Significance of Transcription Factors in Drought Stress Tolerance of Cereal Crops

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Abstract

Drought being a production restrictive factor has become the main threat to international food security. Therefore, understanding the mechanisms underlying the drought response is one of the main scientific agenda for enhancing crop yield. Plants set out different strategies and mechanisms to respond to and tolerate drought stress. The expression of several genes is changed in different plants under drought stress that helps them to optimize their growth and development. Plant hormone abscisic acid (ABA) plays a key role in plant response and tolerance by regulating the expression of many genes under drought stress. Transcription factors being the chief regulator of gene expression play a vital role in stress response. ABA regulates the expression of the majority of the target genes through the ABA-responsive element (ABRE) binding protein/ABRE binding factor (AREB/ABF) transcription factors. Genes regulated by AREB/ABFs comprises a regulon termed as AREB/ABF regulon. In addition to this, drought-responsive genes are also regulated by ABA-independent mechanisms. In ABA-independent regulation, dehydration-responsive element-binding protein (DREB), and NAC regulons play a crucial role by regulating numerous drought-responsive genes. Apart from these key regulons, MYB/MYC, and WRKY, transcription factors family also contributes to drought response and tolerance. Our insight into the transcriptional regulation of drought is still developing. Current findings have suggested the presence of crosstalk between diverse transcription factors functioning under drought stress. In this manuscript, I have reviewed the role of different regulons functioning under drought stress and their crosstalk with each other.

Keywords: Dehydration; Abscisic acid; Transcription factors; Responsive element; Expression

Introduction

Plants are regularly subjected to a broad range of abiotic stresses such as drought, high salinity, heat and extremes of temperature, which seriously affects growth, development and productivity. Of these stresses, drought is one of the most important factors that affect the production of agricultural crops across the worldwide. Drought can cause plant water loss and leaf wilting, and ultimately result in irreversible damaging, plant death. Developing crop performance under a water stress environment is, therefore, the main research focus of plant scientists around the globe. Inadequate water availability induces adaptive physiological responses regulated by changes in the expression of various stress-responsible genes. Plants use complex regulatory pathways to address various stimuli, which include stress sensing, signal transduction, and regulation of stress-responsive genes and/or proteins eventually manifested at the cellular and physiological levels [1].

Transcription factors (TFs) are clusters of proteins that bind to particular regulatory DNA elements situated in gene promoters upstream of transcription initiation sites, repressing or activating many downstream target genes expression. A single TF gene can control the expression of a wide range of target genes (regulon). Transcription factors (TFs) give a possibility for plants to alleviate and respond to biotic and abiotic stresses and are also participate in changing developmental processes. Plant genomes allocate around 7% of their coding sequence to TFs, which shows the complexity of transcriptional regulation. Transcriptome data in many plants advocate that numerous pathways separately respond to stress, showing that stress tolerance or susceptibility is controlled at the transcriptional level by an extremely complex gene regulatory network [1]. TFs concerned with drought response were identified and characterized in different cereal species, such as in rice [2], wheat [3], barley [4], and maize [5]. Underwater limitation in transgenic plants, overexpression of numerous target genes coding for stress-responsive TFs led to enhanced survival rate [6]. The performances of TFs are closely associated with their structure. TFs often comprise a DNA-binding domain (DBD) and a transcriptional activation domain (TAD) [7]. The DBD allows TFs to attach to specific promoter elements of target genes, and TAD intervenes in the control of the downstream gene directly or in association with other proteins. The transcriptional response to water-stress in cereals is controlled by numerous TFs, which have been clustered into some different families based on their structure and binding specificity. The major TFs families are the DRE-binding protein/C-repeat binding factors (DREB/CBF), the NAM/ATAF1/CUC2 (NAC) factors [8], the MYB/MYC family [9], the WRKY family [10], and the basic leucine zipper family (bZIP) [11], and the homeodomain-leucine-zipper (HDZip) family [12].

While plants experience water scarcity, receptors from the cell membrane/cell wall sense the extracellular stress signals and convert them into intracellular secondary messengers such as Ca^{2+} and inositol phosphate [13]. It is well approved that phyto hormones, in particular abscisic acid (ABA), play a considerable role in drought stress-associated transcription, in most cases through modulating phosphorylation-status of transcription factors and other regulatory proteins. The objective of this review is to discuss the involvement of TFs in drought response and adaptation in cereals.

