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REVIEW ARTICLE

Transcription Factors and Their Roles in Signal Transduction in Plants under Abiotic Stresses

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Abstract: In agricultural production, abiotic stresses are known as the main disturbance leading to negative impacts on crop performance. Research on elucidating plant defense mechanisms against the stresses at molecular level has been addressed for years in order to identify the major contributors in boosting the plant tolerance ability. From literature, numerous genes from different species, and from both functional and regulatory gene categories, have been suggested to be on the list of potential candidates for genetic engineering. Noticeably, enhancement of plant stress tolerance by manipulating expression of Transcription Factors (TFs) encoding genes has emerged as a popular approach since most of them are early stress-responsive genes and control the expression of a set of downstream target genes. Consequently, there is a higher chance to generate novel cultivars with better tolerance to either single or multiple stresses. Perhaps, the difficult task when deploying this approach is selecting appropriate gene(s) for manipulation. In this review, on the basis of the current findings from molecular and post-genomic studies, our interest is to highlight the current understanding of the roles of TFs in signal transduction and mediating plant responses towards abiotic stressors. Furthermore, interactions among TFs within the stress-responsive network will be discussed. The last section will be reserved for discussing the potential applications of TFs for stress tolerance improvement in plants.

Keywords: Abiotic stresses, Crop improvement, Genetic engineering, Stress tolerance, Transcriptional factors, Transcriptomic profiling.

1. INTRODUCTION

Abiotic stress factors are recognized as major environmental threats to productivity and quality of crop plants. A number of prevalent abiotic stresses reported to occur around the world include drought [1], salinity [2], extreme temperatures [3], flooding [4], and nutrient deficiencies [5, 6]. Apart from the nutrient stress, the common effects caused by the other mentioned stressors are increase in intracellular Reactive-Oxygen Species (ROS) production and cellular damage [7], alteration in plant metabolism activities and photosynthetic performance [8], and break-down in maintenance of cellular homeostasis and osmotic balance [9, 10]. However, all types of abiotic stress finally result in interference with normal plant growth and development, biomass accumulation, plant productivity, or even cause plant death if the plant defense system is not sufficiently strong to combat the stressor [10, 11]. Taking the impacts of drought and waterlogging on crop yield as examples, a reduction from 20% to 50% in plant productivity can be recorded due to drought (on soybean) and submergence (on barley and wheat), depending on the length and severity of the stress [12-14]. Within the next three decades, food supply crisis is forecasted to be the most serious issue that the humankind has to face with [15]. This is the consequence caused by human activities and/or natural changes that could lead to invasion of salt into more than half of arable land [16, 17]; expansion of severe drought areas [18] and more unpredictable precipitation due to climate change [19].

Plants, depending on species, do have various physiological, metabolic and molecular strategies to minimize the effects imparted by stress on them, either by escaping, avoiding, or tolerating the stress [20, 21]. This also indicates that degree of yield loss and product quality of plants are determined by their defense mechanisms against the stress(es). Currently, boosting the stress tolerance in crop plants is one of the suggested solutions for agricultural biotechnologists in dealing with abiotic stresses.

Engagement of various techniques in research has aided the scientists to draw a global picture of how plants sense the

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environmental stress signal, forward the stress message to the nucleus for subsequently regulating gene expression so that they can generate appropriate responses upon stress exposure. Although insights of the tolerance mechanisms used by plants, as well as specific functions of different participants and their interactions with other members within the network have not yet clearly defined, a number of different components involved in the network has been targeted and used for genetic manipulation. Many attempts have shown promising outcomes, in which the transgenic plants displayed improved stress tolerance. Candidate genes used for engineering can be clustered into two groups – genes that encode functional proteins and genes that encode regulatory proteins [22]. Members belonging to the former group are very diverse, including products that work in maintenance of osmotic balance [23-25], antioxidation and ROS removal [26, 27], and protecting macromolecules such as proteins and DNA from degradation [28, 29]. Regarding the second group of candidate genes, various members within this group have been identified to have a key role in shaping plant behaviours in response to exposed abiotic stresses, including Transcription Factors (TFs), kinases, phosphatases, micro RNAs (miRNAs), and Two-Component Systems (TCSs) [20, 30-33]. The function of the regulatory members is to transmit the stress signal from external environment to the nucleus (like TFs and TCSs) and directly regulate gene expression (like TFs) *via* interacting with the promoters of genes.

This review focuses on the important roles of TFs in conferring stress-tolerant mechanisms in plants and their potential for being used as a resource for crop improvement. The knowledge presented here will be mainly relied on the findings from molecular analyses.

2. TRANSCRIPTION FACTORS AND THEIR REGULATORY FUNCTIONS IN PLANT RESPONSE TO ABIOTIC STRESSES

In plants, environmental stimuli can be firstly recognized by various transcellular membrane sensors, including Ca^{2+} channel and Ca^{2+}-binding proteins [34, 35], histidine kinases [36] and G-protein-coupled receptors [37]. Actions of these detectors lead to the activation of secondary messengers (kinases), or their partners (histidine phosphotransfers, response regulators), mainly *via* phosphorylation mechanism, to transduce the stress signal to subsequent components in the pathway towards the nucleus. Additionally, cellular changes in shape, turgidity, or changes in concentrations of solutes and ROS are also assigned as early stress effects and signals triggering the plant stress responses [38]. A number of previous reviews have demonstrated the participation of various molecules and proteins in the stress signal transduction cascade [39-41]. Regarding TFs, it has been reported that around 5-7% of coding sequences present within a plant genome are used for making this protein group [42, 43]. Based on the specific motifs appearing in their protein structure, the TFs are classified into different families. Among these, many members belong to AP2/EREBP (APETALA2/ethylene-responsive element-binding protein), bZIP (basic leucine zipper) and NAC (NAM-no apical meristem, ATAF-*Arabidopsis* transcription activation factor, and CUC- cup-shaped cotyledon) are particularly known to mediate plant adaptation under various abiotic stress conditions, whereas a smaller number of TFs from other families, such as WRKY and MYB (myeloblastosis), have also been identified to be involved in expression regulation of stress-responsive genes [22]. Table **1** summarizes distinct characteristics of the TF families which will be reviewed in this paper.

