

Journal of Advances in Biology & Biotechnology

Volume 27, Issue 7, Page 853-867, 2024; Article no.JABB.118443 ISSN: 2394-1081

Plant Transcription Factors: An Overview and Its Significance in Abiotic Stress

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

Article Information

DOI[: https://doi.org/10.9734/jabb/2024/v27i71045](https://doi.org/10.9734/jabb/2024/v27i71045)

Open Peer Review History:

This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: <https://www.sdiarticle5.com/review-history/118443>

Review Article

Received: 12/04/2024 Accepted: 18/06/2024 Published: 22/06/2024

ABSTRACT

This study delves into the pivotal role of transcription factors (TFs) in orchestrating plant adaptation to abiotic stress, a critical aspect of plant biology with profound implications for agriculture and environmental sustainability. Through an in-depth exploration, key aspects of TF-mediated abiotic stress responses were examined, including the identification of stress-responsive TFs, their regulatory networks, and mechanisms of action. Additionally, the study elucidated the integration of TFs with stress signalling pathways and their modulation of physiological and biochemical responses to environmental challenges. The importance of understanding TFs in abiotic stress response was underscored, emphasizing their potential for engineering stress-tolerant crops and advancing sustainable agricultural practices. Furthermore, the implications of TF-mediated stress responses for agriculture and environmental sustainability were discussed, highlighting opportunities to enhance crop resilience and mitigate the impact of climate change on global food security. Overall, this study sheds light on the intricate interplay between TFs and abiotic stress adaptation mechanisms, offering valuable insights for future research and practical applications in agriculture and environmental management. This review paper solely discusses about Transcription factors and their domains, WKRY, MYB and NAC families and their involvement in abiotic stress.

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Cite as: K, Satish Chandra, and Deshraj Gurjar. 2024. "Plant Transcription Factors: An Overview and Its Significance in Abiotic Stress". Journal of Advances in Biology & Biotechnology 27 (7):853-67. https://doi.org/10.9734/jabb/2024/v27i71045.

Chandra and Gurjar; J. Adv. Biol. Biotechnol., vol. 27, no. 7, pp. 853-867, 2024; Article no.JABB.118443

Keywords: Transcription factors; domain; abiotic stress; stress-responsive genes; signalling pathways; plant adaptation.

1. INTRODUCTION

(A) Abiotic Stress

Climate changes pose significant challenges to crop production worldwide. Recent data have shown that the Global human population has surpassed 8 billion mark. Furthermore, UN suggested that the figure could potentially escalate to approximately 8.5 billion by the year 2030 and may reach 9.7 billion by 2050 [1]. Environmental changes pose a significant obstacle for the agriculture in order to fulfil the increasing global demand for food production. Raising temperatures and increased frequency of change in weather patterns show major impact on crop growth, development and yield. Abiotic stress poses a significant threat to global food security, with an estimation of 70% of yield losses in major crops [2]. Studies estimate that for every 1degree C rise in global mean temperature could result in 3-10% decrease in crop yield. Drought, heat waves and erratic rainfall patterns have already caused substantial yield loss worldwide [3-5]. Prolonged heatwave across several states, including Punjab, Haryana, and Uttar Pradesh (UP), led to decline in wheat yield by 10-35%. High temperatures can also directly impact physiological processes such as photosynthesis, respiration and reproductive development, leading to yield losses and quality deterioration [6]. The impact of abiotic stress on plants extends beyond the cellular level to influence various aspects of plant growth, development, and productivity. Abiotic stress can inhibit seed germination, reduce plant growth rates, alter root morphology and architecture, decrease leaf area and chlorophyll content, and compromise crop yield and quality [7]. Furthermore, prolonged exposure to abiotic stress can weaken plants, making them more susceptible to biotic stresses such as pest infestations and diseases [8].

