

Feature Review

Open Access

Regulatory Role of Promoter Variants in Cotton Stress-Responsive Genes

Jinhua Cheng, Mengting Luo ✉

Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, China

✉ Corresponding email: mengting.luo@jicau.orgCotton Genomics and Genetics, 2025, Vol.16, No.6 doi: [10.5376/cgg.2025.16.0027](https://doi.org/10.5376/cgg.2025.16.0027)

Received: 07 Sep., 2025

Accepted: 20 Oct., 2025

Published: 10 Nov., 2025

Copyright © 2025 Cheng and Luo, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Cheng J.H., and Lou M.T., 2025, Regulatory role of promoter variants in cotton stress-responsive genes, Cotton Genomics and Genetics, 16(6): 269-277 (doi: [10.5376/cgg.2025.16.0027](https://doi.org/10.5376/cgg.2025.16.0027))

Abstract Cotton, as one of the world's important economic crops, often faces abiotic stresses such as drought, saline-alkali conditions and extreme temperatures. These environmental pressures severely restrict its growth and development as well as the stability of its yield. In recent years, molecular genetic studies have shown that promoter variations play a key role in regulating the expression of stress response genes in cotton. This study systematically reviewed the structure and function of promoters, the classification and characteristics of cotton stress-response genes, as well as the types of promoter variations involved in regulation. It focused on analyzing how promoter polymorphisms lead to transcriptional regulatory differences under stress conditions and affect cotton's adaptability to environmental stress. The molecular mechanisms such as sequence variations in the promoter region, DNA methylation, histone modification, and transcription factor interactions were also deeply explored. Key stress response genes such as *AtDREB1A*, *GhHSP70*, and *GhERF1* were selected, and the specific functional manifestations of their promoter variations in salt tolerance, heat resistance, and drought resistance traits were introduced. This research is expected to provide new ideas for a deeper understanding of the regulatory network of plant environmental adaptability and promote the functional exploration and stress resistance improvement of cotton germplasm resources.

Keywords Cotton (*Gossypium* spp.); Promoter mutation; Stress response gene; Gene expression regulation; Abiotic stress tolerance

1 Introduction

When it comes to which crop is the most "reliable", cotton (*Gossypium* spp.) is definitely on the list. It is not only the most important source of natural fibers in the global textile industry, but also directly related to the basic agricultural economy in many countries. Growing cotton has supported the livelihoods of many families. For some developing countries, it is even a pillar of industry. However, it doesn't mean that having land guarantees good cotton cultivation. Whether it is drought, salinity and alkalinity, high temperature or low temperature, these abiotic stresses have long plagued farmers in cotton-growing areas, causing considerable impacts on yield and quality (Tang et al., 2024).

In recent years, with the continuous improvement of genomics and transcriptomics tools, researchers have gradually drawn a regulatory map of cotton's "self-rescue" in adverse conditions. Transcription factors such as MYB, NAC, AP2/ERF, GLK, and bZIP, as well as some enzyme genes related to stress response, have been successively discovered (Zafar et al., 2022; Gu et al., 2023; Wang et al., 2024). But for these genes to "speak", there must be promoters behind them to cooperate. Especially when facing complex environmental signals, the regulatory role of the promoter region is often more crucial than people imagine. Not all promoters are the same. Some cis element variations can make gene expression stronger or more precise. Genes such as *GhNAC2* or *GhHSP70-26* have multiple regulatory elements related to hormone or stress responses in their promoter regions. Once such structures change, they may directly affect the binding sites of transcription factors (Hamid et al., 2024; Naresh et al., 2024). Bao et al. (2020) pointed out that sequence changes at some key positions might be the cause of differences in gene expression and thus the varying degrees of tolerance. Interestingly, the launcher is not only a "console" but also a "transformation entry point". Shaban et al. (2018) and Guo et al. (2023) found that if the response capabilities of certain promoter components are precisely controlled, the performance of cotton in adverse conditions can be significantly enhanced. In other words, these variations are not only the research subjects but also likely to be the breakthrough points for future stress-resistant breeding.

This study will systematically explore the regulatory role of promoter variations in cotton stress-responsive genes and review the current understanding of promoter structures and their impact on gene regulation under stress conditions. Identify the key promoter variations related to enhancing the stress resistance of cotton; Evaluate the potential of these variations to improve cotton through molecular breeding and genetic engineering. By clarifying the mechanism by which promoter variations regulate the expression of stress response genes, this study aims to provide a theoretical basis for breeding cotton varieties with stronger stress resistance, thereby supporting sustainable cotton production and economic stability while addressing environmental challenges.

