7: 1830.
https://doi.org/10.3389/fpls.2016.01830

Zhang M., Cheng S., Wang H., Wu J., Luo Y., Wang Q., Wang F., and Xia G., 2017, iTRAQ-based proteomic analysis of defence responses triggered by the necrotrophic pathogen *Rhizoctonia solani* in cotton, Journal of Proteomics, 152: 226-235.
https://doi.org/10.1016/j.jprot.2016.11.011

Zhang Z., Zhao J., Ding L., Zou L., Li Y., Chen G., and Zhang T., 2016, Constitutive expression of a novel antimicrobial protein, *Hcm1*, confers resistance to both Verticillium and Fusarium wilts in cotton, Scientific Reports, 6(1): 20773.
https://doi.org/10.1038/srep20773

Zheng Q., Lin R., and Zheng C., 2024, Transcriptomics in the study of antiviral innate immunity, In: Methods in molecular biology, pp.83-91.
https://doi.org/10.1007/978-1-0716-4108-8_10

Zhu Y., Zhao M., Li T., Wang L., Liao C., Liu D., Zhang H., Zhao Y., Liu L., Ge X., and Li B., 2023, Interactions between *Verticillium dahliae* and cotton: pathogenic mechanism and cotton resistance mechanism to Verticillium wilt, Frontiers in Plant Science, 14: 1174281.
https://doi.org/10.3389/fpls.2023.1174281