agronomy

Review

The Role of Stress-Responsive Transcription Factors in Modulating Abiotic Stress Tolerance in Plants

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Abstract: Abiotic stresses, such as drought, high temperature, and salinity, affect plant growth and productivity. Furthermore, global climate change may increase the frequency and severity of abiotic stresses, suggesting that development of varieties with improved stress tolerance is critical for future sustainable crop production. Improving stress tolerance requires a detailed understanding of the hormone signaling and transcriptional pathways involved in stress responses. Abscisic acid (ABA) and jasmonic acid (JA) are key stress-response hormones in plants, and some stress-responsive transcription factors such as ABFs and MYCs function as direct components of ABA and JA signaling, playing a pivotal role in plant tolerance to abiotic stress. In addition, extensive studies have identified other stress-responsive transcription factors belonging to the NAC, AP2/ERF, MYB, and WRKY families that mediate plant response and tolerance to abiotic stress. These suggest that transcriptional regulation of stress-responsive genes is an essential step to determine the mechanisms underlying plant stress responses and tolerance to abiotic stress, and that these transcription factors may be important targets for development of crops with enhanced abiotic stress tolerance. In this review, we briefly describe the mechanisms underlying plant abiotic stress responses, focusing on ABA and JA metabolism and signaling pathways. We then summarize the diverse array of transcription factors involved in plant responses to abiotic stress, while noting their potential applications for improvement of stress tolerance.

Keywords: Abiotic stress; tolerance; Transcription factor; Abscisic acid; Jasmonic acid

1. Introduction

Stress-responsive transcription factors play essential roles in abiotic stress responses and stress tolerance [1,2]. Therefore, these stress-responsive transcription factors may be important targets for developing crops with enhanced abiotic stress tolerance [3]. Plant stress hormones, such as abscisic acid (ABA) and jasmonic acid (JA), regulate plant abiotic stress responses [4,5]. ABA signaling pathways activate target transcription factors, such as the basic leucine zipper (bZIP) ABA-responsive element binding factor (ABF) transcription factors, and JA signaling pathways activate the basic helix-loop-helix (bHLH) MYC transcription factors. These transcription factors control ABA- and JA-dependent expression of stress-responsive genes, as demonstrated using knock-out and overexpression systems [6–8]. In addition, experimental and computational approaches have identified other stress-responsive transcription factors belonging to the NAC, AP2/ERF, MYB, and WRKY families, which are not direct components of ABA and JA signaling pathways but are essential for plant abiotic stress responses. In this review, we describe the roles of ABA and JA metabolism and signaling pathways, and of ABA and JA signaling-specific bZIP and bHLH transcription factors in plant abiotic stress responses. We also summarize other stress-responsive transcription factor families, such as NAC, AP2/ERF, MYB, and WRKY, which are involved in abiotic stress tolerance, and discuss studies using these transcription factors to improve abiotic stress tolerance in plants.

2. ABA Signaling and ABF Transcription Factors

2.1. ABA Metabolism

The key stress hormone ABA mediates plant responses to abiotic stress. For example, ABA mediates stress-induced modulation of plant development, such as root growth inhibition, leaf senescence, and stomatal closure [9,10]. ABA is biosynthesized through the enzymatic activity of 9-cis-epoxycartotenoid dioxygenase (NCED), abscisic aldehyde oxidase (AAO), cytosolic short-chain dehydrogenase/reductase (SDR), and MOLYBDENUM COFACTOR SULFURASE (MCSU), which mediate the production of xanthoxin, an ABA precursor, and the conversion of xanthoxin to ABA [11,12]. Abiotic stress promotes ABA biosynthesis [13]. Mass transcription of the genes encoding the key ABA biosynthetic enzymes is largely responsible for ABA production in response to abiotic stresses such as drought and osmosis, and many stress-responsive transcription factors, including members of the bZIP, MYC, NAC, AP2/ERF, and MYB families, are involved in the transcription of ABA biosynthesis genes [14–19]. ABA degradation also controls cellular ABA levels. The formation of ABA-glucose ester by UDP glucosyltransferase (UGT) is involved in ABA degradation, but ABA hydroxylation by cytochrome P450 monooxygenase 707A family members (CYP707As) appears to be largely responsible for ABA degradation [20]. Similar to the ABA biosynthetic genes, expression of *CYP707As* is regulated by abiotic stresses, such as drought, salinity, and oxidative stress. Moreover, knock-out or knock-down of *CYP707As* increase ABA levels, suggesting that CYP707A-mediated ABA degradation is an important process controlling cellular ABA levels [20–22]. The finding that ABA response and abiotic stress tolerance is altered in plants with knock-out or overexpression of ABA biosynthetic genes, including *NCED*, indicates that ABA metabolism is an essential step controlling plant abiotic stress responses [23]. Although ABA transport has not been fully elucidated, the results showing that ABA accumulates in roots and xylem sap in response to drought suggest that ABA synthesized in roots is transported to shoots through xylems [24,25].