2 Structure and Function of Promoters

2.1 Definition and basic structure of promoters

The promoter is not a strange new concept. It is a fragment on DNA close to the starting point of a gene, like a switch, used to regulate whether the gene is "turned on". Whether RNA polymerase and various transcription factors can "find the door" lies in this region. However, this structure is not simply a single board; it is often composed of several areas: In the core area in the middle, "classic elements" such as the TATA box and the CAAT box can often be seen. There are also proximal and distal control areas embedded with various CRE components, which are responsible for dealing with different TFs. No matter which section it is, if any one is missing, the transcription starting point may not be accurately identified, let alone smoothly transferred.

2.2 The role of promoters in gene transcription regulation

Many people know that transcription initiation relies on RNA polymerase, but to "invite" it to the right position, the promoter is the key. This place is not only its stopover point, but also a venue for the collection of various transcription factors (Khan et al., 2023). The CRE element in the promoter is like an "interface" prepared for different signals. Who binds it, how it binds it, and for how long, these determine whether the gene is activated throughout the day or in phases (Cai et al., 2020). The expression pattern sometimes comes from organizational specificity, sometimes it only becomes active when triggered by the external environment, and even can be artificially designed to be activated whenever one wants. Also, don't underestimate the sequence structure of the promoter. Details such as GC content and motif arrangement often affect transcriptional efficiency and accuracy (Bansal et al., 2014). In crops like cotton that often have to cope with environmental changes, the regulatory power of promoters is the most important link.

2.3 Types and sources of promoter variants

The promoter sequence is not static; it undergoes various variations. These variations sometimes result from the accumulation of natural selection, sometimes are induced mutations by humans, or may be "assemblies" designed in the laboratory (Bao et al., 2020). For instance, some promoters are inherently "all-weather", like the CaMV35S, which can be expressed by any organization. However, there are also some that are more "selective", only lighting up at the leaves, roots or a certain developmental stage. There is another category that only speaks up when there is something to do. Once stimulated by the environment or hormones, they will be activated (Kummari et al., 2020). Synthetic promoters are more like "customized products", allowing researchers to combine various components as needed to achieve more precise control. There are also many forms of variation, ranging from simple SNPS, insertions/deletions to large fragment rearrangements, and even artificial assembly of new components. These changes may not only affect the binding ability of TF, but also alter the "character" of the entire promoter, thereby making the gene expression stronger, weaker or responding faster. There have been many examples of this in crops such as cotton.

3 Characteristics and Function of Cotton Stress-Responsive Genes

3.1 Classification of cotton stress-responsive genes

Over the years, with more research, it has been found that the types of genes mobilized by cotton in response to stress are indeed quite numerous. In addition to the well-known transcription factors, such as DREB, MYB, NAC, bZIP, WRKY and GARP families (Wang et al., 2024), there are also some "familiar faces" involved in regulating metabolism, synthesis or defense. Such as SAMS, LEA, CDKs, PLA1, *RF2* and *P5CS*, etc. (Figure 1) (Gu et al., 2023; Fang et al., 2025). The specific functions of these genes are also quite scattered. Some are responsible for

signal transduction, some for regulating transcription, and others contribute to osmotic protection, antioxidation, or maintaining cell membrane stability. However, to truly make a detailed classification, it is necessary to take into account their performance under different pressures.

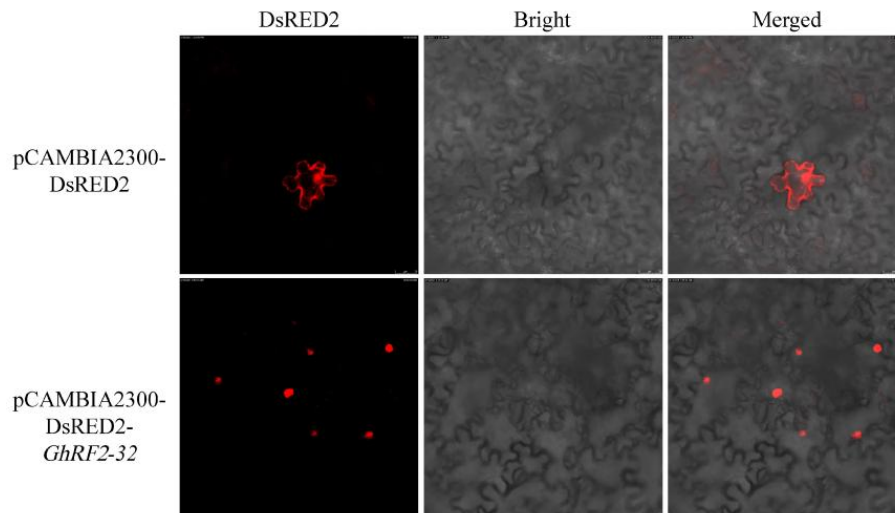


Figure 1 Subcellular localization of pCAMBIA 2300-DsRED2-*GhRF2-32* fusion protein (Adopted from Gu et al., 2023)

3.2 Major stress types

Among various environmental stresses, salinity, drought and low temperature pose the most challenges to cotton. Just talking about salt and drought, these two stresses are sufficient to cause the imbalance of water regulation and ion disorder in plants, ultimately leading to a decrease in yield (Kilwake et al., 2023). The problem of low temperatures is even more "insidious", especially during the emergence and seedling stages, when the damage to cotton often comes suddenly and severely. Although stresses such as high temperature, water accumulation and heavy metals also exist, the current research attention is still less than that of the former three. Although different types of stress have their own characteristics, they are not completely isolated at the gene expression level. The initiation of many stress response genes is crossed, showing certain commonalities or complementarities (Wang and Zhang, 2024).

