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Genome-Wide Identification of WRKY Transcription Factors in Chickpea and Their Roles in Stress Responses

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Abstract WRKY transcription factors play pivotal roles in regulating plant responses to various biotic and abiotic stresses. In this study, a comprehensive genome-wide identification and analysis of WRKY transcription factors were conducted in *Cicer arietinum* (chickpea), a key legume crop with growing importance in stress biology. Using advanced bioinformatics tools, we identified and annotated the complete set of *WRKY* genes in the chickpea genome, classifying them into groups I, II, and III based on conserved domains and structural features. The chromosomal distribution, gene structures, and phylogenetic relationships were analyzed to provide insights into their evolutionary patterns. Expression profiling under drought, salinity, and pathogen stress conditions (e.g., Fusarium and Ascochyta) revealed several stress-responsive *WRKY* genes with distinct tissue-specific and developmental expression patterns. We further explored their regulatory networks, including interactions with key signaling molecules (ABA, JA, SA) and crosstalk with other transcription factor families. A detailed case study highlighted the role of selected *WRKY* genes in drought tolerance, supported by phenotypic assessments under water-deficit conditions. Functional validation through overexpression, gene silencing, and omics approaches-such as transcriptomics and CRISPR/Cas-based editing-provided strong evidence for the functional roles of specific *WRKY* genes. This study underscores the significance of WRKY transcription factors in stress adaptation and sets the foundation for their application in marker-assisted selection and breeding of stress-resilient chickpea varieties.

Keywords Chickpea (*Cicer arietinum*); WRKY transcription factors; Abiotic and biotic stress; Gene expression profiling; Functional genomics

1 Introduction

Chickpeas (*Cicer arietinum* L.) are not unfamiliar on people's dining tables, especially today when nutritional intake and food security are increasingly valued. This leguminous plant is not only rich in protein and minerals, but also thrives well in arid and semi-arid regions, which has drawn it worldwide attention. However, everything has two sides. Despite its drought resistance and strong adaptability, in actual production, it still frequently encounters challenges such as drought, saline-alkali land and diseases, and the problem of unstable yield has never been well solved.

In fact, chickpeas are not only food crops; their value in scientific research is also constantly rising. As a "model student" among leguminous plants, it has been widely used to study the coping mechanisms of plants under adverse conditions. Especially in recent years, with the development of genomic and transcriptomic technologies, scientists have been able to identify a number of genes related to stress response, and the WRKY transcription factor is one of the more notable ones (Kumar et al., 2016).

When it comes to transcription factors (TFS), they are almost ubiquitous in plants, just like sound engineers, controlling the "switches" of different genes. Among them, the WRKY family stands out particularly among plants due to its conservative WRKY domain and zinc finger domain. They have a distinct feature, that is, they can bind to the W-box element in the promoter of the target gene, thereby regulating those downstream genes related to plant development and stress response (Jiang et al., 2017; Cheng et al., 2021; Ma and Hu, 2024; Wang et al., 2024). However, this combination is not always an "activating" effect; it could also be an "inhibitory" one.

One core feature of WRKY transcription factors is that the networks they are involved in are very complex, and they play a versatile role in regulating plants' responses to environmental stresses such as pathogen invasion, drought, salinity and temperature. They can both regulate upwards and downwards. This "bidirectional regulation" enables them to play a key role in plants' adaptation to environmental changes (Wani et al., 2021). In chickpeas, some *WRKY* genes exhibit different expression patterns when exposed to various adverse conditions, which further confirms their significance in adverse adaptation (Mashaki et al., 2019).

Based on these backgrounds, we conducted this study. The aim was not to provide a general overview but to systematically sort out the genome-wide characteristics of the WRKY family members in chickpeas, including their structure, evolutionary relationships, and expression traits. In addition, we also attempted to delve into the functions of several key WRKY members in actual stress responses, hoping to provide some valuable ideas for subsequent molecular improvement breeding.

2 Structural and Functional Classification of Chickpea *WRKY* Genes

2.1 Domain architecture and WRKY motifs (WRKYGQK)

The name "WRKY" comes from a very short but crucial heptapeptide sequence - WRKYGQK. This small motif remains almost unchanged in all chickpea WRKY transcription factors, with only a very few cases showing variations (Kumar et al., 2016). This is not surprising, as it is the key to their ability to combine with DNA. This WRKY motif does not exist in isolation; it usually appears together with a zinc finger structure, and this combination enhances the binding stability of proteins and DNA. In addition, in the analysis of the chickpea WRKY protein, some other conserved motifs were also discovered, but these structures are often specific to the groups. This might also explain why the functions of the WRKY family are so diverse.