2.2. ABA Signaling and ABF Transcription Factors

The ABA signaling pathway initiates with recognition of ABA by a complex including Pyrabactin Resistance 1 (PYR1)/PYR-Like (PYL)/Regulatory Component of ABA Receptor (RCAR) and signal transduction by Protein Phosphatase Type 2Cs (PP2Cs), and SNF1-Related Protein KINASES TYPE 2s (SnRK2s) [26]. These activate the ABA signaling-specific ABA-Responsive Element Binding Factor (ABF) transcription factors, which belong to a distinct subfamily of bZIP transcription factor, and regulate the expression of ABA-responsive genes, leading to the establishment of stress-specific transcription [27–29]. SnRK2s activate ABFs through direct phosphorylation. In the absence of ABA, PP2Cs inhibit the kinase activity of SnRK2s, thus blocking activation of the ABFs. When plants are exposed to abiotic stress, ABA biosynthesis is promoted, resulting in formation of the PYR/PYL–PP2C complex, which inhibits PP2C activity, thus activating SnRK2s to phosphorylate and activate ABFs [30] (Figure 1). The activated ABFs directly bind to the ABA-responsive element (ABRE), a major *cis*-element in ABA-responsive genes [31], and activate the transcription of other stress-responsive transcription factors, such as NACs and AP2/ERFs, which are also responsible for the expression of stress-responsive genes [32]. This transcriptional cascade changes the genome-wide transcription profile, inducing the plant defense system, to adapt to and survive the abiotic stress, suggesting that stress-responsive bZIPs, including ABFs, are essential components of the plant response and tolerance to abiotic stress [33,34].

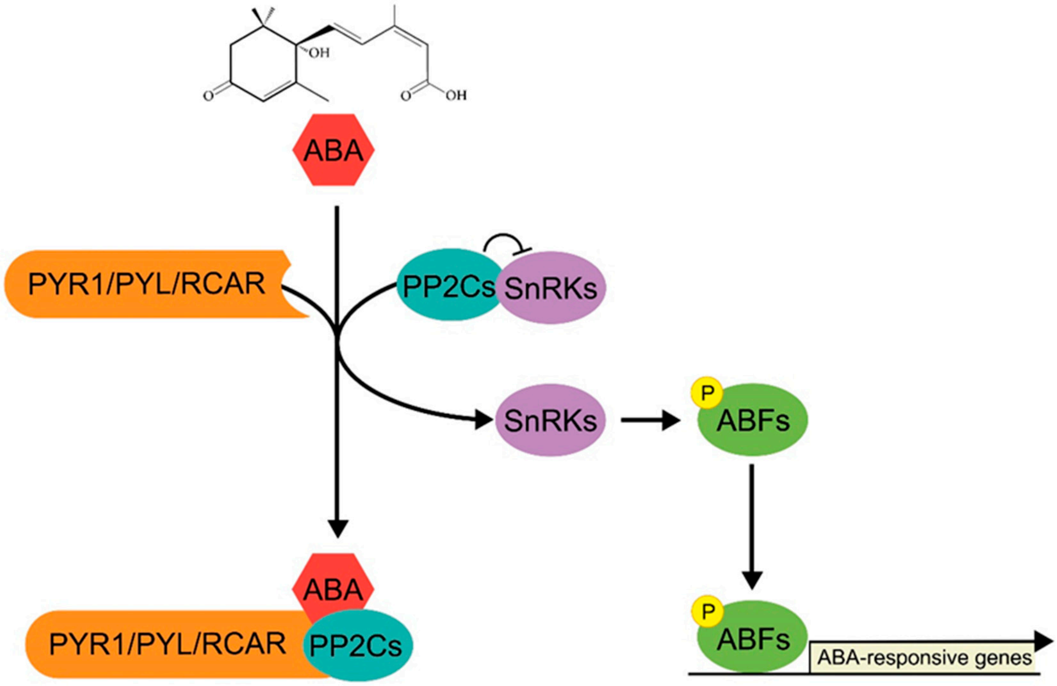

Figure 1. A schematic of ABA signaling pathway. In response to ABA, ABA receptor PYR1/PYL/RCAR forms a complex with PP2Cs, and activates SnRKs, the kinases that determine the activity of ABF transcription factors. SnRK-mediated phosphorylation of ABF promotes expression of ABA-responsive genes and ABA response.