3.3 The role of stress-responsive genes in stress tolerance

Not all genes can be called "stress responses", but once they are included in this category, it usually means that they do play a key role in regulating cotton's resistance to external stress. Whether by initiating signal transduction or activating protective mechanisms (such as accumulating osmotic substances and enhancing antioxidant capacity), these genes are involved in regulating physiological states to help cotton "resist". Transcription factors such as DREB and bZIP are often regarded as signal "switches", while genes related to LEA protein and proline synthesis are more like "executors", providing support at the cellular level (Fang et al., 2025). Genes like these, once overexpressed or knocked down, will directly change the performance of cotton under stress such as salt, drought and cold, which also provides an operable target for subsequent breeding or molecular engineering (Guo et al., 2022).

4 The Impact of Promoter Variants on Cotton Stress-Responsive Gene Expression

4.1 Changes in transcription factor binding due to promoter variants

Whether there are many cis control elements or not, and whether their positions are reliable or not, will actually change due to a small variation of the starter. Like *GhNAC2*, its promoter region is home to many components related to hormones and abiotic stress, and the corresponding hormones are also numerous - gibberellin, ethylene, auxin, abolic acid are all within the regulatory range, as well as stress factors such as mannitol and NaCl (Naresh et al., 2024). The combination of these components not only affects which transcription factors can bind, but also determines whether they are expressed in the leaves or activated at the root tips, and whether they respond to stress or remain low-key all the time. Another example is *GhHSP70-26*, whose promoter insertion deletion

variation alters the binding patterns of TFS such as GhFLZ, GhABF3, and GhRVE8, resulting in differences in activation under drought or hormonal treatment. The more you look, the more you will find that similar stress response elements are enriched in the promoters of genes such as NAC, ERF, *P5CS*, CKX, and VLN. (Deep & Pandey, 2024; Hamid et al., 2024). Ultimately, when the structure of the promoter changes, the set point of TF also changes accordingly, and this kind of influence is hard to ignore.

4.2 Gene expression differences caused by promoter variants

Not every promoter variation will bring about significant effects, but the M-650 insertion/deletion in *GhHSP70-26* can be regarded as a "positive example" - whether in the field or in transgenic experiments, this variation almost always corresponds to higher expression and stronger drought resistance. The research team tested using the GUS fusion gene and other reporter systems and it was clear that the expression levels of specific promoter fragments would change after stress or hormone treatment, with some enhanced and some inhibited (Guo et al., 2023). Similar situations can also be observed in the large families of NAC, ERF, *P5CS*, and CKX. The expression differences under different tissues and pressures are often associated with those minor variations in the promoter. Some allelic promoter types can make genes "more easily awakened" and more likely to respond immediately (Sun et al., 2018; Zafar et al., 2022). Of course, not all variations can lead to good results; some may even disrupt the original rhythm of expression.

4.3 The relationship between promoter variants and stress response pathways

If the promoter only adjusts one gene, it's not that troublesome. The problem is that it affects the whole situation. Transcription factors such as WRKY, TCP, and triple helix proteins often recognize motifs such as W-box, TCP elements, GT-box, or MYB sites, and subsequently regulate a whole set of defense mechanisms including ABA pathways, osmotic regulation, and antioxidation (Wang et al., 2019; 2023). When variations occur around these sites, it is often not just the expression of one gene that is driven, but rather affects the activation rhythm of the entire stress pathway. These changes can sometimes enhance the drought resistance, salt tolerance or cold tolerance of cotton, but they may also make the response slow or excessive. In other words, although the promoter seems to be just a sequence segment, it actually influences the entire regulatory network behind it. Combining transcriptome and functional studies to decode these variations can provide a clearer reference path for subsequent targeted breeding.

5 Molecular Mechanisms of Promoter Variants

5.1 The impact of sequence diversity in promoter regions on gene expression regulation

The promoter region of cotton is actually not "quiet" at all. Especially in gene families such as *P5CS*, CNGC, and CKX, cis-regulatory elements (CAREs) are densely packed. Elements like MYB, ABRE, and Cat-box that respond to hormonal and abiotic stresses can be seen everywhere (Zhao et al., 2022). Their existence determines how transcription factors bind and what patterns gene expression ultimately exhibits. What truly sets cotton apart in adverse conditions is the diversity of the promoters themselves - variations such as SNPS, indels, and structural rearrangements can all alter these binding sites, thereby changing gene activity. For instance, some haplotypes or EQTs have been confirmed to be directly linked to salt resistance or cold resistance (Hamid et al., 2024; Fang et al., 2025). However, not every mutation works. Whether it can "make a sound" depends on where it lands. It is precisely these regional differences that support the functional differentiation among the members of the genetic family and also give cotton the confidence to adapt to various complex environments.