2.1. Many AP2/EREBP TF Members are Identified as Positive Regulators of Abiotic Stress Responses in Plants

AP2/EREBP is a TF superfamily which is found mainly in plants albeit AP2-homologues have also been found in other non-plant species [44, 45]. Based on the number of AP2/ERF domains and other signatures present in the protein, this superfamily is divided into five categories, known as (i) AP2 TFs carrying two AP2/ERF domains, (ii) RAV (related to ABI3/VP1) TFs with an AP2/ERF domain and a B3 DNA-binding domain, (iii) ERF (ethylene-responsive element binding factor) with an AP2/ERF domain, (iv) DREB (dehydration-responsive element binding proteins)/CBF (CRT (C-repeat)-binding factor) with an AP2/ERF domain but being different in amino acid sequence from that of the AP2/ERF domain of ERF TFs, and (v) Soloist [46-48]. The last subgroup has been recently added to classify any members that possess AP2 domain but display a more diverse sequence and structure in comparison with the ERF TFs [46, 49]. The AP2 and ERF domains sharing similarity in sequence were firstly recognized in *Arabidopsis* and tobacco, respectively [50, 51]. Their 3D-structure analysis revealed the presence of a β-sheet at the N-terminal and an α-helix at the C-terminal of the domain [52]. However, specific sequence of each TF determines its DNA-binding affinities to different genes [53, 54]. Although the *cis*-binding elements have been well identified for ERF, DREB and RAV TFs, the characterization of the DNA-binding domain of AP2 members is under progress [46, 55]. According to a number of investigations, AP2 TFs are suggested to bind to an AT-rich DNA domain or bind to sequence GACC (A/G)N(A/T)TCCC(A/G) ANG(C/T) [55-57]. Up-to-date, genome-wide analyses of putative TFs belong to AP2/EREBP family have been intensively performed in model and many economically important plants, including cabbage (*Brassica oleracea*) [58], wheat (*Triticum aestivum*) [59], *Arabidopsis*, rice (*Oryza sativa*) [60, 61], peanut (*Arachis hypogaea* L.) [62] and soybean (*Glycine max*) [63]. Preliminary investigation of expression of the identified AP2/EREBP TFs encoding genes, either in different plant tissues or different growing conditions, have been also conducted in these studies to provide a first glance into their possible functions.

In addition to their vital regulatory roles in plant growth and development, and in plant response to biotic stresses, involvement of TFs belonging to AP2/EREBP superfamily, mainly ERF- and DREB-type members, in regulating plant adaptive mechanisms to abiotic stresses has also been reported [64-68]. Salient examples as evidence for the participation of ERF TFs are rice Sub1 and RAP2.2 in plant response to flooding [69, 70], wheat TaPIE1 to freezing stress [71], tomato TSRF1 to drought stress [72], rice OsERF1 to salinity stress [73], *Arabidopsis* ERF1 to drought, salinity and heat stress

Table 1. Distinct features of major transcription factor (TF) families that have members involved in abiotic stress-responsive pathways in plants.

TF Family	Classes/Sub-families	DNA Binding Sequences (*cis*-element sequences)	Note	References
AP2/EREBP	DREB/CBF ERF AP2 RAV Soloist	(A/G)CCGAC AGCCGCC not yet identified CAACCA	—	[46-48]
bZIP	ABI AREB/ABF	PyACGTGG/TC CACGTGGC	—	[74, 75]
MYB	MYB-related R2R3-MYB R1R2R3-MYB 4R-MYB	CNGTT(A/G) C(G/T)T(A/T)GTT(A/G)	—	[76-78]
WRKY	Groups I to III	TTGACC/T TGCGCTT TTTTCCAC	—	[79-81]
NAC	NAC-a to NAC-h	CGT(G/A) CACG	Plant-specific	[82, 83]

[84], and soybean GmERF3 to salinity, drought and hormonal treatments [85]. Regarding DREB TFs, previous studies showed that they were able to bind to the DRE (dehydration–responsive element)/CRT regions that are commonly found in the promoters of genes that respond to drought, salinity and adverse temperature conditions [45, 86-88]. Taking studies on *DREB1*s and *DREB2*s from various plant species as examples, *Arabidopsis DREB1* (*AtDREB1*) genes had induced expression in plants upon cold treatment, whereas expression of *Arabidopsis DREB2A* (*AtDREB2A*) and *DREB2B* (*AtDREB2B*) was upregulated by other abiotic stresses including, dehydration and salinity [66, 89]. An investigation by Oh *et al.* in 2005 revealed an interesting finding about *Arabidopsis* DREB1A, in which the rice (cv. Nakdong) transgenic plants overexpressing *AtDREB1A* conferred tolerance mainly to drought and salinity instead of cold as observed with *Arabidopsis* transgenic plants ectopically overexpressing the same gene [66, 90]. On the other hand, overexpression of *AtDREB1A* in other rice cultivars (cv. Kita-ake and cv. Nipponbare) showed that the transgenic plants displayed improved tolerance to drought, salt and cold stresses [91]. With specific study on AtDREB2A by Sakuma *et al.*, additional participation of this TF in heat-stress responsive pathway in plants was revealed [86]. When examining rice *DREB*s (*OsDREB*s), expression of *OsDREB1A* has been shown to be up-regulated in plant response to cold stress, and its overexpression resulted in enhanced tolerance to drought, salinity and cold stresses in both transgenic *Arabidopsis* and rice plants [91, 92]. Additionally, a study by Dubouzet *et al.* also revealed that dehydration and high salinity treatments led to an increase in *OsDREB2A* expression [92]. Similarly, another investigation on soybean DREB (GmDREB2) suggested the involvement of this TF in plant response to drought, high salt and abscisic acid (ABA) since application of these treatments induced *GmDREB2* expression [93].