Understanding the molecular mechanisms underlying plant responses to abiotic stress is essential for developing strategies to enhance stress tolerance and improve crop resilience. Plants have evolved sophisticated mechanisms to perceive and respond to abiotic stress at the molecular, cellular, and physiological levels. These include stress signal perception, activation of stress signalling pathways,

transcriptional reprogramming, synthesis of stress-related proteins (such as chaperones, Osmo protectants, and antioxidants), and activation of stress-responsive metabolic pathways [6]. Recent developments in the fields of molecular biology, genomics, and biotechnology have shed light on the genetics of plant abiotic stress tolerance. Plant responses to abiotic stress have been linked to important genes, transcription factors, signalling molecules, and regulatory networks that have been discovered by researchers [9]. Using this knowledge, researchers are creating crop types that are more productive and resistant to harsh environmental conditions through the use of genome editing, marker-assisted breeding, and genetic engineering [10].

(B) Transcription Factors in Plants

Plants being sessile organisms, have the need to protect themselves from various biotic and abiotic stresses surrounding them to survive in the adverse conditions, plants have various mechanisms which include tolerance, avoidance and resistance. These mechanisms are governed by various biochemicals which are the products of many genes that are expressed under specific conditions. The expression of these stress responsive genes is regulated by specialized proteins called transcription factors (TF). They act as molecular switches, capable of either activating or repressing the transcription of targeted genes. These master regulators (TFs) binds to specific DNA sequence (promotor region) of a gene for transcription initiation and regulation of gene expression [11]. Genome of the plants consist large compliments of TF genes. The model plant *Arabidopsis thaliana* encodes over 1500 transcription factors, representing more than 5% of its total genome complement [12]. Several families of TFs have been identified and extensively studied in plants. Among them, dehydration responsive element binding (DREB), basic leucine zipper (bZIP) domain, MYB, NAC, Zinc-finger, heat shock factors (HSF), WRKY, and nuclear factor-Y(NF-Y) have been recognised as major players in stress tolerance mechanisms [13]. TFs also plays an integral role in gene regulatory mechanisms crucial for growth, development, and metabolic pathways of the plant.

Table 1. Role of TF in plant developmental stages

(C) Mechanisms of TF-Mediated Abiotic Stress Tolerance

TFs Regulating Stress-Responsive Genes: In plants, transcription factors (TFs) are essential for controlling how genes that respond to stress are expressed. Target genes implicated in stress tolerance processes are either transcriptionally activated or repressed as a result of certain TFs being activated or upregulated in response to abiotic stressors. In the promoters of stressresponsive genes, for instance, TFs like AREB/ABF (ABA-Responsive Element-Binding Factor) and DREB (Dehydration-Responsive Element-Binding) bind to cis-acting regions to activate the transcription of these genes and improve stress tolerance. Similarly, to help plants adapt to abiotic challenges, TFs from the WRKY, NAC, and bZIP families control the expression of genes related to osmotic adjustment, antioxidant defence, and ion homeostasis [21].

Crosstalk between TFs and Stress Signalling Pathways: Abiotic stress responses mediated by TF often entail communication across many signalling pathways. As integrators of stress signals, transcription factors take in information from several signalling pathways, including as calcium, ABA, and MAPK signalling. Plants are

able to prioritise resources for stress adaption and adjust their responses to various abiotic stressors thanks to the crosstalk between TFs and stress signalling pathways. For instance, stress-responsive gene expression is regulated by ABA-responsive transcription factors (TFs) in conjunction with elements of the ABA signalling pathway, whereas stress-induced phosphorylation cascades trigger gene expression modulation by MAPK-regulated TFs [22].

Role of TFs in Plant Adaptation to Abiotic Stress: By controlling the expression of genes that respond to stress and coordinating physiological and biochemical reactions, transcription factors are essential in facilitating plant adaptation to abiotic stressors. The
production of protective proteins such production of protective proteins such chaperones and late embryogenesis abundant (LEA) proteins, the detoxification of reactive oxygen species (ROS), osmotic adjustment, and the preservation of cellular ion homeostasis are all regulated by TFs. By means of these processes, TFs aid in improving stress tolerance, encouraging plant survival, and guaranteeing productivity in the face of challenging environmental circumstances [23].