5.2 The role of DNA methylation and histone modifications in promoter variants

Not all expression differences can be attributed to the sequence itself; epigenetic factors can also be quite "troublesome". Mechanisms such as DNA methylation and histone modification often act as "switches" in stress responses. Changes in the methylation level of the promoter region can alter the openness of chromatin, thereby affecting whether transcription factors can approach, sometimes inhibiting expression and sometimes activating. In cotton, heat stress can cause an increase in histone markers such as H3K4me2 and H4K5ac, corresponding to enhanced expression of a batch of heat shock factors and proteins (Zhang et al., 2020). In addition, regulatory molecules such as JmjC demethylases and histone acetyltransferases (HATs) also change in expression under

stress conditions, and their own promoters are also rich in stress response elements. These modifications can change at any time. They are not only flexible but also reversible, providing cotton with an operational space to quickly respond to sudden environmental changes.

5.3 Interaction between transcription factors and promoter variants

A minor variation on the promoter can sometimes precisely trigger an entire regulatory chain, especially at the binding sites of transcription factors. TFS such as MYB, bZIP, NAC, and WRKY are the "main force" in the cotton stress response. Whether they can successfully bind to the promoter region often depends on whether these sequences have mutations (Naresh et al., 2024). Studies have found that specific promoter haplotypes do indeed alter the efficiency of TF binding and further affect the expression patterns of related genes, such as directly influencing the salt tolerance of cotton (Lin and Zhu, 2024). Looking deeper, the methylation state of DNA is also involved. Some TFS are highly sensitive to methylation, and some are even directly excluded (Heberle & Bardet, 2019). Therefore, promoter variations, TF binding, and methylation modifications are constantly interacting and in real-time dynamic state. This coordination enables the gene expression of cotton to remain "online" in complex environments.

6 Case Study: Promoter Variants in Specific Cotton Stress-Responsive Genes

6.1 Variants in the *AtDREB1A* promoter and salt tolerance

The DREB family has long made an appearance in various studies on responses to coercion, and *GhDREB1A* is no exception. Its expression pattern under salt stress has been confirmed to be related to salt tolerance. In fact, not only cotton, but also in many crops, once the expression level of DREB genes is increased, the related downstream stress response genes will also become active, thereby making the plants more tolerant of salt. However, the promoter of DREB itself is not simple either - it usually contains multiple cis-regulatory elements related to stress and hormones, becoming one of the key nodes in the regulatory network. A few years ago, there were studies suggesting that CRISPR/Cas9 could be used to directly target these promoters for targeted modification, with the aim of achieving more precise expression (Mahmood et al., 2019). Meanwhile, GWAS and transcriptome data have increasingly linked DREB genes to the salt tolerance of cotton, especially in those salt-tolerant varieties, where the expression levels are more pronounced (Wang et al., 2023; Li et al., 2025).

6.2 Variants in the *GhHSP70* promoter and heat tolerance

In terms of heat resistance, the *GhHSP70-26* promoter also performs quite "representative". For instance, some studies have found that there is a 22 bp deletion (M-1590-Del22, Hap2) at the -1590 bp site upstream of its promoter region. This variation leads to upregulation of gene expression under heat stress, resulting in stronger heat tolerance. Even better, this kind of variation is not only manifested in cotton - when applied to *Arabidopsis thaliana*, plants with the Hap2 promoter also showed higher activity after heat induction and ABA treatment, indicating that the function of this site is indeed solid (Guo et al., 2023). Interestingly, this natural variation can also serve as a molecular marker for breeding screening, and its practicality is not low. In addition, an insert-deletion variation (M-650-In360) also occurred in another region of the gene promoter (-650 bp). This structural difference is also associated with the improvement of drought resistance, which once again indicates from the side that the promoter variation is not an "embellishment", but a part of regulation.

6.3 Variants in the *GhERF1* promoter and drought tolerance

When it comes to drought response, genes like *GhERF1* in the ERF family cannot be avoided. Its promoter structure is already quite rich, with a dense array of stress response elements inside, and the expression regulation is also rather complex. In arid environments, the expression of such genes will be controlled layer by layer. According to the results of transcriptome and co-expression network analysis, ERF genes are often upregulated in drought-tolerant cotton strains. The higher the expression, the more "resilient" the plants are in water-deficient environments (Figure 2) (Mahmood et al., 2019; Wang et al., 2023). Given this, it is no wonder that there are now studies attempting to enhance the expression of *GhERF1* by modifying the promoter structure - after all, this approach seems more stable and easier to apply to actual breeding.