The pivotal functions of ABFs in the ABA response and abiotic stress tolerance have been well documented in *Arabidopsis thaliana*. The transcription of *ABF1*, *2*, *3*, and *4* is strongly upregulated by ABA or abiotic stress, and overexpression of *ABF3* and *4* promotes the expression of ABA-responsive genes, such *ABA-INSENSITIVE 1* (*ABI1*) and *ABI2*, which encode PP2Cs, and whose mutations cause defects in ABA-dependent stomatal closure [35–37]. Furthermore, overexpression of *ABF3* and *4* significantly improves drought tolerance. For example, most wild-type plants withered by approximately 10 days of drought stress, whereas *ABF3*- and *4*-overexpressing transgenic plants survived the drought stress [36]. In contrast to the *ABF3*- and *4*-overexpressing plants, the *abf2 abf3 abf4* triple mutant exhibited reduced drought tolerance compared to wild-type plants, and large-scale transcriptome analysis showed that expression of stress-responsive genes is impaired in the triple mutant [27]. These studies indicate that ABFs play an essential role in the plant response to abiotic stress. Moreover, *ABF3* and *4* are predominantly expressed in roots, suggesting that *ABF3* and *4* are involved in ABA response in roots [27,36]. Despite the functional redundancy of ABFs in ABA response and stress tolerance, it is likely that their functions do not completely overlap [36,38].

ABFs mediate stress-induced changes in plant development. For example, abiotic stress accelerates flowering and shortens the plant life cycle. A recent study by Hwang et al. revealed that *ABF3* and *4* regulate flowering time by controlling the expression of the floral integrator *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) [38]. Mutant plants that lack expression of *ABF3* and *4* exhibit reduced expression of *SOC1* and showed an ABA-insensitive late flowering phenotype, whereas transgenic plants ectopically expressing ABF3 or 4 displayed an early flowering phenotype. Together with the result that *SOC1* is a direct downstream target of ABF3 and 4 transcription factors, these findings suggest that stress-responsive ABFs mediate ABA-dependent modulation of plant growth and development under stress conditions.

The function of ABFs in abiotic stress tolerance is conserved in plants. For example, ABA and abiotic stress upregulate the *Fagopyrum tataricum* FtbZIP5 and *Poncirus trifoliata* PtrABF bZIP transcription factors. *FtbZIP5*-overexpressing *Arabidopsis* plants exhibited improved tolerance to drought, salinity, and oxidative stress by modulating the antioxidant system [39]. Similar to *FtbZIP5*, overexpression of *PtrABF* enhanced abiotic stress tolerance in tobacco [40]. This indicates functional conservation of stress-responsive bZIPs in plants, suggesting that modulation of the stress-responsive bZIPs could be a good strategy for development of crops with improved stress tolerance. For example, ABA and abiotic stress induce the expression of rice (*Oryza sativa*) *OsbZIP23* [41] and transactivation assays showed that OsbZIP23 is a transcriptional activator. Overexpression of *OsbZIP23* increased sensitivity to ABA and improved the tolerance to abiotic stress, including drought and salinity.

Other stress-responsive rice bZIPs showed similar functions in abiotic stress tolerance to that of OsbZIP23. For example, OsbZIP12 and OsbZIP71 conferred drought tolerance by increasing sensitivity to ABA, and OsbZIP46 and OsbZIP72 improved drought tolerance in rice and *Arabidopsis* [36,42–46]. *ZmbZIP4* is a stress-responsive maize (*Zea mays*) bZIP transcription factor with high sequence similarity to OsbZIP23 [47]. Similar to *OsbZIP23*, overexpression of *ZmbZIP4* increased ABA levels and enhanced abiotic stress tolerance by activating the transcription of stress-responsive genes. Interestingly, ZmbZIP4 also affects expression of genes involved in root development in maize, such as *ZmLRP1*, *ZmSCR*, *ZmIAAs*, and *ZmARFs*, and *ZmbZIP4*-overexpressing transgenic plants formed longer roots with an increased number of lateral roots. These results suggest that ZmbZIP4 positively regulates plant abiotic stress responses and is involved in root development in maize [47].