Large-scale studies on expression profiling of DREB/CBF TFs under various abiotic stress conditions have been already conducted in different plant species. For example, analyses by Fowler and Thomashow on expression of 8000 *Arabidopsis* genes upon cold stress treatment using microarray approach systematically revealed direct and indirect regulons of *Arabidopsis* AtDREB1A (CBF3), AtDREB1B (CBF1) or AtDREB1C (CBF2) (*i.e.* target genes regulated directly by CBF TFs or by another protein whose expression is regulated by the AtDREBs) [94]. The identified genes assumably regulated by these AtDREBs encode a wide range of products, including TFs (RAP2.1, RAP2.6), sugar transporter, water channel proteins, galactinol synthases, and LEAs (late embryogenesis abundant)/dehydrins (COR6.6, ERD10, COR47, COR78 *etc.*) or other types of cryoprotectant proteins. This study also provided evidence of multiple regulatory pathways involved in plant response to cold stress, as there were genes with altered expression taking place as early as the change in the expression of *AtDREB* genes, or due to the trigger of cold stress instead of the overexpression of *AtDREB*s. Additional finding supporting this was the participation of various TFs belonging to different families [94]. Meanwhile, interpretation from microarray data revealed that overexpression of *AtDREB2A* could induce a subset of genes that are responsive to not only drought and salinity (*e.g.* genes encoding LEA proteins, dehydrins and COR15A) but also heat stress (*e.g.* genes encoding for TF AtHsfA3, and heat-shock proteins HSP70 and HSP18.2) [86]. AtHsfA3 is known to regulate expression of a number of heat-shock proteins encoding genes. The confirmation of AtHsfA3 as a member of the DREB2A regulon and identification of AtHsfA3-regulated genes were subsequently conducted [95]. Besides, other research groups already attempted to analyze dynamic changes on metabolites in transgenic *Arabidopsis* plants overexpressing *AtDREB1A* or *AtDREB2A* under normal and stress conditions to get a better insight into metabolic pathways regulated by these TFs [96, 97]. The results showed that *AtDREB1A*-overexpressing and *AtDREB2A*-overexpressing plants displayed different metabolite profiles when they were exposed to dehydration or low temperature conditions [96]. These findings partially explain why these two transgenic lines showed differential tolerance abilities towards dehydration and cold stresses [66, 96, 98, 99]. Other results from DREB2-related studies indicated that abundance of the transcripts is not sufficient to achieve biological effects since biological activity of a TF might also depend on post-transcriptional modification processes [100, 101]. Another example for large-scale study is the expression profiling of *DREB* members in apple (*Malus domestica*) using Genevestigator and qRT-PCR conducted by Zhao *et al.* to identify potential genes for improving abiotic stress tolerance in plants by gene-transfer techniques, particularly against drought, salinity and low temperature conditions [88].

2.2. Other Important TF Families Involving in Abiotic Stress-Responsive Pathways in Plants

2.2.1. bZIP TFs

In addition to AP2/EREBP, various members of other TF families, including bZIP, MYB, WRKY and NAC, are also reported to have pivotal functions in mediating plant responses against various abiotic stresses. The explanation why some of the bZIP TFs are master regulators for plant stress responses is due to their capacity of binding specifically to ABRE (ABA-responsive element) sequence, the *cis*-acting sequence found within promoter regions of many stress-responsive genes controlled by ABA, especially under osmotic conditions [75]. In addition, expression of these *bZIP*s themselves can be induced by ABA treatment, and activities of the corresponding TFs could be also modulated by this phytohormone [75, 102]. These findings collectively indicate that these specific bZIP TFs function in ABA-dependent pathways, and thus they were named ABRE-binding proteins (AREBs) or ABRE-binding factors (ABFs). So far, the majority of abiotic stress-responsive bZIPs identified have been known to function in drought-responsive pathways, in which AREB1 (ABF2), AREB2 (ABF4) and ABF3 are well known master regulators in *Arabidopsis* [90, 103, 104]. In addition, in another independent study, gene ontology annotation and MapMan analyses were carried out to get details about functional regulation of *Arabidopsis* bZIP TFs, including bZIP1 and bZIP53 in salt-treated roots [105]. The results revealed that *bzip1 bzip53* double mutant caused effects on the expression of stress-related marker genes, such as *Senescence-associated1* (*SEN1*), *Dark-induced2* (*DIN2*), *EARLI1*, *RD29B* and a subset of genes involved in amino acid catabolism. This finding suggested a reprogramming role in root metabolism of these two TFs in adaptation to salt stress conditions [105]. When performing Digital Gene Expression Profiling (DGEP) for two soybean cultivars with contrasting drought-tolerant abilities, *GmbZIP110* was identified to be induced significantly under salinity [106]. Subsequent functional characterization of GmbZIP110 indicated that the TF could positively regulate expression of many stress-related genes and lead to the accumulation of proline, an osmoprotectant. This result suggested that GmbZIP110 could be used to improve salinity tolerance in plants by genetic engineering approach [107].