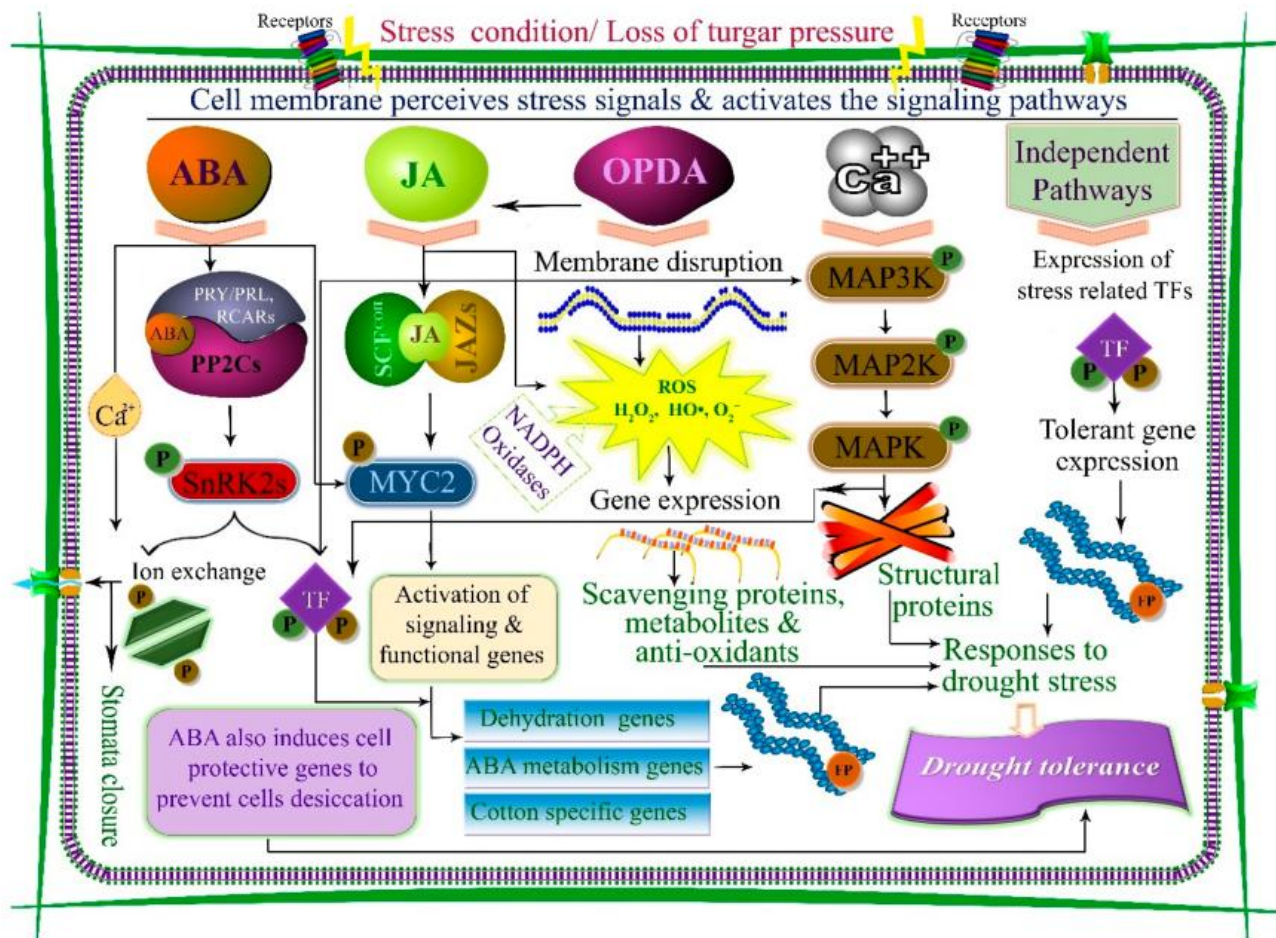


Figure 2 Drought-induced cellular and molecular signaling pathways to enhance drought tolerance in plants (Adopted from Mahmood et al., 2019)

7 Applications of Promoter Variants in Cotton Improvement

7.1 Using promoter variants to enhance cotton stress tolerance

Not all resilience improvement measures rely on radical gene editing. Sometimes, the details of the "regulatory layer" such as promoter variations are even more crucial. Especially under drought, high temperature or saline-alkali stress, some naturally occurring promoter variants or variations modified through engineering means can more flexibly regulate gene expression. Some only function in specific tissues, while others are activated only when stress occurs. A certain insertion/deletion site of the *GhHSP70-26* promoter is linked to improving the drought and heat tolerance of cotton and is regarded as a target worthy of close attention in breeding (Guo et al., 2023). Another example is the *GhNAC2* promoter, which can "respond" to various hormones and adverse signals. Using it to drive the expression of downstream beneficial genes is a feasible path to enhance overall adaptability (Naresh et al., 2024). Although these regulatory changes may seem like mere "patchwork", when combined with marker-assisted selection and molecular breeding techniques, their effects are no worse than those of gene knockout.