3. JA Signaling and MYC Transcription Factors

3.1. JA Metabolism

JA regulates plant responses to environmental stresses and modulates development under stress conditions [48,49]. JA, a cyclopentane fatty acid, and was initially isolated as a methyl ester from *Jasminum grandiflorum*. JA is biosynthesized from linolenic acid via the octadecanoid pathway involving a variety of enzymatic components, such as lipoxygenase (LOX), allene oxide synthase (AOS), allene oxide cyclase (AOC), and 12-oxo-PDA reductase (OPR) [50,51]. The free acid form of JA, which is produced through the octadecanoid pathway, is further metabolized into the JA-isoleucine conjugate (JA-Ile) or methyl jasmonate (MeJA) through the activity of jasmonate-amido synthetase 1 (JAR1) and jasmonate methyl transferase (JMT), respectively [52,53]. JA-Ile is an active form of JA that interacts with JA receptors to promote the JA-dependent stress response [54]. In response to abiotic stress, the expression of JA biosynthesis genes is dynamically upregulated, leading to increases in endogenous JA levels. For example, cold temperature stress rapidly activated the JA response by inducing expression of JA biosynthesis genes such as *LOX, AOS*, and *AOC* in *Arabidopsis* and rice [55,56]. Furthermore, exogenous JA treatments improved freezing tolerance, and the JA-deficient mutants *lox2* and *aos* exhibited reduced tolerance to freezing compared to wild-type plants [55]. In addition, transgenic *Arabidopsis* plants overexpressing wheat (*Triticum aestivum*) *AOC1* (*TaAOC1*) showed enhanced tolerance to salt stress by activating JA biosynthesis [57,58]. These studies support the view that JA is a key hormone mediating plant responses and tolerance to abiotic stress, indicating that JA metabolism is a key step controlling the JA response in plants. Similar to ABA, JA transport remains largely unknown. A radioisotopic labeling experiment suggested that JA is transported both through phloem and xylem [59]. However, a recent study using a micrografting experiment suggested shoot-to-root JA transport mainly though phloem, and this finding is partially supported by phloem-specific accumulation of JA biosynthetic enzymes such as LOX and AOS [60,61].

3.2. JA Signaling and MYC Transcription Factors

Early studies on JA revealed that the expression of genes involved in plant defenses is rapidly and dynamically regulated by exogenous JA treatment, indicating the existence of a JA-specific signaling pathway and the integral role of JA in modulating stress-related transcription networks [62,63]. In *Arabidopsis*, identification of JA signaling components, including the JA receptor CORONATINE INSENSITIVE 1 (COI1) and the JA signaling repressors JASMONATE ZIM-DOMAIN proteins

(JAZs), have extended our understanding of the JA signaling pathway and establishment of JA-dependent transcription. In response to abiotic stress, JA, especially JA-Ile, activates JA signaling through interaction with COI1. This interaction induces 26S proteasome-mediated proteolysis of JAZs. In the absence of JA, the activity of the MYC2 transcription factor, which governs the expression of JA-dependent stress-responsive genes, is suppressed through its interaction with JAZ proteins. The degradation of JAZs liberates MYC2, which then activates the expression JA-responsive genes [64–67] (Figure 2). This indicates a pivotal role of MYC2 in the JA response, and the finding that expression of *MYC2* is regulated by diverse abiotic stresses, including drought and salinity, suggests that MYC2 is involved in the plant response and tolerance to abiotic stress [68–70]. MYC2 was identified in a mutant screen for insensitivity to exogenous JA, and further characterization revealed that MYC2 is a key component of the JA signaling pathway [71]. MYC2 contains a conserved bHLH domain required for the formation of homo- or hetero-dimers with other JA-responsive MYCs such as MYC3 and MYC4 [72]. The basic region of the MYC2 protein is responsible for its interaction with DNA (G-box; 5′-CACGTG-3′) [73]. Expression of *MYC2* is involved in the plant response and tolerance to abiotic stress such as oxidative stress. Ascorbate is a major reactive oxygen species (ROS) scavenger in plants [74]. Exogenous JA treatment increases ascorbate levels by inducing ascorbate biosynthesis genes such as *DEHYDROASCORBATE REDUCTASE* and *ASCORBATE PEROXIDASE*, and knock-out mutant plants that lack MYC activity display reduced expression of genes involved in oxidative stress tolerance [69,75]. This suggests that MYC2 positively regulates oxidative stress tolerance, and the result that *MYC2*-overexpressing transgenic plants show improved tolerance to oxidative stress further supports this.