2.2.2. MYB TFs

Another important group of regulators in plant defense pathways against abiotic stresses are MYB TFs, which are distinguished from members of other TF families by their specific binding to the MYB-binding sites (MBS) [108]. Members of MYB family are grouped into four classes according to number of repeats found in the MYB domain, namely MYB-related, R2R3-type MYB, R1R2R3-type MYB and 4R-MYB [76-78]. Similarly to AP2/EREBP and bZIP TFs, MYB regulators that have been identified to have positive effects on plant stress tolerance mainly function against drought and salinity stresses [20, 109-111], although a few reports revealed the application of MYBs in improving plant tolerance to adverse temperature conditions [112, 113].

The majority of MYB- and abiotic stress-related studies have focused on the roles of R2R3-type MYB proteins, the largest subgroup in MYB TF family in plants. Taking reports from several recent studies as examples, overexpression of *Arabidopsis AtMYB44* has been shown to improve salt and drought stress tolerance in both *Arabidopsis* and soybean transgenic plants, probably by preventing excessive ROS accumulation [114, 115]. Another R2R3-type MYB in *Arabidopsis* that has been identified to function in plant response to ABA, drought, flowering and seed germination is AtMYB37. Overexpression of *AtMYB37* in *Arabidopsis* caused hypersensitive response to ABA and differential expression of a subset of ABA-responsive genes, as shown by qRT-PCR analyses. Additional positive attribute of the AtMYB37-overexpressing plants was the increase in seed yield, suggestively due to the plants having good biomass accumulation at vegetative stage prior to switching to the reproduction stage. Therefore, this gene may be promising for both crop adaptation to drought stress and improvement of plant productivity [116]. In another independent study examining *PtsrMYB* gene from trifoliate orange (*Poncirus trifoliata*), whose sequence shares high similarity with *AtMYB109*, the authors reported that its expression was up-regulated by dehydration, salt, cold and ABA treatments [109]. Transgenic tobacco plants overexpressing *PtsrMYB* showed increased dehydration-tolerant features, including a decrease of leaf water loss and lower accumulation of malondialdehyde and ROS [109]. In red wild einkorn (*Triticum urartu*), *TaMYB19* expression was highly up-regulated by NaCl, low temperature, polyethylene glycol (PEG), and ABA treatment [117]. This study further showed that the better drought tolerance of the *TaMYB19*-overexpressing transgenic *Arabidopsis* plants might be attributed to the up-regulation of stress-responsive genes *RD29A* (*responsive to dehydration 29A*), *RD22* and *MYB2*. These findings also suggested the involvement of TaMYB19 in both ABA-mediated and ABA-independent stress-signaling pathways. On the other hand, LeAN2 of tomato (*Lycopersicum esculentum*), an anthocyanin-associated R2R3-MYB, acts as a positive regulator of anthocyanin biosynthetic pathway by inducing the expression of several structural genes related to anthocyanin accumulation [113]. Overexpression of *LeAN2* in tomato conferred heat tolerance to transgenic plants [113].

Taken together, these findings suggest that genetic engineering of plants using *MYB* genes could stimulate typical or general pathways related to abiotic stress responses, leading to improved plant tolerance to various abiotic stresses.

2.2.3. WRKY TFs

The third TF family worthy to be mentioned in this section is the WRKY family, of which the main feature is the presence of the WRKY domain with conserved motif WRKYGQK [79]. Members of the *WRKY* family have been identified in a number of plants, including 74 in *Arabidopsis* [118], 197 in soybean [115], 81 in rice [119] and 71 in pepper (*Capsicum annuum*) [120]. In wheat, 48 putative drought-responsive *WRKY* genes were revealed from data comparison of *de novo* transcriptome sequencing data obtained from wheat growing under unstressed and drought stress conditions [121]. In addition, the authors reported that *Arabidopsis* transgenic plants overexpressing *TaWRKY1* and *TaWRKY33* showed enhanced expression of stress-related downstream genes, including *ABA1*, *ABA2*, *ABI1*, *ABI5* and *RD29A*. These might reliably explain why the transgenic plants had higher rate of germination and root growth in comparison to the wild-type counterparts under drought and ABA treatment. Application of both RNA-seq and qRT-PCR, a recent study identified *WRKY* genes that differentially responded to water-deficient stress in white pear (*Pyrus bretschneideri*) [122]. Digital transcriptomic analysis resulted in the construction of single-end cDNA libraries from salicylic acid, methyl jasmonate, salt, low temperature, wounding, and pathogenic-treated samples for sequencing and screening stress-responsive *WRKY* genes in black cotton wood (*Populus trichocarpa*) [123]. In grapevine (*Vitis vinifera*), a total of 59 *VvWRKY* genes was identified and classified into sub-families based on features of WRKY domain and zinc/finger motif. Using publicly available microarray data and qRT-PCR, 15 grapevine *VvWRKY* genes were noted to be cold-upregulated and three of them (*VvWRKY28*, *42*, and *55*) also showed inducible transcription under ABA treatment, suggesting their participation in cold response *via* either ABA-dependent or -independent pathway [124]. Additionally, a study of Expressed Sequence Tags (ESTs) of 10 unigenes (*TaWRKY44-53*) in wheat revealed the up-regulation of *TaWRKY44* by treatments with PEG, NaCl, low temperature, ABA, hydrogen peroxide (H_2O_2) and gibberellin. Transgenic tobacco plants overexpressing *TaWRKY44* resulted in induced expression of several ROS-related genes and stress-responsive genes in transgenic plants under drought, high salinity, and mannitol-triggered osmotic stress, suggesting a positive regulatory role of TaWRKY44 in plant response to these stressors [125]. By using qRT-PCR and RACE-PCR (rapid amplification of cDNA ends-PCR), *GhWRKY17* in cotton (*Gossypium hirsutum*) was isolated and further characterized by molecular techniques [126]. The expression of this gene was up-regulated to the highest levels in cotton plants that had been treated with 4-hour dehydration, 6-hour high salt, 6-hour H_2O_2 and 4-hour ABA treatments prior to getting reduced. When overexpressing *GhWRKY17* in *Nicotiana benthamiana*, the transgenic plants displayed significantly decreased plant tolerance to drought and salt stress, as evidenced by physiological and molecular analyses performed in this study [126]. According to their results, GhWRKY17 was suggested to be a negative regulator involved in both ABA and ROS signaling pathways.