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General and specific TFs: Eukaryotic transcription require transcription factors along with RNA polymerase for the initiation of the mechanism [27]. Those transcription factors that controls the primary step of gene expression (transcription) by transcription pre-initiation complex (PIC) formation and guide RNA polymerase towards the promotor regions are basal or General transcription factors (GTFs) [28,29]. GTFs ensure that the transcription mechanism is properly positioned and activated to initiate the transcription mechanism. Most common GTFs that involved in transcriptional initiation are TFIIA, TFIIB, TFIID, TFIIE, TFIIF, TFIIH and TATA binding protein (TBP) a component of TFIID [30]. TFIID binds to the TATA region located 20-25 nucleotides upstream to the transcriptional initiation site with the help of TATA binding protein (TBP) and assemble other GTFs along with RNA polymerase [31].

Specific transcription factors (STFs) binds to cisregulatory elements (enhancer and repressors sequence) of the gene promotor and regulate the rate of transcription [32]. These regulatory regions (activators and repressor DNA sequence) that governs the transcription rates exists proximal to the sites where transcription initiates [33]. They alter the levels of gene expression in response to external stimuli to maintain homeostasis.

Domains of TFs: Plant transcription factors consist of DNA-binding domain, Transcriptional regulation domain, Oligomerization domain and nuclear localization signal (NLS) domain in their structure.

DNA-binding domain (DBD) of the transcription factors consists of a highly conserved amino acid residue that recognize DNA bases at promotor region, specifically at transcription factors binding sites (TFBS). Other residues of the domain enhance the transcription factors by binding with either phosphate or deoxyribose moiety [34]. Plant TFs are classified into various families on basis of structure resemblance in the DNA binding domain. bZIP, AP2IEREBP, NAC, WRKY families, the trihelix DNA binding proteins, the auxin response factors (ARFs), MYB and MADs families are major TF families found in plants [12].

Transcriptional regulation domain either function as activators or repressors depending on weather to initiate or inhibit the transcription of the specific gene [35]. This result in increase or decrease in the transcription of the gene, protein synthesis and alters cellular function. Activation domain (AD) interacts with other proteins such as coactivators along with GTFs and enhance the transcription mechanism [36]. Most of the activation domain are rich in either acidic amino acids, proline, or glutamine residues [37]. Repression domain (RD) form complexes with corepressors and actively interferes with transcription initiation complex to repress the gene transcription [38].

Many transcription factors form a dimer or multimers by protein -protein interaction between transcriptional factor subunits. Oligomerization domain of TFs facilitate the formation of these complexes (homo or hetero oligomers) which enhance the specificity, affinity of DNA binding and transcriptional activity by exposing and masking regulatory domain [35].

Nuclear localization signal (NSL) sequence ensures that the transcription factor is transferred from cytoplasm to nucleus to interact with DNA and regulate gene expression [39]. Certain plant TFs do not possess NSL, they are transported into nucleus through dimer formation with proteins that possess these signals [40].

2. WRKY TF

WRKY TF family is considered one of the largest families found in plants. They play a pivotal role in regulating plant biotic and abiotic stress defense mechanism and governs various developmental and physiological processes within plants [41].

First WRKY TF, Sweet potato factor1(SPF1) gene, was discovered in 1994 in Ipomea batatas [42]. Subsequently, the transcription factors ABF1 and ABF 2 were discovered in the wild oat species Avena sativa and were shown to play regulatory role in seed germination [43]. Later as more genomes of different crops became available, numerous members of the WRKY TF families have been identified in various species, including 104 in Populus, 45 in hordeum vulgara, 55 in Cucumis sativus, 74 in Arabidopsis thaliana, 55 in solanum Lycopersicon and 102 in Oryza sativa [44].

Structure of the WRKY TF consists of 60 amino acids with N- terminal (amino terminal) DNA binding domain (DBD) and C-terminal (carboxyl terminal) Zinc-finger motifs (ZFM) [45]. The DNAbinding domain (DBD) consists of conserved WKRY heptapeptide amino acid sequence WRKYGQK located within N-terminal b strand [46]. Presence of this conserved sequence is the characteristic feature of the WRKY protein. WRKY TF recognize the W-Box sequence in the promotor region of the specific stress response gene and regulate its expression. The W-Box sequence, which is commonly known as the target recognition sequence for WRKY domains, consists of the nucleotide sequence TTTGACY, where Y can be either T or C [43]. Zn-finger structure found in C-terminal of WRKY proteins are predominantly of C2H2 and C2HC type [47]. Based on the number of DNA binding domains (WKRY domains) and the structure of their Zincfinger motifs, WRKY TFs can be categorized into three distinct groups: Group I,II,III [48]. Group I proteins typically contain two WRKY domains and one C2H2 Zinc- finger motifs. In contrast, the WRKY proteins in groups II and III possess only a single WRKY domain. The distinguishing feature is that the Zinc-finger motif in group II is a C2H2 type, while Group III has C2HC type [49].