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Drought-Responsive Signaling Pathways

Plant hormones play vital roles in relating to the stress-responsive signaling flow. ABA is an important plant hormone that utilized as a link between environmental stress reception and adaptive transcriptional program such as the regulation of cellular mechanisms, carbohydrate and lipid metabolism. It is the essential regulator of abiotic stress predominantly drought resistance in plants, and a direct intricate gene regulatory network enabling plants to survive with water deficit [14]. ABA induces the expression of many genes, including late-embryogenesis-abundant (LEA) genes. ABA-dependent signalling pathway has been shown as the system that intervenes stress adaptation by bringing on at least two different regulons: (1) the AREB/ABF (ABA-responsive element-binding protein/ABA-binding factor) regulon; and (2) the MYC (myelocytomatosis)/MYB (myeloblastosis regulon [15]. Whereas ABA-independent regulons are: (1) the CBF/DREB regulon; and (2) the NAC (NAM, ATAF and CUC) [16]. Nevertheless, besides, some investigations have revealed the presence of both ABA-dependent and – independent pathways of the stress response that function through AP2/EREBP (ERF) family subsets [17]. Beside these recognized regulons, an enormous other TFs are also participated in abiotic stress response, thus playing a critical role in conferring stress survival to plants. Even though these diverse stress-responsive TFs usually function separately, it is certainly likely that a few levels of cross-talk present between them [18].

There are three main pathways through which drought and ABA-mediated signals are perceived via various receptors. The primer receptor PYR/PYL/ RCARs binds ABA and inactions the type 2C protein phosphates (PP2Cs), which leads to the buildup of SNF1-RELATED PROTEIN KINASES (SnRK2s) [19] (Figure 1). SnRK2s in turn trigger ABA-responsive TFs such as Arabidopsis AREB1, AREB2, and AREB3. These TFs regulate ABA-dependent gene expression take part in several physiological processes such as the movement of stomatal guard cells, thus escalating the tolerance to drought. Protein-coupled receptor-type G proteins (GTGs) like GTG1/GTG2 have participated in the second ABA reception pathway, which was initially reported in Arabidopsis. GTG1/GTG2 proteins are membrane-localized receptors with functions in seedling and pollen tube growth and development, acting through voltage-dependent anion channels. The third ABA receptor is the H subunit of Mg-chelatase (CHLH/ABAR), which regulates the lipid metabolism linked to drought tolerance in plants [19].

Major Families of Cereal TFs Involved in Drought Response

Transcription factors are categorized into several family groups mostly based on characteristic amino acid sequences of its conserved DBDs [20]. Among these, the families DREB/CBF, NAC, MYB, WRKY, and bZIP are the main TFs that play a part in drought.

DREB/CBF Family

The dehydration responsive element binding proteins (DREBs) family is a part of the AP2/EREBF superfamily of TFs that induce a set of abiotic stress-related genes, thus conferring stress tolerance to plants. These take part in the ABA-independent pathways that trigger stress-responsive genes. DREB/CBF TFs contains around 60 amino acid long AP2 DBD which specifically bind to dehydration-responsive C-repeat (DRE/CRT) cis-element (5'-TACCGACAT-3') and activate expression of genes (Figure 2). In DREB family members, AP2 is an extremely conserved domain throughout the plant kingdom. It possesses two conserved motifs: the YRG and RAYD motifs. The YRG motif is assumed to determine DNA binding and the RAYD motif, which makes α-helix on the C-terminus [21]. DREB/CBF TFs were primarily identified in the promoter of the drought-responsive gene rd29A [22]. They were also found other plant species such as Brassica napus, Triticum aestivum, Atriplex hortensis, and Oryza sativa [23]. DREB1 and DREB2 are two major subgroups of the DREB subfamily, participated in two different signal transduction pathways under cold and dehydration, respectively [24].
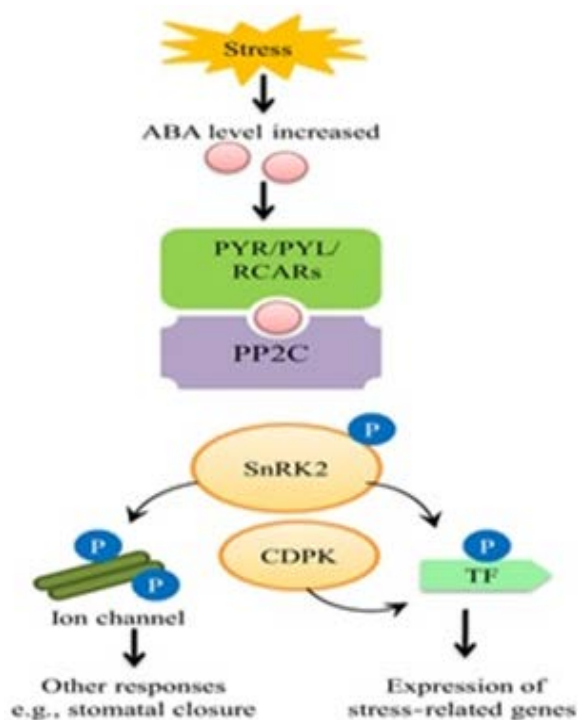