2.2 Classification into groups (I, II, III) based on structural features

To group members of the WRKY family, there are actually two main considerations: one is how many WRKY domains they have, and the other is which type the zinc finger motif belongs to. According to this standard, the *WRKY* gene of chickpeas is divided into three groups: I, II and III. Among them, Group I is rather special, featuring two WRKY domains and one C2H2-type zinc finger. Group II has only one WRKY region, which is also of the C2H2 type, but it is further subdivided into several subgroups from IIa to IIe. Group III, on the other hand, had a C2HC-type zinc finger, which was a unique feature of theirs (Waqas et al., 2019). This classification is not merely a formal difference; to some extent, it also reflects the variations in the evolutionary paths and functional directions of these proteins (Figure 1).

2.3 DNA-binding properties and target W-box elements

What exactly is the role of the WRKY protein? Simply put, their most core function is to recognize and bind to certain specific DNA sequences, such as the W-box in the promoter region of the target gene (the core sequence is usually TTGACC/T). The WRKYGQK motif here is the key to determining their recognition ability. Experiments have confirmed that proteins like CaWRKY50 can move into the cell nucleus, precisely lock onto and bind to the W-box, thereby activating or inhibiting some genes involved in the stress response (Kumar et al., 2016). Not only that, structural simulations and molecular dynamics studies also show that this combination not only has strong specificity but also good stability. Moreover, several amino acid residues that play a key role have also been identified (Konda et al., 2018).

3 Genome-Wide Identification and Annotation of *WRKY* Genes in Chickpea

3.1 Bioinformatics tools used for *WRKY* gene identification

It is not easy to find these *WRKY* genes from the very beginning. Researchers usually have to start with existing public databases, such as iTAK. With the help of these platforms, they then use a complete set of bioinformatics tools to conduct subsequent identification and analysis - including finding sequences, extracting motifs, predicting gene structures, etc. For instance, MEME Suite is used to discover conserved motifs, GSDS is a common tool for analyzing exon and intron structures, while tools like MEGA and MUSCLE are employed for sequence alignment and the establishment of phylogenetic trees. Although this process sounds standard, there may still be steps in the

middle that require manual verification. For instance, for some gene loci with ambiguous boundaries, further positioning needs to be done in combination with genomic annotation information.