7.2 Promoter engineering in genetically modified cotton

The core of transgenic technology is not merely about "what genes to add", but rather "how to regulate their expression". In cotton breeding, some naturally derived or designed inducible promoters are being used to precisely regulate the expression timing and position of target genes. The advantage of doing so is that it can reduce some common side effects and also enhance the resistance of cotton to adverse environments (Shan et al., 2019). A representative case is that the expression of the IPT gene was controlled by the aging-inducing promoter *SAG12*. As a result, not only did the salt tolerance of cotton increase, but the antioxidant capacity was also significantly enhanced, and even the ion balance was more stable (Shan et al., 2019). In addition, tools like

CRISPR/Cas are not limited to gene knockout or insertion. Fine-tuning of the promoter region directly has gradually become a new strategy. For example, some studies have improved the heat resistance of cotton by weakening the activity of the GhCKI promoter (Li et al., 2025). So, the "operating space" of the promoter is not small. If used well, it can precisely exert force.

7.3 Potential of combining promoter variants with precision breeding technologies

In terms of promoters, it is not merely an "auxiliary" regulation. When combined with tools like CRISPR/Cas, the breeding efficiency can be further enhanced by one level. In the past, we always paid more attention to genes themselves, but now we are more inclined to conduct targeted optimization on "regulatory switches". By introducing or editing promoter elements, the target genes can be expressed "just right", neither too much nor too little, especially suitable for those pathways related to adverse adaptation (Shi et al., 2023). Khan et al. (2023) mentioned that modifying promoters with the CRISPR system can not only yield novel alleles but also directly enhance traits such as salt tolerance and drought tolerance. If combined with rapid breeding methods and multi-omics analysis, the entire process will be faster and more accurate. The ultimate outcome is not merely the improvement of a single trait, but rather the possibility of superimposing multiple stress resistances and pushing them together to the practical stage, thus providing more confidence in dealing with complex environments.

8 Conclusion

How crucial is promoter variation in the process of cotton coping with stress? In fact, there are already quite a few answers to this question. Representative genes like *GhNAC2* and *GhHSP70-26*, as well as transcription factor families such as ERF, NAC, bZIP, and MYB, contain a large number of cis elements in their promoter regions that respond to hormones and abiotic stresses. Once the environment encounters problems, It can regulate how, when and how much genes are expressed (Guo et al., 2023; Naresh et al., 2024). However, whether there is variation and where it occurs are what truly determine the differences in expression. GWAS and functional verification methods have linked many promoter variations (such as SNPS and indels) to drought resistance, salt tolerance and heat tolerance. The impact of many variations on cotton traits is real. For this reason, promoter engineering, molecular marker selection and other techniques are increasingly being used for cotton improvement.

But when it comes to how to proceed next, it's far from the time to "wrap it up". The promoter variations of many cotton germplasm resources remain unclear. Whether there is a real impact on their functions and to what extent, many have not been verified. By incorporating eQTL and GWAS analyses and running them again under different developmental stages and environmental backgrounds, more regulatory factors may be unearthed. At the same time, it is also necessary to clarify the relationship between the changes in the promoter sequence and the binding of transcription factors as well as epigenetic modifications. If this step is not thoroughly understood, the regulatory network will remain a "black box". However, on the other hand, tools like CRISPR/Cas do offer an idea - since there is a way to precisely rewrite the promoter, it might indeed be possible to customize alleles with "novel expression patterns" in the future.

Of course, challenges are not absent. Whether promoter variations can be stably inherited and whether they will definitely lead to good outcomes still need to be verified in practice. The multi-gene control and environmental dependence already make stress resistance "elusive". You may move one site, and the result will be a domino effect. Not to mention the difficulties such as the transformation efficiency, expression fluctuations, and network interaction of the promoter sub-project, which are all realistic problems right before us. However, as long as the ideas can be integrated with tools such as precision breeding, rapid breeding, and molecular markers, the breeding efficiency and the implementation speed of stress-resistant varieties are likely to increase significantly. Today, with the increasing pressure of climate change, this path is worth continuing down.

Acknowledgments

We would like to express our gratitude to the reviewers for their valuable feedback, which helped improve the manuscript.

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.