2.2.4. NAC TFs

NACs, which form a plant-specific TF family, have been well-established as key regulators of plant response to abiotic stress. In study conducted by De Clercq and his colleagues, five transmembrane domain–containing ANAC TFs (ANAC013, 016, 017, 053, and ANAC078) in *Arabidopsis* were found to have involvement in MRR (mitochondrial dysfunction stimulon) – mediated regulation for the expression of *MDS* (*mitochondrial dysfunction stimulon*) genes, *via* interaction with the MDM (mitochondrial dysfunction motif) *cis*-element located in the promoter regions of the *MDS* genes [127]. MRR pathway is essential for effective communication between nucleus and mitochondria to regulate gene expression in response to environmental stress. Among the identified TFs, *in planta* function analysis has been performed for ANAC013, in which the *ANAC013*-overexpressing *Arabidopsis* plants conferred elevated oxidative stress tolerance against methyl viologen and rotenone [127]. In another study, genome-wide analysis in potato (*Solanum tuberosum*) revealed the presence of 110 genes belonging to the *NAC* family (*StNAC*s), among which fourteen encoded TFs were predicted to have membrane-bound activity [128]. The tissue-specific, biotic and abiotic stress-, as well as hormone-responsive expression patterns of *StNAC*s were examined by using bioinformatic tools [128]. In chickpea (*Cicer arietinum*), 19 out of 71 identified *CaNAC* genes have been shown to be involved in dehydration responses [129]. In another study in rice, *SNAC3* was shown to be induced by drought, high temperature, salinity and ABA treatments. Overexpression of *SNAC3* in rice enhanced tolerance of transgenic plants to high temperature, drought, and methyl viologen-induced oxidative stress. Consistently, silencing *SNAC3* by RNAi caused increased sensitivity to these stresses [130]. MlNAC5, a NAC TF from *Miscanthus lutarioriparius* has been showed to play a positive regulatory role in plant response to drought and cold stresses as the transgenic *MlNAC5*-overexpressing *Arabidopsis* plants displayed enhanced tolerance ability to these stress conditions through transcriptionally activating stress-responsive genes and increasing in hypersensitivity to ABA [131].

2.3. Interactions of TFs in Stress Signaling Pathways

It is obvious that networks of abiotic stress signal transduction in plants are complicated. The challenge for obtaining comprehensive understanding of TF functions in plant signaling pathways is due to the fact that one environmental stimulus can trigger a number of secondary stress signals in plant cells, and each of these secondary stress signals might be forwarded through a distinct signaling pathway. However, these pathways might have crosstalk at some nodes during the cascades of signal transduction or eventually result in regulation of the same target genes [132, 133]. To deal with this, molecular analyses of stress-inducible genes using full-length cDNA microarrays, RNAseq or oligo arrays are several approaches to explore the existence of crosstalk in abiotic stress signaling pathways towards a single stress or various stresses [128, 134-136]. By using such strategies, it has been found out that there is crosstalk in plant responses to drought and salt stress rather than to drought and cold stress. Findings supporting for this judgment were that the majority of drought-inducible genes were also induced by high salinity and ABA treatments, while only 10% of drought-inducible genes could be induced by cold [137]. TFs from various families can regulate plant responses to abiotic stresses either independently of ABA (such as CaNAC05 and CaNAC41) [129] or dependently on this hormone (such as AtAREB1 and GhWRKY17) [126, 138]. Alternatively, they can function in both ABA-dependent and ABA-independent pathways (such as TaMYB19, MbDREB1 and DREB2A) [48, 117, 139].

The crosstalk can be achieved *via* indirect interactions between TFs and major *cis*-elements present in the same promoter of target genes. For example, promoter of abiotic-stress responsive *RD29A* contains both DRE/CRT and ABRE *cis*-elements for binding by DRE/CRT-binding TFs (AtDREB1 and AtDREB2) and ABRE-binding TFs (AtAREB1 and AtAREB2), respectively. These TFs have been shown by transactivation experiments in *Arabidopsis* to function cooperatively in regulating expression of the target gene [140]. This study also revealed that the degree of *RD29A* transcriptional activity depends on the combination of DREB/AREB regulators simultaneously binding to the *cis*-elements in the promoter. Meanwhile, another independent study on TF binding to *Arabidopsis RD29A* promoter indicated that this promoter also contains the binding site (name NACRS) for ANAC096 and this TF could bind directly with AtAREB1 and AtAREB2 due to proximity of NACRS and ABRE regions [141]. Besides, analyses by Oh *et al.* indicated that the presence of higher number of ABRE or higher number of DRE sequence present in the promoter region, which contain both these *cis*-elements, would result in the tendency that the target gene will be strongly regulated by DREBs or by AREBs [90]. Taken together, the interaction of TFs are complicated and studies on understanding of their cooperative acting mechanisms in regulating gene expression in plant responses to different stress conditions are still under progress.