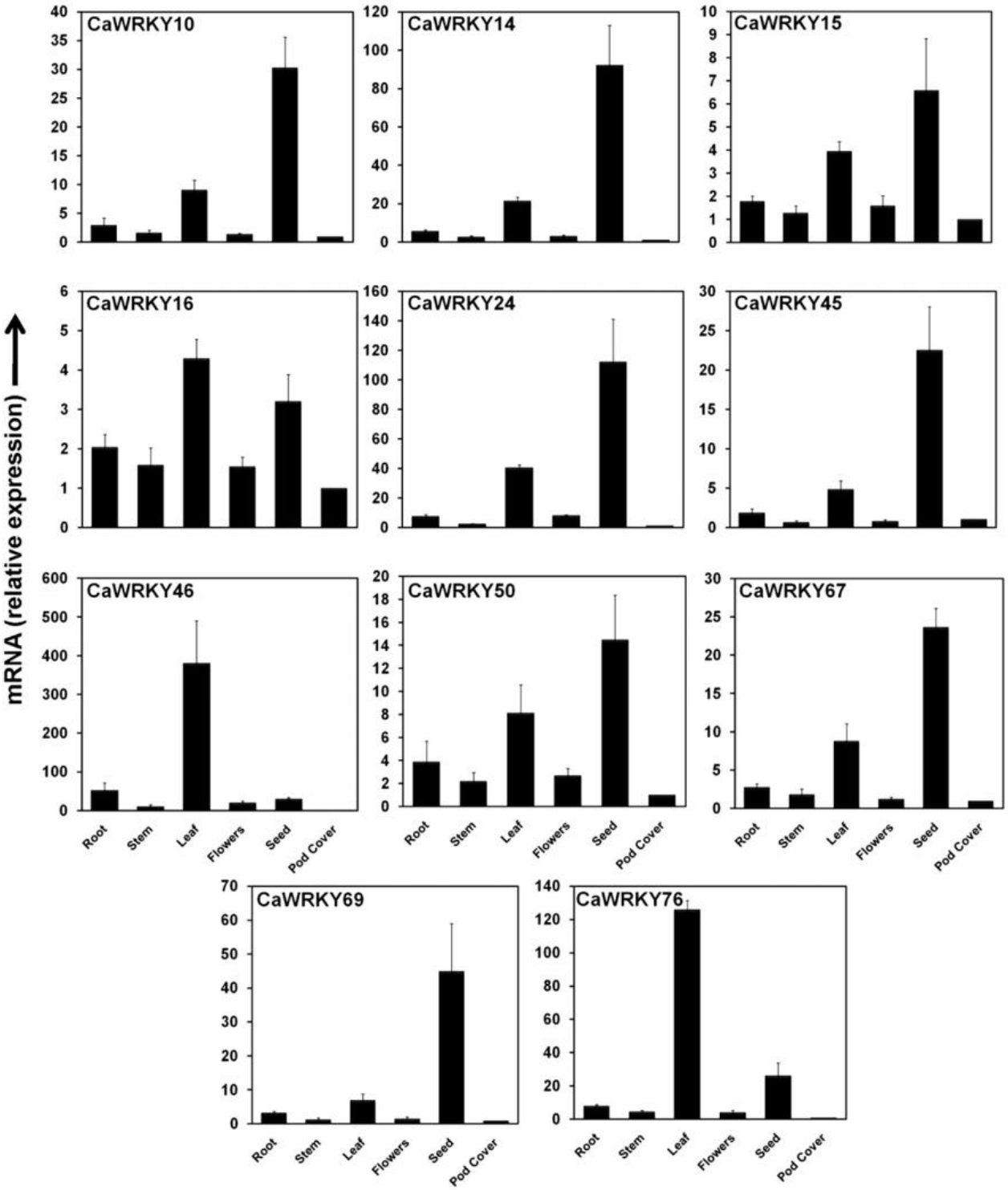

Figure 1 Expression analysis of group-III WRKY genes in different tissues of C. arietinum. The samples of chickpea were collected from 4-week-old plants for the root, stem, and leaf tissues. Bloomed flowers were sampled at reproductive stage while pod cover and seeds were collected at the same time points. The mRNA level expression was analysed by qRT-PCR using chickpea β-tubulin gene as internal control. The relative mRNA level was calculated with respect to the pod cover. The results presented here were obtained from three biological replicates with three technical replicates each. The error bars represent ±SD of means (Adopted from Kumar et al., 2016)

3.2 Genomic distribution and chromosomal localization

How are these *WRKY* genes distributed on the chromosomes of chickpeas? According to current research, the number is approximately between 61 and 78, and the results of different analyses vary slightly. For instance, a study analyzed 70 non-redundant *WRKY* genes and found that they were distributed on almost all chromosomes except chromosome 8 (Shende et al., 2021). This distribution is not concentrated and clustered but rather scattered, indicating that the *WRKY* gene is widely distributed throughout the genome. Another interesting finding is that during the amplification of the WRKY gene family, fragment repeats play a more significant role, while tandem repeats are less common.

3.3 Gene structure analysis and phylogenetic relationships

The structures of different *WRKY* genes actually vary significantly. Some contain 2 to 7 introns, while a very few even have no introns at all. From the structural analysis, it can be seen that in addition to the WRKY conserved structural domain, there are also some group-specific motifs, which provide clues for their functional differentiation. After the evolutionary tree was constructed, the researchers classified these WRKY proteins into three major categories (I, II, III) and their further subcategories, in a classification manner similar to that of other plants. More importantly, this phylogenetic relationship not only helps clarify the evolutionary origins among genes, but also indicates that these genes have been subjected to certain purification selection pressure during amplification, especially those collateral homologous genes.

4 *WRKY* Gene Expression in Chickpea under Abiotic and Biotic Stresses

4.1 *WRKY* gene expression in response to drought and salinity

In dry or saline-alkali environments, chickpeas do not completely "silence", and the WRKY transcription factor in their bodies is often rapidly activated. According to the results of transcriptome and whole-genome analysis, many WRKY members show upregulated expression in roots and stems, not only during drought but also under cold stress. However, the expression differences among different genotypes are still quite obvious. Under extreme drought conditions, the expression of the *WRKY* gene in drought-tolerant strains is often more intense, while in sensitive strains, although it is also upregulated, the extent is not as high. This implies a possibility: WRKY is very likely involved in the regulatory pathway that enhances the stress resistance of chickpeas. Of course, one point cannot be overlooked - not all members of WRKY were involved, and some members hardly changed under such coercion.