References

- Bansal M., Kumar A., and Yella V., 2014, Role of DNA sequence based structural features of promoters in transcription initiation and gene expression, *Current Opinion in Structural Biology*, 25(1): 77-85.
<https://doi.org/10.1016/j.sbi.2014.01.007>
- Bao Y., Mei Y., Xu X., Liu Y., and Wu Z., 2020, Changes in the promoter of a defender against apoptotic cell death gene affect its expression in upland cotton, *Journal of Systematics and Evolution*, 59(5): 1018-1026.
<https://doi.org/10.1111/jse.12569>
- Cai Y., Kallam K., Tidd H., Gendarini G., Salzman A., and Patron N., 2020, Rational design of minimal synthetic promoters for plants, *Nucleic Acids Research*, 48(21): 11845-11856.
<https://doi.org/10.1101/2020.05.14.095406>
- Deep A., and Pandey D., 2024, Genome-wide analysis of VILLIN gene family associated with stress responses in cotton (*Gossypium* spp.), *Current Issues in Molecular Biology*, 46(3): 2278-2300.
<https://doi.org/10.3390/cimb46030146>
- Fang H., Gao X., Wu Y., Zhang K., Wu Y., Li J., Qian D., Li R., Gu H., Mehari T., Shen X., and Wang B., 2025, Unveiling the role of *GhP5CS1* in cotton salt stress tolerance: a comprehensive genomic and functional analysis of *P5CS* genes, *Plants*, 14(2): 231.
<https://doi.org/10.3390/plants14020231>
- Gu H., Zhao Z., Wei Y., Li P., Lu Q., Liu Y., Wang T., Hu N., Wan S., Zhang B., Hu S., and Peng R., 2023, Genome-wide identification and functional analysis of *RF2* gene family and the critical role of *GhRF2-32* in response to drought stress in cotton, *Plants*, 12(14): 2613.
<https://doi.org/10.3390/plants12142613>
- Guo X., Ullah A., Siuta D., Kukfisz B., and Iqbal S., 2022, Role of WRKY transcription factors in regulation of abiotic stress responses in cotton, *Life*, 12(9): 1410.
<https://doi.org/10.3390/life12091410>
- Guo Y., Chen Q., Qu Y., Deng X., Zheng K., Wang N., Shi J., Zhang Y., Chen Q., and Yan G., 2023, Development and identification of molecular markers of GhHSP70-26 related to heat tolerance in cotton, *Gene*, 874: 147486.
<https://doi.org/10.1016/j.gene.2023.147486>
- Hamid R., Jacob F., Ghorbanzadeh Z., Nekouei M., Zeinalabedini M., Mardi M., Sadeghi A., Kumar S., and Ghaffari M., 2024, Genomic insights into CKX genes: key players in cotton fibre development and abiotic stress responses, *PeerJ*, 12: e17462.
<https://doi.org/10.7717/peerj.17462>
- Héberlé É. and Bardet A., 2019, Sensitivity of transcription factors to DNA methylation, *Essays in Biochemistry*, 63(6): 727-741.
<https://doi.org/10.1042/EBC20190033>
- Khan Z., Khan S., Ahmed A., Iqbal M., Mubarik M., Ghouri M., Ahmad F., Yaseen S., Ali Z., Khan A., and Azhar M., 2023, Genome editing in cotton: challenges and opportunities, *Journal of Cotton Research*, 6(1): 3.
<https://doi.org/10.1186/s42397-023-00140-3>
- Kilwake J., Umer M., Wei Y., Mehari T., Magwanga R., Xu Y., Hou Y., Wang Y., Shiraku M., Kirungu J., Cai X., Zhou Z., Peng R., and Liu F., 2023, Genome-wide characterization of the SAMS gene family in cotton unveils the putative role of *GhSAMS2* in enhancing abiotic stress tolerance, *Agronomy*, 13(2): 612.
<https://doi.org/10.3390/agronomy13020612>
- Kummari D., Kummari D., Palakolanu S., Kishor P., Bhatnagar-Mathur P., Singam P., Vadez V., and Sharma K., 2020, An update and perspectives on the use of promoters in plant genetic engineering, *Journal of Biosciences*, 45(1): 119.
<https://doi.org/10.1007/s12038-020-00087-6>
- Li H., Liu L., Kong X., Wang X., Si A., Zhao F., Huang Q., Yu Y., and Chen Z., 2025, Time- course transcriptomics analysis reveals molecular mechanisms of salt- tolerant and salt- sensitive cotton cultivars in response to salt stress, *International Journal of Molecular Sciences*, 26(1): 329.
<https://doi.org/10.3390/ijms26010329>
- 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>
- Mahmood T., Khalid S., Abdullah M., Ahmed Z., Shah M., Ghafoor A., and Du X., 2019, Insights into drought stress signaling in plants and the molecular genetic basis of cotton drought tolerance, *Cells*, 9(1): 105.
<https://doi.org/10.3390/cells9010105>
- Naresh R., Srivastava R., Gunapati S., Sane A., and Sane V., 2024, Functional characterization of *GhNAC2* promoter conferring hormone- and stress- induced expression: a potential tool to improve growth and stress tolerance in cotton, *Physiology and Molecular Biology of Plants*, 30(1): 17-32.
<https://doi.org/10.1007/s12298-024-01411-2>
- Shaban M., Ahmed M., Sun H., Ullah A., and Zhu L., 2018, Genome- wide identification of lipoxygenase gene family in cotton and functional characterization in response to abiotic stresses, *BMC Genomics*, 19(1): 599.
<https://doi.org/10.1186/s12864-018-4985-2>
- Shan Y., Zhao P., Liu Z., Li F., and Tian X., 2019, An isopentyl transferase gene driven by the senescence- inducible *SAG12* promoter improves salinity stress tolerance in cotton, *Journal of Cotton Research*, 2(1): 15.
<https://doi.org/10.1186/s42397-019-0032-3>