A TF can interact with other proteins, including kinases and other TFs, in a single stress-responsive pathway. Usually, the communication between protein-protein is achieved *via* phosphorylation-based mechanism. Example to illustrate the interaction between TF and kinase is the requirement of mitogen-activated protein kinase MPK3 for MYB44 function in enhancing tolerance of *Arabidopsis* transgenics to salinity [142]. Another evidence supporting this is the interaction between SnRK2 kinases (SnRK2D, SnRK2E and SnRK2I) and downstream AREB/ABF TFs (AREB1, AREB2 and ABF3) in regulating expression of the *DREB2A* gene *via* ABA-mediating dehydration stress signaling pathway [139, 143]. Regarding TF-TF interaction, by using yeast two-hybrid assay, direct interaction in a physical manner has been identified for DREBs and AREBs/ABFs. Specifically, in *Arabidopsis*, DREB2C could interact with AREB1, AREB2 and ABF3, while DREB1A and DREB2A with AREB1 and AREB2 [144].

In addition, several TFs have also been assigned as multi-functional regulatory proteins working in both biotic and abiotic stress pathways. Illustrating examples for this include NACs from rice (OsNAC6) and *Arabidopsis* [ATAF1 (*Arabidopsis* transcription activation factor 1) and ATAF2] [145-147]; MYBs from wheat (TaPIMP1) and rice (OsMYB4) [148, 149]; and WRKY TFs from rice (OsWRKY45) and grapevine (VvWRKY11) [150, 151].

3. APPLICATIONS OF TFs IN CROP IMPROVEMENT

To increase plant adaptation to stress(es) by transgenic approach, TFs have been considered an excellent target for manipulation. The advantage of using TFs is due to the fact that under environmental stress conditions, genes encoding TFs usually acquire early and appropriate alteration in transcriptional activity. Furthermore, since plant stress tolerance capacity is determined by multiple genes, using a functional gene encoding a single particular product seems to be less effective than using a TF-encoding gene in improving plant stress resistance. Each TF is a master regulator of a set of genes that include both regulatory and functional stress-responsive genes, some of which are even regulated by different pathways in response to various stimuli. Also, due to this nature of TF characteristics, enhancement of plant defense not only to a single stress but also to multiple stresses; a scenario that is commonly seen in fields, could be achieved. Table **2** summarizes several successful stories of development of transgenic crop plants with improved abiotic stress tolerance using TF-encoding genes over the last two years. In addition to the genes isolated from intensively studied sources, such as *Arabidopsis*, rice, legume and maize, genes retrieved from other plant species also showed promising results for being used as targets in engineering (Table **2**). For example, *DREB1* gene from the cold-tolerant plant *Adonis amurensis* (*AaDREB1*) had been cloned and transferred to rice and *Arabidopsis* under the control of constitutive promoter *35S*. The analyses revealed that the *AaDREB1*-overexpressing rice and *Arabidopsis* plants became more tolerant to not only low temperature but also drought and high salinity stress conditions [152].

TFs related to several large families as AP2/EREBP, bZIP, MYB, WRKY and NAC have been found to be widely used in applied research. Among these, DREB proteins should be noted as highly potential TF candidates for engineering and should be further investigated, since attempts with various DREB members from different species have shown promising outcomes towards improvement of plant tolerance to abiotic stresses, especially drought, salinity and cold conditions [88, 91, 92, 153-156]. Nevertheless, a smaller number of TFs from other families, such as bHLH (basic helix–loop–helix), HD-Zip (homeodomain-leucine zipper), MYC (myelocytomatosis related proteins), NF-Y (nuclear factor Y), HSF (heat shock factor) and GRAS (GAI – Gibberellin-acid insensitive, RGA – Repressor of GA1, SCR - Scarecrow), also displayed potential applications to cope not only with popular abiotic stresses like drought and salt [157-160] but also with other stresses such as nutrient deficiency [161], high light, heat shock [162] and anoxia [163]. Therefore, it might be worth investigating members of these families more thoroughly in the future.

A common strategy to find target TFs for engineering is by screening stress-responsive genes, followed by analyzing structure of the gene promoters so that appropriate TFs regulating the gene expression *via* interaction between *trans*- and *cis*- acting elements could be identified [86, 92, 164]. Alternatively, shortlist of potential genes including TFs could be established based on transcriptome profiling data obtained from plant tissues that were placed under non-stressed *versus* stressed conditions. In addition, following expression analysis to identify potential gene(s), *in planta* functional analysis of this/these gene(s) is still required for selecting the best candidates for genetic engineering. Fully characterizing post-transcriptional regulation and mode-of-action of the potential TFs is also necessary to obtain complete understanding about the TF functions and their interactions with other partners. To serve for functional analyses of TFs of interest, generation of mutant and overexpressing lines in both model (*e.g. Arabidopsis*, tobacco and rice) and crop species is usually made. Several TF-encoding genes in *Arabidopsis* confer similar abiotic stress tolerance capacity when being introduced to crop plants. HARDY (HRD), which is a TF belonging to the DREB IIIb subgroup, is an example for this [60]. *Arabidopsis* overexpressing *HRD* produced thicker leaves with more mesophyll cells, resulting in drought resistance. When transformed into rice, overexpression of this gene resulted in a transgenic plants with significantly improved drought tolerance and water use efficiency under both well-watered and drought conditions. Furthermore, these transgenic plants exhibited higher photosynthetic assimilation and reduction in transpiration, thus leading to increased biomass production under normal greenhouse conditions [165].