4.2 Role in pathogen defense (e.g., Fusarium, Ascochyta)

It's not only environmental stress that triggers WRKY's response; when pathogenic bacteria come, they will also "step in". For instance, when chickpeas are attacked by *Fusarium acuminatum* or Trichospora, studies have found that the expression of many *WRKY* genes changes significantly, especially between disease-resistant and susceptible strains. Some members, like WRKY40, were significantly induced in resistant varieties, and its increased expression was usually accompanied by enhanced disease resistance (Chakraborty et al., 2018). In addition, some studies have focused on epigenetic regulatory mechanisms such as histone acetylation in the promoter region and found that they are also involved in the regulatory process of WRKY. More interestingly, when the *WRKY* gene of these chickpeas was transferred into model plants, the antibacterial ability of those plants was also enhanced (Priyadarshini et al., 2023). From this perspective, WRKY is not "fighting alone"; they might be an indispensable part of the pathogen defense system.

4.3 Tissue-specific and developmental expression patterns

The *WRKY* gene is not expressed everywhere and functions at any time in chickpeas. Their "switches" are often linked to tissue type or developmental stage. Some are only active in the roots, while others are expressed only in the stems or specific leaf tissues. What is more complex is that some WRKY proteins exhibit similar expression profiles under various stress scenarios, suggesting that they may be involved in relatively universal response mechanisms. In contrast, there are also some that will only be activated under specific coercion. Such a "dual control of time and space" model enables chickpeas to flexibly respond to changes in the external environment, avoiding treating all stimuli equally and wasting resources.

5 Regulatory Networks and Downstream Targets of WRKY Transcription Factors in Chickpea

5.1 Interaction with signaling molecules (ABA, JA, SA)

The *WRKY* gene is indeed very active in the regulation of adverse signals, but their "selectivity" is also worth noting. Take CaWRKY70 as an example. It binds to the promoters of salicylic acid (SA) signal-related genes, such as *NPR1*, *PR2*, *PR10*, etc., thereby influencing the immune response and systemic acquired resistance (SAR) of plants. However, it's not the case that the more the better. Experiments have found that once CaWRKY70 is overexpressed, it will instead inhibit the endogenous SA level and the expression of its response genes, resulting in a decline in the plant's resistance to Fusarium. Another case is WRKY40, whose promoter is activated during jasmonic acid (JA) treatment and pathogen infection, but remains indifferent under SA induction (Li et al., 2024). This indicates that WRKY's hormonal response has a distinct "preference" and does not consume all signaling pathways.

5.2 Crosstalk with other transcription factor families

It is not entirely accurate to say that WRKY is the core regulator. Often, they are more like a "node" in the network, working together with other families of transcription factors. For instance, they will interact with families such as ERF, MYB, NAC, and bZIP. CaWRKY70 and CaWRKY54 have been found to jointly participate in regulating defense and stress pathways, sometimes cooperating and sometimes checking and balancing each other. More interestingly, CaWRKY70 can also suppress the CaMPK9-CaWRKY40 signal path, demonstrating the role of an "intervener" (Phukan et al., 2016; Rai et al., 2024). This complex relationship where you are in me and I am in you might precisely be the key for plants to strike a balance between growth and defense.

5.3 Regulation of stress-responsive gene cascades

WRKY's participation in defense responses relies not on single-point output but on a complete set of "cascading mechanisms". They can recognize W-box elements, thereby regulating a whole set of downstream stress-related genes. In chickpeas, WRKY members such as Ca-08086 have been found to co-express with some key gene modules, which are involved in typical defense responses such as callose deposition and chitin induction. More interestingly, these networks exhibit distinct activation states across different chickpea genotypes (disease resistance vs. susceptibility) (Chakraborty et al., 2019; Konda et al., 2019). This not only indicates the significance of WRKY, but also reflects their "differentiated" strategies in regulatory directions, with some activating and others inhibiting.

6 Case Study: *WRKY* Gene Involvement in Drought Stress Tolerance in Chickpea

6.1 Selection and characterization of drought-responsive *WRKY* genes

Not all stress response genes are significantly expressed under drought conditions, but WRKY transcription factors are often the most active among them. Through the joint analysis of whole-genome and transcriptome data, researchers found that WRKY was upregulated in different genotypes, but to varying degrees. Especially when water is severely scarce, the expression of WRKY in drought-tolerant chickpeas is often more intense, while that in drought-tolerant ones is relatively lower (Kumar et al., 2019; Waqas et al., 2019). This difference is not accidental. Multiple RNA sequencing and qPCR studies have shown that those *WRKY* genes with high expression levels are likely to be associated with enhanced drought resistance. Although other transcription factors are also involved in regulation, such as bZIP or MYB, WRKY is often among the first to be upregulated in the early stages of drought stress.