Role of WRKY TF in abiotic stress: Analysis of plant genome database has uncovered the presence of distinct WRKY encoding expressed sequence tags (ESTs) [50]. These WRKY ESTs have been isolated from diverse range of plant tissues, including roots, flowers, seeds, and vascular tissues. Furthermore, WRKY ESTs have been identified in plant samples subjected to drought, salinity stress, or pathogen infection. This extensive distribution of WRKY genes across various cell types and physiological conditions suggests that the WRKY TF family may be involved in regulating broad spectrum of biological processes within plants. Despite the significant progress made in understanding the roles of WRKY proteins in biotic stress response, their role in abiotic stress is comparatively less known. The expression of WRKY genes appear to be induced under a variety of abiotic stress conditions, suggesting that WRKY transcription factors may be involved in regulating the signaling pathways and transcriptional reprogramming that occurs when plants encounter different environmental changes [49]. This indicates that WRKY proteins play a central role directing the complex molecular responses that allow plants to adopt and acclimate to various abiotic stress.

In response to drought stress, certain droughttolerant plant varieties have ability to increase their production of oligosaccharides through the metabolic processing of sucrose [44]. Oligosaccharides act as osmolytes such as proline, glycine betaine, helping plant cells to retain water and maintain their structural integrity. This accumulation of oligosaccharides serves to enhance the plants overall drought resistance and capacity to withstand periods of water deficiency. Plants experience dehydration during drought stress. Dehydration can lead to accumulation of reactive oxygen species like H2O2, which cause oxidative damage to cellular components. To prevent dehydration, plants undergo certain mechanisms that aims to increase the water uptake, reduce the rate of water loss, or protect the plant cells from elevated levels of hydrogen peroxide(H2O2) [50]. For example, WRKY53, a group III WRKY protein play a role in modulating the stomatal movement and behavior, likely through mechanisms involved in reduction of H2O2 levels and promotion of starch metabolism within the guard cells [51]. Cotton (Gossypium hirsutum) WRKY protein GhWRKY41 when transferred to tobacco revealed that the overexpression of GhWRKY41 enhanced the tolerance to drought and salt stress by regulating stomatal conductance and reactive oxygen species (ROS) levels [52]. HaWRKY76 (Helianthus annus), a group II WRKY protein of sunflower was found to provide tolerance to drought and waterlogging in transgenic Arabidopsis [53]. Transgenic Arabidopsis plants expressing soyabean (Glycine max) transgenic factor GmWRKY54 was found to confer tolerance to both salt and drought stress whereas GmWRKY21 exhibits enhanced tolerance to cold stress [54]. Wheat transgenic factor TaWRKY2 binds with the promotor of drought-responsive gene RD29B and enhance its expression [55]. Arabidopsis transcription factor AtWRKY57 similarly binds with RD29A and NCED3 gene promotors and positively regulates its expression [56]. NCED3 gene is responsible for increase in Abscisic acid (ABA) during stress condition which promotes stomatal closure and enhance various drought and salinity tolerance mechanisms.

3. NAC TF

The acronym NAC originates from the initial letters of the first three identified proteins that possess a specific domain, known as NAC domain. These proteins were discovered in

different plant species: NAM (no apical meristem) in Petunia, ATAF1/2 and CUC2(cup-shaped cotyledon) in Arabidopsis [63]. By advancement in plant genome sequencing technologies numerous NAC genes have been unvieled across diverse plant species at genome level which include 117 in Arabidopsis, 151 in rice, 152 in maize ,71 in chickpea, 110 in potato [64].