- Sheri V., Mohan H., Jogam P., Alok A., Rohela G., and Zhang B., 2025, CRISPR/Cas genome editing for cotton precision breeding: mechanisms, advances, and prospects, *Journal of Cotton Research*, 8(1): 4.
<https://doi.org/10.1186/s42397-024-00206-w>
- Shi L., Su J., Cho M., Song H., Dong X., Liang Y., and Zhang Z., 2023, Promoter editing for the genetic improvement of crops, *Journal of Experimental Botany*, 74(15): 4349-4366.
<https://doi.org/10.1093/jxb/erad175>
- Sun H., Hu M., Li J., Chen L., Li M., Zhang S., Zhang X., and Yang X., 2018, Comprehensive analysis of NAC transcription factors uncovers their roles during fiber development and stress response in cotton, *BMC Plant Biology*, 18(1): 150.
<https://doi.org/10.1186/s12870-018-1367-5>
- Tang R., Zhou X., Weng S., Wang F., Li R., Xie Q., Li Z., Xie S., Cao A., Zhuo L., Wang M., and Li H., 2024, Genome-wide analysis of GLK gene family in four cotton species provides insights into their involvement in cotton abiotic stress response, *Agriculture*, 14(11): 2086.
<https://doi.org/10.3390/agriculture14112086>
- Wang J.M., and Zhang J., 2024, Assessing the impact of various cotton diseases on fiber quality and production, *Field Crop*, 7(4): 212-221.
<https://doi.org/10.5376/fc.2024.07.0021>
- Wang M., Wang L., Yu X., Zhao J., Tian Z., Liu X., Wang G., Zhang L., and Guo X., 2023, Enhancing cold and drought tolerance in cotton: a protective role of *SikCOR413PM1*, *BMC Plant Biology*, 23(1): 577.
<https://doi.org/10.1186/s12870-023-04572-6>
- Wang N., Xu S., Sun Y., Liu D., Zhou L., Li Y., and Li X., 2019, The cotton WRKY transcription factor (GhWRKY33) reduces transgenic Arabidopsis resistance to drought stress, *Scientific Reports*, 9(1): 724.
<https://doi.org/10.1038/s41598-018-37035-2>
- Wang Z., Peng Z., Khan S., Qayyum A., Rehman A., and Du X., 2024, Unveiling the power of MYB transcription factors: master regulators of multi-stress responses and development in cotton, *International Journal of Biological Macromolecules*, 276: 133885.
<https://doi.org/10.1016/j.ijbiomac.2024.133885>
- Zafar M., Rehman A., Razzaq A., Parvaiz A., Mustafa G., Sharif F., Mo H., Youlu Y., Shakeel A., and Ren M., 2022, Genome-wide characterization and expression analysis of *Erf* gene family in cotton, *BMC Plant Biology*, 22(1): 134.
<https://doi.org/10.1186/s12870-022-03521-z>
- Zhang J., Feng J., Liu W., Ren Z., Zhao J., Pei X., Liu Y., Yang D., and Ma X., 2020, Characterization and stress response of the JmjC domain-containing histone demethylase gene family in the allotetraploid cotton species *Gossypium hirsutum*, *Plants*, 9(11): 1617.
<https://doi.org/10.3390/plants9111617>
- Zhao J., Peng S., Cui H., Li P., Li T., Liu L., Zhang H., Tian Z., Shang H., and Xu R., 2022, Dynamic expression, differential regulation and functional diversity of the CNGC family genes in cotton, *International Journal of Molecular Sciences*, 23(4): 2041.
<https://doi.org/10.3390/ijms23042041>
- Zheng J., Zhang Z., Zhang N., Liang Y., Gong Z., Wang J., Ditta A., Sang Z., Wang J., and Li X., 2024, Identification and function analysis of GABA branch three gene families in the cotton related to abiotic stresses, *BMC Plant Biology*, 24(1): 57.
<https://doi.org/10.1186/s12870-024-04738-w>

**Disclaimer/Publisher's Note**

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.