6.2 Experimental setup and phenotypic observations under water deficit

To verify the functions of these genes, the experimental design must be close to real drought scenarios. The common practice is to select two strains, drought-tolerant and drought-tolerant, and create a water-deficient environment by treating with polyethylene glycol or cutting off water supply. The monitoring of gene expression is carried out at multiple time points, mainly using semi-quantitative or real-time PCR techniques. In terms of appearance, drought-resistant varieties are more "resilient" during stress - they are less likely to wilt and recover

quickly after rewatering. And such phenotypic changes are often associated with the high expression of WRKY. Interestingly, some non-Wrky stress genes are also up-regulated, but their changes do not seem as stable or significant as those of WRKY (Borhani et al., 2019).

6.3 Implications for chickpea improvement through *WRKY* gene manipulation

Not every gene is suitable for breeding targets, but WRKY is clearly an exception. With the support of expression data and the results of functional verification, such genes naturally become the key focus of molecular breeding. Regulating the expression of WRKY through genetic modification, gene editing or traditional molecular marker breeding methods has been proposed as a feasible strategy to enhance the drought resistance of chickpeas. Especially if the expression profile information of WRKY can be integrated into the breeding process, it may not be far off to select and breed new germplasms adapted to arid regions (Figure 2) (Sen et al., 2017). Of course, all of this still needs to be based on a deeper understanding of the regulatory mechanism of the *WRKY* gene.

7 Functional Validation through Transgenic and Omics Approaches

7.1 Overexpression and silencing studies in model plants

To verify the function of the *WRKY* gene, it is not necessary to start with the chickpeas themselves. Often, researchers will first conduct overexpression or silencing experiments using model plants such as tobacco. For instance, after CaWRKY50 was overexpressed in tobacco, the plants showed signs of early flowering and accelerated senescence. This indicates that it not only participates in the response to adverse conditions but is also related to the growth and development of plants. Similarly, once CaWRKY70 is overexpressed in chickpeas, it supposes the salicylic acid pathway and multiple defense responses, resulting in the plants being more susceptible to Fusarium infection. But things are not black and white. For instance, when researchers silenced the downstream gene *CaHDZ12*, the plants became more vulnerable to drought and salt. Although such experiments ostensibly only regulate the expression of a few genes, they actually reveal the key position of WRKY in the adversity regulatory network (Chakraborty et al., 2020).

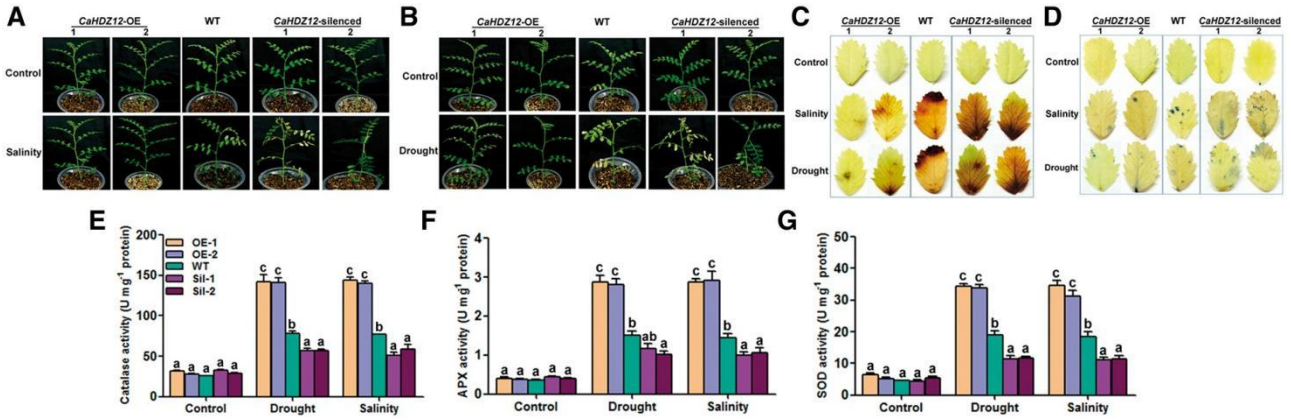

Figure 2 Functional characterization of CaHDZ12 transformed chickpea plants under salt and drought stresses. (A & B) Phenotype of control, CaHDZ12-OE and CaHDZ12-silenced chickpea plants treated with 200 mM NaCl (salinity) or kept for 10 days without water (drought). (C) DAB staining represents the extent of H_2O_2 production in CaHDZ12-OE and silenced plants under above mentioned conditions. (D) NBT staining represents the extent of formation in CaHDZ12-OE and silenced plants under above-mentioned conditions. (E) Analysis of antioxidant enzyme activities (CAT, SOD, APX) in CaHDZ12-OE and silenced plants before and after stress treatments. Data are means ± SEM from three biological replicates. Significant difference of transformed plants compared with WT plants is done by one way ANOVA using Duncan's multiple range test (DMRT); significance level indicates $P < 0.05$ (Adopted from Sen et al., 2017)