NAC domain consists of approximately 150 amino acids located within the N-terminal region which function is to facilitate DNA binding within the cell nucleus and promote dimer formation; Cterminal site of the NAC domain plays a crucial role in transcriptional regulation mechanism [64]. X-ray crystallographic studies made on ANAC019 (Arabidopsis thaliana NAC019) and SNAC1 (stress responsive NAC1 of rice) have shown that the structure of NAC domain consists of a novel transcription factor fold comprising twisted beta-sheet surrounded by a few helical elements [65]. NAC transcription factors binds with their promotors and regulate the down stream target genes during stress conditions. CACG core sequence, recognized as a NAC recognition sequence (NACRS) has been identified in promotor regions of ERD1 gene (early response to dehydration 1) in Arabidopsis enabling the NAC TF to bind and modulate its expression during drought response [66]. NAC TF play a pivotal role by involving in plant signaling pathways during stress conditions. For instance, 33 NAC genes in Arabidopsis exhibited altered expression under salt stress [67],38 NAC genes in soyabean responded to drought [68] and 40NAc genes in rice were modulated by drought and salinity.

4. MYB TF

MYB TF family is regarded as one of the extensive protein families found in plants. First plant MYB gene -C1 gene was identified in maize [14]. Structure consists of highly conserved Nterminal MYB DNA-binding domain (DBD) repeats (R1, R2, R3; R represent repeat). Each repeat comprises approximately 52 amino acid residues that adopt a three-dimensional structure consisting of three alpha helices [69]. On basis of Terminal MYB domain repeats MYB TF is classified into four different classes- 1R (R1 type MYB), R2R3MYB, 3RMYB(R1R2R3MYB) and 4RMYB (four R1/R2). Majority of plant MYB TF belong to R2R3 MYB class containing 2 repeats in their N-terminal domain. R2R3 MYB TF play a major role in pant specific processes such as metabolism (primary and secondary), cell

Table 4. Role of NAC TF in abiotic stress

Table 5. Role of MYB TF in abiotic stress

development and response to both biotic and abiotic stresses [88]. Extensive research efforts have been led to identification of MYB genes across various plant species. Notably, Model plant Arabidopsis consists of 204 MYB genes, 197 in rice, 279 in populus, 279 in grapevine and 180 in Brachipodium [89]. R2R3 MYB TF play a significant role in signal transduction pathways associated with various phytohormones, including salicylic acid, abscisic acid, gibberellic acid, and jasmonic acid [90]. Notably ABA plays a major crucial role in facilitating stomatal closure and enabling the adaptation of vegetative tissue to abiotic stresses such as drought and salinity. For example, AtMYB60 and AtMYB96 in Arabidopsis act through the abscisic acid (ABA) signalling pathway to regulate stomatal movement and enhance drought tolerance [91].

5. CONCLUSION

Throughout this discussion, we explored the intricate role of transcription factors (TFs) in plant adaptation to abiotic stress. The discovery of stress-responsive transcription factors (TFs), their control over stress-responsive genes, their interaction with stress signalling pathways, and their modification of physiological and biochemical reactions are important aspects. We also spoke about the various ways that TFs support plant resilience and stress tolerance under harsh environmental circumstances. Deciphering the molecular processes behind plant stress adaptation requires an understanding of the involvement of TFs in the abiotic stress response. TFs are key players in the regulation of stress-responsive gene expression, coordinating intricate signalling pathways and physiological reactions to external stimuli. By clarifying the roles of TFs, scientists might create methods for creating stress-tolerant plants that are more resilient to unfavourable environmental circumstances, therefore tackling issues related to global food security. The insights gained from studying TF-mediated abiotic stress responses have significant implications for agriculture and environmental sustainability. Through the use of TF information, scientists may create crop varieties that are more resilient to stress, decreasing yield losses and boosting agricultural output in the face of environmental degradation and climate change. Furthermore, by optimising resource utilisation and reducing the environmental effect of agricultural production, farmers may adopt sustainable agricultural practices by gaining a knowledge of TF-mediated stress responses.

In conclusion, research on transcription factors in the response to abiotic stress offers important insights into the processes of plant adaptation, presenting potential chances to improve environmental sustainability and agricultural output in a changing global context.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

ACKNOWLEDGEMENT

We express our sincere gratitude to all authors contributed to the completion of this paper.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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