A number of factors need to be taken into account in order to identify excellent TF-encoding genes for engineering, including performance of the engineered host (i) under controlled greenhouse *versus* natural field conditions towards a particular type of abiotic stress or towards multiple stresses, and (ii) in maximizing survival rate *versus* minimizing yield loss challenged by the stressor. In addition, choice of promoter used to drive expression of the target gene is another important consideration in order to generate genetically modified plants exhibiting improved stress tolerance characteristics but minimal compromise in development or yield loss. Scientists might consider whether the use of a constitutive promoter (such as *CaMV 35S*, *Actin* and *Ubiquitin*), an inducible promoter (like *RD29A* and *4ABRC*), or a tissue/cell type-specific promoter to express the transfer gene is the optimal solution [166, 167]. To our knowledge, constitutive promoters are the most widely used to overexpress the transgenes [168]. However, constitutive overexpression of several stress-responsive TF-encoding genes may come with pleiotropic effects, such as growth retardation, late flowering or yield reduction, perhaps due to the unnecessary alteration in gene expression caused by the engineered TF under normal growing conditions [91, 114, 138, 169]. In order to manage this problem, the stress-inducible promoters can be an alternative choice of use to allow the transgene to rapidly express upon stress exposure only, while it is completely silenced under normal growing conditions [166]. An example to demonstrate this useful approach is that overexpression of *OsNAC6* in rice under control of either stress-inducible promoter *OsNAC6* or *LIP9* instead of *CaMV 35S* could improve salinity tolerance without any adverse consequence for plant growth and productivity [147]. Similarly, when overexpressing *Arabidopsis DREB1B* using *CaMV 35S* in tomato, enhanced drought tolerance of transgenic plants with side effects on phenotype and seed number was observed [170]. Replacing this promoter by *ABRC1* promoter obtained from barley, could overcome plant growth retardation problem of improved drought-tolerant transgenics under normal conditions [184].

Table 2. Study reports on improving tolerance in crop plants to abiotic stress using transcription factors within the last two years.

TF Family	Target Gene	Source	Recipient	Engineering Approach	Improved Trait(s)	Suggested Mechanisms for Stress Adaptation	References
AP2/ EREBP	*AaDREB1*	*Adonis amurensis*	Rice	Constitutive overexpression	Drought, salinity and freezing ↑	Preventing chlorophyll degradation, accumulation of more soluble sugars and proline	[152]
	OsEREBP1	*Oryza sativa*	Rice	Constitutive overexpression	Drought and submergence ↑	Enhancing jasmonate (JA) and ABA production, thereby preventing H_2O_2 accumulation and up-regulating expression of ABA- and JA-responsive genes	[171]
	AtDREB1A/ CBF3	*Arabidopsis thaliana*	*Citrus macrophylla*	Constitutive overexpression	Salinity ↑	Unclear	[172]
	EaDREB2	*Erianthus arundinaceus*	Sugarcane	Constitutive overexpression	Drought and salinity ↑	Improved membrane stability, increased relative water content (RWC) and chlorophyll content, higher stomatal closure rate and photosynthesis efficiency	[173]
	AtDREB1A	*Arabidopsis thaliana*	Peanut	Stress-inducible overexpression	Drought and salinity ↑	Higher proline accumulation, better osmotic adjustment and RWC maintenance, lower electrolyte leakage and chlorophyll degradation	[174]

(Table 2) contd….

TF Family	Target Gene	Source	Recipient	Engineering Approach	Improved Trait(s)	Suggested Mechanisms for Stress Adaptation	References
bZIP	*PtrABF*	*Poncirus trifoliata*	*Poncirus trifoliata*	Constitutive overexpression	Dehydration ↑	Reducing water loss by down-regulating stomatal development-related genes to decrease stomatal density, enhancing antioxidant enzyme activities and accumulation of various polyamines	[175]
MYB	*OsMYB91*	*Oryza sativa*	Rice	Constitutive overexpression	Salinity ↑	Higher proline, DELLA protein and ABA accumulation, increasing activities of peroxidase and catalase, up-regulating salt-stress-responsive genes	[176]
	OsMYB48-1	*Oryza sativa*	Rice	Constitutive overexpression	Drought and salinity ↑	Higher proline and ABA accumulation, regulating expression of ABA-biosynthetic genes, ABA early signaling genes and ABA late responsive genes	[177]
	LeAN2	*Lycopersicum esculentum*	Tomato	Constitutive overexpression	Heat ↑	Increasing content of D1 protein of photosystem II and photosynthesis rate, up-regulating anthocyanin biosynthesis-related genes, thereby increasing anthocyanin accumulation	[113]
WRKY	*MtWRKY76*	*Medicago truncatula*	*Medicago truncatula*	Constitutive overexpression	Drought and salinity ↑	Higher root-top rate, reducing electrolyte leakage, modulating stress response *via* interaction with ASR (ABA-, stress-, and ripening-induced)-related protein Medtr1g098680.1 and inducing certain abiotic-stress-responsive genes	[178]
	ZmWRKY58	*Zea mays*	Rice	Constitutive overexpression	Drought and salinity ↑	Higher level of RWC, lower membrane damage. ZmWRKY58 interacts with calmodulin ZmCaM2 in stress signal transduction pathway	[179]
NAC	*SNAC3*	*Oryza sativa*	Rice	Constitutive overexpression	Heat and drought ↑	Up-regulating expression of ROS-scavenging-related genes	[130]
	ONAC022	*Oryza sativa*	Rice	Constitutive overexpression	Drought and salinity ↑	Lower water loss and transpiration rate with increased stomatal closure, longer root system, higher accumulation of proline, ABA and soluble sugars, up-regulating ABA early signaling genes and ABA late responsive genes	[180]
	ATAF1	*Arabidopsis thaliana*	Rice	Constitutive overexpression	Salinity ↑	Up-regulating expression of stress-related genes *OsLEA3*, *OsSalT1* and *OsPM1*	[181]
	EcNAC67	*Eleusine coracana*	Rice	Stress-inducible overexpression	Drought and salinity ↑	Better RWC maintenance, probably due to better stomatal and root growth regulation	[182]