7.2 Transcriptomics and proteomics-based validation

Not all gene functions can be verified by transgenic methods, and omics technology offers another approach in this regard. Transcriptome data, especially the expression profiles under abiotic and biological stresses, reveal which *WRKY* genes are involved in the stress response of plants. Among them, some WRKY are frequent visitors who exhibit differential expression under multiple stressful conditions. After further analysis through the

co-expression network, it is also possible to identify which gene modules they jointly respond to stress with. Although this approach cannot directly state "who regulates whom", it can help depict an overall picture. In contrast, proteomics is not as widely used, but it can bridge the gap between the transcriptional level and the protein level, verifying whether the WRKY protein is truly translated and participates in the reaction (Roorkiwal et al., 2020; Naqvi et al., 2024).

7.3 Gene editing tools (e.g., CRISPR/Cas) in WRKY functional analysis

The emergence of CRISPR/Cas9 has brought the functional research of WRKY into an era of "precise operation". Although there haven't been many research cases of directly editing WRKY with CRISPR on chickpeas yet, the application of this technology in other crops is already quite mature, including regulating stress-resistant genes and improving agronomic traits, etc. If the editing advantages of CRISPR are combined with transcriptome or proteome data, it is theoretically possible to lock onto target genes more quickly and achieve targeted modification. That is to say, in the future, to improve the stress resistance of chickpeas, CRISPR may not be absent (Razzaq et al., 2021).

8 Future Directions and Applications of *WRKY* Genes in Chickpea Breeding

8.1 Potential of WRKYs in marker-assisted selection (MAS)

Not all transcription factors are suitable as breeding markers, but WRKY is an exception, especially those that stand out in terms of disease resistance and stress tolerance. Like WRKY40, it was once positioned in important areas related to heat resistance and wilt disease resistance. These loci were not guessed out of thin air but were confirmed step by step through GWAS, QTL analysis and transcriptome data (Priyadarshini et al., 2023). All these pieces of evidence combined make WRKY a highly credible candidate for MAS. Under other environmental conditions such as salt stress, EST-SSR molecular markers related to WRKY have also been developed, which further indicates their usability in molecular breeding (Tarinejad et al., 2024). Of course, some members of the WRKY family may not be so "useful", which requires more meticulous screening.

8.2 Integration into stress-resilient chickpea breeding programs

To truly utilize these genetic markers, a systematic breeding process is needed in coordination. Nowadays, multi-omics technology is developing rapidly, and many studies have begun to attempt to apply WRKY linkage markers to actual breeding. For instance, in high-temperature or severe wilt environments, previous studies have cultivated chickpea strains with better performance through marker-assisted backcrossing and genomic selection (Mohanty et al., 2024; Soorni et al., 2025). However, this plan is not universally applicable. The performance of some varieties in specific regions still needs to be verified. However, the overall trend is clear - WRKY is gradually transforming from a research subject in the laboratory to a practical tool that can be used in the field.

8.3 Challenges and prospects in translating genomics to field application

Ultimately, transforming genomic data into actual agronomic traits is no easy task. Although the *WRKY* gene seems "versatile", their regulatory networks are often complex, involving multiple pathways. The upregulation of one gene may both enhance resistance and bring about negative growth effects. Moreover, the field environment itself is highly variable, and the interaction between genes and the environment can easily mask the original expression trend. In addition, the promotion of genetically modified crops is still subject to regulatory restrictions in many regions. However, with the emergence of CRISPR/Cas9, high-throughput phenotypic platforms, and more systematic field validation methods, these challenges are no longer insurmountable obstacles (Javed and Gao, 2023). With these technologies as support, the practical application prospects of the *WRKY* gene are actually closer to reality than ever before.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Borhani S., Vessal S., Bagheri A., and Shokouhifar F., 2019, Differential gene expression pattern of drought responsive transcription factors in chickpea: an expressional analysis, Journal of Plant Growth Regulation, 39: 1211-1220.
https://doi.org/10.1007/s00344-019-10056-5