Figure 1: Sequential steps involved in ABA dependent signalling cascade for drought stress tolerance in crop Plants. Under drought stress, the cellular ABA level increases, and ABA then binds to PYR/PYL/RCARs, which in turn bind and inactivate PP2Cs. The SnRK2s autoactivate when they dissociate from PP2Cs. Activated SnRK2s phosphorylate downstream targets and trigger ABA-induced physiological and molecular responses.
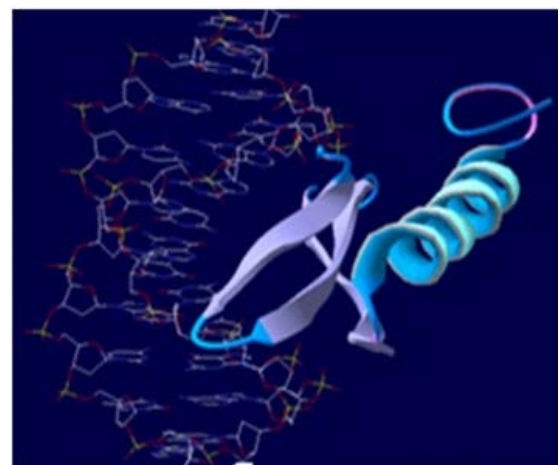

Figure 2: Schematic representation of secondary structure and recognition site of DREB/AP2/ERF families. (1) three-stranded antiparallel ß-sheet packed with a-helix; binding to DNA major groove (2) DRE/CRT, A/GCCGC (3) 333 aa (4) a DBD.

TaDREB1 was found to be inducible by drought, salt, low temperature, and ABA in different wheat cultivars [25]. The transgenic barely having TaDREB2 and TaDREB3 [26] demonstrated enhanced tolerance in drought and low-temperature environment. In rice, 13 transcriptional factors including seven DREB1 types and six DREB2 types were isolated and analyzed. ZmDREB1A [27], and ZmDREB2.7 [28] transcription factors contributed to drought tolerance in maize.

NAC Family

The NAC family of plant-specific TFs is one of the largest in the plant genome, with 149 members in rice, [29]. The NAM/ATAF/CUC (NAC) TFs possess a unique feature, a conserved N-terminus DBD and diversified C-terminus regulatory domain and they are distributed across the plant kingdom [20] (Figure 3). NAC is a short form of three genes designated as no apical meristem (NAM), Arabidopsis transcription activation factor (ATAF), and cup-shaped cotyledon (CUC). The cis-element of NAC TF [NAC recognized sequence (NACRS)] was also identified in Arabidopsis [30]. TaNAC2 [31] and TaNAC69 [32] genes are highly expressed under water deficiency and salinity in wheat crop. In maize, ZmNAC052, Zma000584, Zma006493, Zma001259z [33], and ZmSNAC1 showed improved transcription levels of underwater deficiency, demonstrating their potential role in drought tolerance regulation. Besides, the overexpression of OsNAC045, OsNAC6/SNAC2 and SNCA1 [34] encouraged ABA sensitivity and provided drought tolerance in transgenic rice. Hence NAC TFs play an indispensable role in physiological adaptation for successful plant propagation under abiotic stress conditions.