(Table 2) contd….

TF Family	Target Gene	Source	Recipient	Engineering Approach	Improved Trait(s)	Suggested Mechanisms for Stress Adaptation	References
Others	*OsGRAS23*	*Oryza sativa*	Rice	Constitutive overexpression	Drought and oxidative ↑	Up-regulating expression of anti-oxidation and defense response-related genes, increasing activities of superoxide dismutase and peroxidase	[159]
	Cdt-NF-YC1	*Cynodon dactylon x Cynodon transvaalensis*	Rice	Constitutive overexpression	Drought and salinity ↑	Up-regulating expression of ABA-biosynthesis-related genes as well as certain ABA-dependent and ABA-independent stress responses-related genes, thereby lowering electrolyte leakage and chlorophyll degradation but maintaining higher RWC	[183]

Another solution to cope with undesirable traits is to consider cell or tissue type-specific promoters. However, the number of research studies on comparative effects of this kind of promoters and constitutive promoters is relatively limited. In rice, a root-specific promoter, *RCc3*, has been investigated and compared with the constitutive promoter *GOS2* in terms of controlling the expression of different rice *NAC* genes to improve the plant drought tolerance capacity [185-187]. According to these reports, during the vegetative stage, the transgenic rice lines overexpressing *OsNAC5* [187], *OsNAC9* [186] and *OsNAC10* [185] driven by any of these promoters displayed better tolerance to drought stress than the wild-type rice plants. Nevertheless upon to the stress exposure at the reproductive stage of growth, the transgenic rice plants employing *RCc3* promoter conferred higher grain yields in comparison with the transgenic counterparts under the control of *GOS2* promoter. Further analyses revealed that the former transgenic plants with root-specific overexpression resulted in significantly larger roots and better filling rate, which have been suggested to be important characteristics for the plants in minimizing yield penalty [185-187]. In addition, using loss-of-function mutants as a less common approach, TFs that negatively regulate stress responses can be targeted for engineering to enhance plant stress tolerance. AtMYB14 [188] and AtMYB15 [189] were two MYB TFs that had been identified to negatively regulate the expression of downstream cold-stress-responsive genes *AtDREB1A*, *AtDREB1B* and *AtDREB1C* in *Arabidopsis*. When knocking down any of these genes by using miRNA, the mutant plants became more tolerant to freezing stress [188, 189]. More recently, ERF11 TF from *Betula platyphylla* (BpERF11) has been similarly shown to act as a negative regulator in plant response to salt and mannitol applications [190]. Furthermore, the *BpERF11*-knockdown lines obtained by using RNAi strategy exhibited improved tolerance to these abiotic stress conditions in comparison with the non-transgenic and *BpERF11*-overexpressing plants.

Noticeably, a number of transgenic plants possessing manipulated TF encoding genes have already been tested under field conditions to precisely evaluate the improvement of stress tolerance, mainly against drought. One of the most well-known examples is the enhanced performance of the *SNAC1*-overexpressing rice plants on tested fields under drought [191]. In comparison with the non-transgenic rice plants, the transgenics displayed higher seed-setting rate as well as postponed leaf rolling and reduced water loss [191]. Other field trial data that have been published with positive results of improved drought tolerance and higher productivity under the drought-prone areas include rice transformed with various constructs, namely *OsCc1:AP37* [65], *RCc3:OsNAC5* [187], *RCc3:OsNAC9* [186] and *RCc3:OsNAC10* [185]; maize transformed with *OsRACT:ZmNF-YB2* [157]; peanut transformed with *RD29A:AtDREB1A* [192]; and soybean with *35S:AtMYB44* [115].

CONCLUSION

Drought, high salinity and cold are among the serious abiotic stresses, which cause yield loss worldwide. Therefore, the need for production of stress-tolerant crops needs to be quickly implemented with genetic engineering being at the forefront. Among the target genes for manipulation, the use of TFs has been suggested as they have potential to evoke a new revolution in biotechnology, upon which novel crop cultivars with improved resistance to abiotic and/or biotic stresses could be successfully generated. However, although there have been numerous reports on development of robust stress tolerant phenotypes by overexpressing a TF-encoding gene in the target host plant under controlled growth conditions at various developmental stages, the number of field trials of testing and validating the performance of these genetically modified varieties under natural conditions during their whole life span is still limited. Consequently, this hinders the identification of novel crop varieties that can be commercially launched into the market. In parallel with phenotypic and productivity examination, another challenge remains for the scientists is to work out the mechanisms controlled by various complex pathways that participate in shaping the behavior of the engineered plants under normal, single stress or multiple stress conditions. Studies at large scales using omic data are believed to have essential contribution in accelerating the speed of acquiring such knowledge.

CONFLICT OF INTEREST

The authors declare no conflict of interest, financial or otherwise.

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