Chakraborty J., Ghosh P., Sen S., and Das S., 2018, Epigenetic and transcriptional control of chickpea WRKY40 promoter activity under *Fusarium* stress and its heterologous expression in *Arabidopsis* leads to enhanced resistance against bacterial pathogen, Plant Science, 276: 250-267.
https://doi.org/10.1016/j.plantsci.2018.07.014

Chakraborty J., Ghosh P., Sen S., Nandi A., and Das S., 2019, CaMPK9 increases the stability of CaWRKY40 transcription factor which triggers defense response in chickpea upon *Fusarium oxysporum* f. sp. *ciceri* Race1 infection, Plant Molecular Biology, 100: 411-431.
https://doi.org/10.1007/s11103-019-00868-0

Chakraborty J., Sen S., Ghosh P., Jain A., and Das S., 2020, Inhibition of multiple defense responsive pathways by CaWRKY70 transcription factor promotes susceptibility in chickpea under *Fusarium oxysporum* stress condition, BMC Plant Biology, 20: 319.
https://doi.org/10.1186/s12870-020-02527-9

Cheng Z., Luan Y., Meng J., Sun J., Tao J., and Zhao D., 2021, WRKY transcription factor response to high-temperature stress, Plants, 10(10): 2211.
https://doi.org/10.3390/plants10102211

Javed T., and Gao S., 2023, WRKY transcription factors in plant defense, Trends in Genetics, 39(10): 787-801.
https://doi.org/10.1016/j.tig.2023.07.001

Jiang J., Ma S., Ye N., Jiang M., Cao J., and Zhang J., 2017, WRKY transcription factors in plant responses to stresses, Journal of Integrative Plant Biology, 59(2): 86-101.
https://doi.org/10.1111/jipb.12513

Konda A., Farmer R., Soren K., P.S., S., and Setti A., 2018, Structural modelling and molecular dynamics of a multi-stress responsive WRKY TF-DNA complex towards elucidating its role in stress signalling mechanisms in chickpea, Journal of Biomolecular Structure and Dynamics, 36: 2279-2291.
https://doi.org/10.1080/07391102.2017.1349690

Konda A., Sabale P., Soren K., Subramaniam S., Singh P., Rathod S., Chaturvedi S., and Singh N., 2019, Systems biology approaches reveal a multi-stress responsive WRKY transcription factor and stress associated gene co-expression networks in chickpea, Current Bioinformatics, 14(7): 591-601.
https://doi.org/10.2174/1574893614666190204152500

Kudapa H., Barmukh R., Garg V., Chitikineni A., Samineni S., Agarwal G., and Varshney R., 2023, Comprehensive transcriptome profiling uncovers molecular mechanisms and potential candidate genes associated with heat stress response in chickpea, International Journal of Molecular Sciences, 24(2): 1369.
https://doi.org/10.3390/ijms24021369

Kumar K., Srivastava V., Purayannur S., Kaladhar V., Cheruvu P., and Verma P., 2016, WRKY domain-encoding genes of a crop legume chickpea (*Cicer arietinum*): comparative analysis with *Medicago truncatula* WRKY family and characterization of group-III gene(s), DNA Research, 23: 225-239.
https://doi.org/10.1093/dnares/dsw010

Kumar M., Chauhan A., Yusuf M., Sanyal I., and Chauhan P., 2019, Transcriptome sequencing of chickpea (*Cicer arietinum* L.) genotypes for identification of drought-responsive genes under drought stress condition, Plant Molecular Biology Reporter, 37: 186-203.
https://doi.org/10.1007/s11105-019-01147-4

Li S., Khoso M., Wu J., Yu B., Wagan S., and Liu L., 2024, Exploring the mechanisms of WRKY transcription factors and regulated pathways in response to abiotic stress, Plant Stress, 12: 100429.
https://doi.org/10.1016/j.stress.2024.100429

Ma Z., and Hu L., 2024, WRKY transcription factor responses and tolerance to abiotic stresses in plants, International Journal of Molecular Sciences, 25(13): 6845.
https://doi.org/10.3390/ijms25136845

Mashaki K., Ghomi A., Nezhad K., Yamchi A., Soltanloo H., Thudi M., and Varshney R., 2019, Transcription factors evaluation in a transcriptome analysis on chickpea (*Cicer arietinum* L.) under drought stress, Journal of Crop Breeding, 11(30): 133-141.
https://doi.org/10.29252/jcb.11.30.133