MYB/MYC Family

MYB is a cluster of ancient TFs that existed in eukaryotes such as fungi, animals, and plants known to have various functions [35]. Both MYC/MYB TFs participate in the ABA-dependent pathway of stress signalling for the up-regulation of the abiotic stress-responsive genes. MYC and MYB TFs build up only after ABA accumulation. MYBC1 was the first known gene in a plant, isolated from Zea mays [36]. MYB TFs possess a conserved DBD called MYB domain differentiated by one to three imperfect repeated amino acid sequences (R1, R2, and R3). Each repeat sequence contains about 50–53 amino acids which form three α-helixes [37] (Figure 4). These three α-helices resulted in a helix-turn-helix structure while intercalating in the major groove of DNA. The MYB TFs are mainly categorized into three classes based on the number of the MYB domain repeats: R1-MYB having one MYB repeat, R2R3-MYB containing two flanking repeats, and
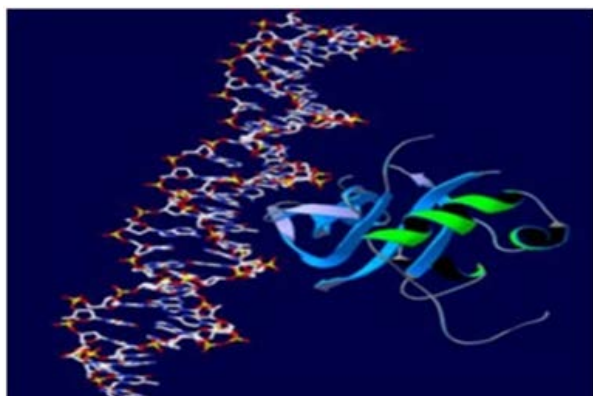

Figure 3: Schematic representation of secondary structure and recognition site of NAC family.(1)Twisted six-stranded β sheet packed with a helix; bind to the major groove of DNA (2)NACR, TCN7ACACGCATGT (3) 350 aa (4) 150aa DBD
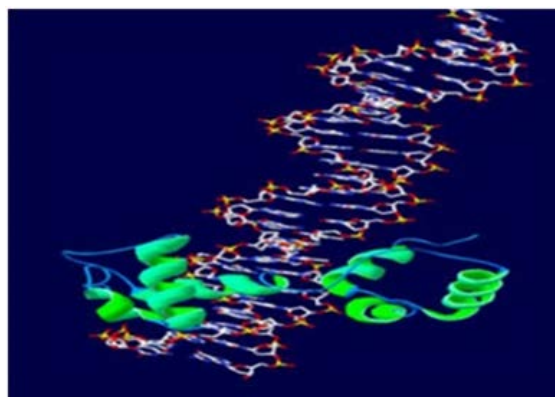

Figure 4: Schematic representation of secondary structure and recognition site of MYB families. MYB (1) helix- turn –helix (HTH); bind to the major groove of DNA (2) MYB/MYC, TAACNA/G (3) 310 aa (4) 50-53 aa DBD.

R1R2R3-MYB comprising three contiguous repeats [38]. These TFs contribute to responses to dehydration or drought [39]. The R2R3 family possesses the largest number of MYB genes [40] have revealed that there are about 183 MYB genes in the rice genomes. ZmMYB-R1 was induced by ABA and drought, in maize [41]. The overexpression of rice genes OsMYB3R-2, OsMYB4, and OsMYB48-1 improved the adaptive response to drought and other stresses in transgenic plants. TaMYB3R1 and TaMYB30-B were found to be potentially taking part in drought adaptation in wheat [42].

WRKY Family

WRKY proteins belong to the superfamily WRKY-GCM1 of zinc finger TFs [43]. They exist in several plant species and were reported to be contributed to several biotic and abiotic stress responses [44]. WRKY family members possess a strongly conserved WRKY domain with 60 amino acids consisted of two motifs. One is the conserved WRKYGQK motif on the N-terminus and the other one is a zinc-finger-like motif on the C-terminus [45] (Figure 5). Based on the different number of WRKY domains and the variable structure of the zinc-finger-like motif, WRKY families are grouped into three key categories. Group I has two WRKY domains, while groups II and III have one WRKY domain. WRKY domain binds to the W box ([T][T]TGAC[C/T]) of target gene promoters to change transcription. The zinc finger motifs of the WRKY domain in group III are different from those of groups I and II [46]. OsWRKY11 was identified to have participated in drought and heat response [47]. OsWRKY45 was assumed to be responsive to ABA and considered to function in stomatal closure to develop drought and salt tolerance [48]. HvWRKY38 was demonstrated to have a role in drought and cold response in barely [49]. In wheat, the overexpression of TaWRKY2 and TaWRKY10 led to improved drought and salt adaptation in transgenic plants [50].