Mohanty J., Yadav A., Narnoliya L., Thakro V., Nayyar H., Dixit G., Jha U., Prasad P., Agarwal P., and Parida S., 2024, A next-generation combinatorial genomic strategy scans genomic loci governing heat stress tolerance in chickpea, Plant, Cell & Environment, 48(4): 2706-2726.
https://doi.org/10.1111/pce.15186

Naqvi R., Mahmood M., Mansoor S., Amin I., and Asif M., 2024, Omics-driven exploration and mining of key functional genes for the improvement of food and fiber crops, Frontiers in Plant Science, 14: 1273859.
https://doi.org/10.3389/fpls.2023.1273859

Phukan U., Jeena G., and Shukla R., 2016, WRKY transcription factors: molecular regulation and stress responses in plants, Frontiers in Plant Science, 7: 760.
https://doi.org/10.3389/fpls.2016.00760

Priyadarshini P., Sahu S., Kalwan G., Yadava Y., Nagar R., Rai V., Bharadwaj C., Gaikwad K., and Jain P., 2023, Unravelling the mechanism of Fusarium wilt resistance in chickpea seedlings using biochemical studies and expression analysis of *NBS-LRR* and *WRKY* genes, Physiological and Molecular Plant Pathology, 124: 101958.
https://doi.org/10.1016/j.pmpp.2023.101958

Rai N., Sarma B., and Rai S., 2024, Transcriptional regulation of biotic and abiotic stress responses: challenges and potential mechanism for stress tolerance and chickpea improvement, Tropical Plant Biology, 17: 83-107.
https://doi.org/10.1007/s12042-024-09354-4

Razzaq M., Aleem M., Mansoor S., Khan M., Rauf S., Iqbal S., and Siddique K., 2021, Omics and CRISPR-Cas9 approaches for molecular insight, functional gene analysis, and stress tolerance development in crops, International Journal of Molecular Sciences, 22(3): 1292.
https://doi.org/10.3390/ijms22031292

Roorkiwal M., Bharadwaj C., Barmukh R., Dixit G., Thudi M., Gaur P., Chaturvedi S., Fikre A., Hamwieh A., Kumar S., Sachdeva S., Ojiewo C., Tar'an B., Wordofa N., Singh N., Siddique K., and Varshney R., 2020, Integrating genomics for chickpea improvement: achievements and opportunities, Theoretical and Applied Genetics, 133: 1703-1720.
https://doi.org/10.1007/s00122-020-03584-2

Sen S., Chakraborty J., Ghosh P., Basu D., and Das S., 2017, Chickpea WRKY70 regulates the expression of a homeodomain-leucine zipper (HD-Zip) I transcription factor CaHDZ12, which confers abiotic stress tolerance in transgenic tobacco and chickpea, Plant and Cell Physiology, 58: 1934-1952.
https://doi.org/10.1093/pcp/pcx126

Shende R., Singh R., Kumar A., and Sengar R., 2021, Genome-wide analysis of WRKY transcription factors family in chickpea (*Cicer arietinum* L.), Legume Research, 45(6): 700-710.
https://doi.org/10.18805/LR-4352

Soorni J., Loni F., Daryani P., Amirbakhtiar N., Pourhang L., Pouralibaba H., Khoshro H., Ramandi H., and Shobbar Z., 2025, Developing resistance to Fusarium wilt in chickpea: from identifying meta-QTLs to molecular breeding, The Plant Genome, 18(1): e70004.
https://doi.org/10.1002/tpg2.70004

Tarinejad A., Alamholo M., and Azad D., 2024, A study on chickpea (*Cicer arietinum* L.) EST under salinity stress and development of EST-SSRs molecular markers, Genetika, 56(3): 381-399.
https://doi.org/10.2298/gensr2403381t

Wang S., Wu G., and Wei M., 2024, Functional mechanisms of WRKY transcription factors in regulating plant response to abiotic stresses, Chinese Journal of Biotechnology, 40(1): 35-52.
https://doi.org/10.13345/j.cjb.230298

Wani S., Anand S., Singh B., Bohra A., and Joshi R., 2021, WRKY transcription factors and plant defense responses: latest discoveries and future prospects, Plant Cell Reports, 40: 1071-1085.
https://doi.org/10.1007/s00299-021-02691-8

Waqas M., Azhar M., Rana I., Azeem F., Ali M., Nawaz M., Chung G., and Atif R., 2019, Genome-wide identification and expression analyses of WRKY transcription factor family members from chickpea (*Cicer arietinum* L.) reveal their role in abiotic stress-responses, Genes & Genomics, 41: 467-481.
https://doi.org/10.1007/s13258-018-00780-9