bZIP (AREB/ABF) Family

The basic leucine zipper (bZIP) family is another immense group of TFs that take part in diverse functions such as hormone and sugar signalling and organ development [51]. bZIP proteins usually comprise a basic section for DNA binding and a conserved leucine zipper dimerization motif [52] (Figure 6). These TFs in particular bind to a DNA sequence with a core cis-element ACGT-like TACGTA (A-box), GACGTC (C-box), CACGTG (G-box), and an ABA-responsive element (ABRE) [51]. In plants, bZIP transcription factors provide a different subset of TFs which regulate processes including light and stress signalling, seed maturation, pathogen defence, and flower
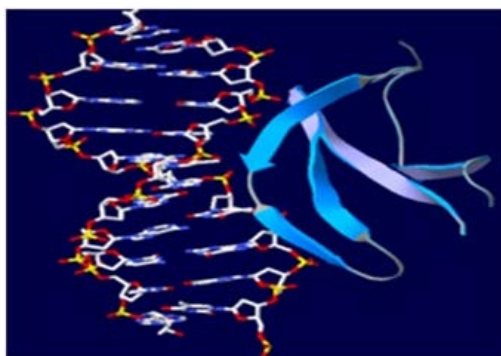
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Figure 5: Schematic representation of secondary structure and recognition site of WRKY families. (1) Five stranded antiparallels β sheet; bind to the major groove of DNA by β sheet rim W-box TTGAC (C/T) (3) 679aa (4) 60aa DBD
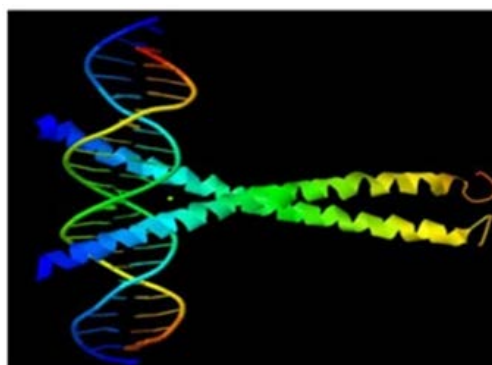

Figure 6: Schematic representation of secondary structure and recognition site of bZIP families. Dimerization of two α-helix monomers bound to DNA major groove (2) ABRE,ACGT 3) 55 aa (4) 16 aa DBD
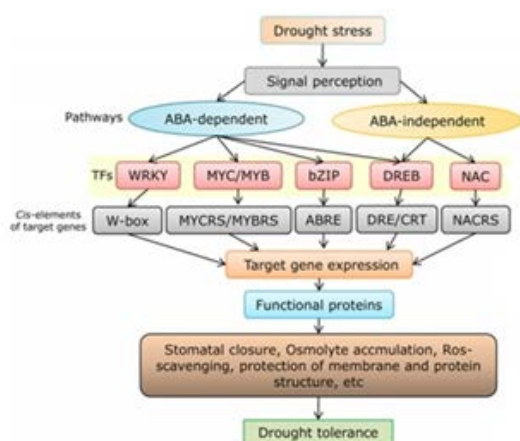

Figure 7: Major transcriptional regulatory networks of transcription factors involved in drought stress through ABA-dependent and –independent pathways.

development. Several bZIP members were known to participate in transducing ABA-dependent stress signals and were known as ABRE binding proteins (AREBs) or ABRE binding factors (ABFs). The AREB or ABFs are bZIP (basic leucine zipper) TFs that bind to the ABRE motif and activate ABA-dependent gene expression were first isolated in a yeast one-hybrid screening [53].

Several bZIP proteins were confirmed to be contributing to abiotic stress response in cereal crops, for instance, 141 in barley, 89 in rice & 171 in maize, and they were categorized into 11 groups A, B, C, D,

E, F, G, H, I, S, and U according to the phylogenetic trees and DNA binding motif in maize, rice, and barely. The overexpression of bZIP TFs was recognized to be the response to drought stress in several kinds of cereal. In barley, 11 HvbZIP members were well known to be down-or up-regulated by drought. The overexpression of ZmbZIP37, OsbZIP12 and TabZIP60 in maize, rice and wheat respectively, have shown high expression level in drought stress condition. Similarly, the overexpression of TabZIP60 enhanced drought and frost tolerance in transgenic Arabidopsis [51].

TFs Target Gene Network Activated in Response to Drought

TFs are involved in target gene network regulation through their DBD interaction with different gene promoter cis-elements mediated by ABA-dependent or ABA-independent signal transduction pathway (Figure 7). The majority of DREB family members such as OsDREB1A and TaDREB1 were found to be activated in ABA-independent pathways [23]. They can improve stress tolerance by activating the expression of downstream genes determined by DRE/CRT cis-element. Their expression products in cells safeguard from stresses by increasing the membrane stability and correction of protein folding. However, current studies indicated that some members of DREB also involve in ABA-dependent pathways. DREBs in different species might possess various preferences in regulating the expression of downstream genes with different core elements in their promoters. The rice OsDREB1A, e.g., prefers to interact with the CRT/DRE core element GCCGAC of genes such as cor15A, rd29A, and rd17 instead of core element ACCGAC, while the Arabidopsis DREB1A and maize ZmDREB1A have equal competition for recognizing core element GCCGAC and core element ACCGAC in the downstream genes [23].

In the WRKY family, more than 10 TFs isolated from rice were got to express together under drought and cold stresses, but the downstream genes were still not determined. TaWR- KY44 from wheat was identified to recognize the core element (TTGACC/TTAACC) in the promoter region of downstream genes and up-regulate genes encoding stress-defensive proteins such as NtERD10C, to increase plants survival rate in drought [54-57].

Members of the MYB family regulate the expression level of various target genes participated in the ABA-dependent and independent pathways (Figure 7). The overexpression of OsMYB48-1 was existed to regulate genes such as OsPP2C68, RAB21, and OsNCED4, respectively, contributing to ABA early signaling, late response, and the ABA synthesis pathway, contributing to increased drought tolerance under water deficiency. TaMYB30-B was known to induce the expression of stress-inducible genes rd29A and ERD1, contributed to the ABA-independent pathway [42]. Members of the bZIP family were also known to regulate downstream gene transcription via the ABA-dependent and independent pathway. OsbZIP52 was believed to bind to G-box cis-elements and down-regulated genes such as OsLEA3 and OsTPP that can enhance drought or cold tolerance in rice via the ABA-independent pathway. The expression of downstream genes LEA3 and Rab16 was activated by the transcription factor OsbZIP12 under water stress mediated by the ABA synthesis pathway [55, 58-61].

The majority of TFs in the NAC family involved in the ABA synthesis pathway (Figure 7). OsNAC5 and OsNAC6 can recognize a core sequence (CACG) of the downstream gene OsLEA3 and regulate the gene expression that altered root structure and conferred strong drought tolerance through the ABA signaling pathway. OsNAC6 also play a part in up-regulating the transcription of genes encoding peroxidase, which can catalyze a series of oxidative reactions. Some TFs

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even contribute to both ABA-dependent and independent pathways. For instance, TaNAC67 was supposed to up-regulate 10 abiotic stress-responsive genes such as rd29A and rd29B, which were individually associated with ABA-independent and-dependent pathways and four ABA-responsive genes such as ABI1 [31], thus enhance stress tolerance in plants.

Conclusion

In response to abiotic stresses such as drought, a lot of genes are regulated, and their gene products serve in conferring stress tolerance to plants. Considering the molecular mechanisms of plant responses to abiotic stresses is very essential as it makes it possible in utilizing them to advance stress tolerance and output. This manuscript summarizes the role of important plant TFs namely; ABRE, MYC/MYB, CBF/DREBs and NAC that regulate various stress-responsive gene expression. TFs play a crucial role in regulating gene transcription via various signal pathways to allow plants to acclimatize to diverse environments and abiotic stresses such as drought. Those TFs can recognize and interact with specific cis-elements of target genes through DBDs. Some TFs can up-/down-regulate downstream gene transcription, which encodes a member of TFs integrated into phytohormone signalling pathways, developing a complex hierarchic regulatory network. ABA, the main plant hormones, acts as key regulators in balancing plant growth and abiotic stress response. TFs, as the node of the cellular stress network and growth process, function as the interface of different phytohormone signal transduction pathways. These networks of signal pathways are regulating the activity of stress response TFs and other stress-relative genes, which in turn adjust physiological processes, such as stomatal movement, cuticle formation, and carbohydrate and lipid metabolism, to limit water loss and adapt to drought conditions. TFs can be genetically engineered to generate transgenic with higher tolerance to drought, salinity, heat and cold using different promoters. Besides, considering TFs as candidate genes inbreeding and other crop improvement programs will confer us a clear understanding of abiotic stress linked signal transduction events and ultimately will direct us to develop crop varieties advanced in stress tolerance by genetic manipulation.

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