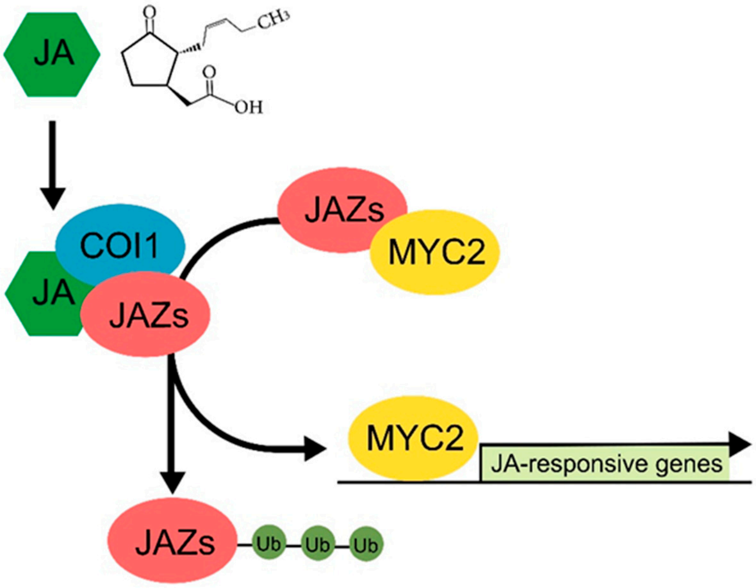

Figure 2. A schematic of JA signaling pathway. MYC2 is a key transcription factor responsible for expression of JA-responsive genes. In the absence of JA, the transcription activity of MYC2 is suppressed by direct interaction with JAZs. In JA condition, JA interacts with the JA receptor COI1 and provokes ubiquitin (Ub)-mediated proteolysis of JAZs, leading to activation of MYC2 and expression of JA-responsive genes.

MYC transcription factors, which are characterized by the basic helix-loop-helix (bHLH) domain, belong to a subfamily of bHLH transcription factors [76,77]. The family of bHLH transcription factors is widespread in eukaryotes, and has expanded in plants [78,79]. Based on the sequence similarity of the bHLH domain, it has been suggested that *Arabidopsis* contains approximately 160 bHLH transcription factors, and many bHLH transcription factors, including AtbHLH17, AtbHLH68, and AtbHLH122, are involved in plant abiotic stress responses [80–83]. The function of bHLH transcription factors in abiotic stress tolerance is conserved in plants, as supported by studies showing that heterologous expression of *F. tataricum FtbHLH2* and *3*, and *Populus euphratica PebHLH35* in *Arabidopsis* enhanced tolerance to abiotic stresses, such as cold, drought, and oxidative stress [82,84,85].

In rice, OsbHLH148 has a similar activity to MYC2 [86]. OsbHLH148 directly interacts with JAZ proteins, suggesting that OsbHLH148 act as a JA signaling component in rice. The expression of *OsbHLH148* is rapidly upregulated by JA and diverse abiotic stresses such as drought, salinity, cold, and wounding. Furthermore, transgenic rice overexpressing *OsbHLH148* exhibited increased transcript levels of *DEHYDRATION-RESPONSIVE ELEMENT-BINDING PROTEINS* (*OsDREBs*), which are involved in the drought-stress response, and displayed enhanced tolerance to drought [86]. This suggests that stress-responsive bHLH transcription factors, including MYC2 and OsbHLH148, play an essential role in plant response and tolerance to abiotic stress. Indeed, studies using stress-responsive bHLH transcription factors, such as INDUCER OF CBF EXPRESSION 1 (ICE1) and ICE2, support this [55,87].

In addition, stress-responsive bHLH transcription factors, including MYC2 and OsbHLH148, are involved in ABA-mediated stress tolerance [86,88]. Expression of *MYC2* and *OsbHLH148* is strongly upregulated by ABA and ABA-related stresses. In addition, MYC2 promotes the expression of ABA and the dehydration-responsive gene *rd22* by directly interacting with its promoter, and *myc2* mutant plants show reduced sensitivity to ABA [88]. These results suggest that JA interacts with ABA to modulate stress response and tolerance, and stress-responsive bHLH transcription factors are involved in the JA–ABA crosstalk. This idea is supported by increasing evidence showing that ABA is involved in modulation of stress tolerance by stress-responsive bHLH transcription factors [89–91]. In addition, the results showing that activation of JA biosynthesis by jasmonic acid methyltransferase (JMT) promotes ABA production, and that the ABA receptor PYL6/RCAR9 interacts with MYC2 also support this [92,93].

4. Other Transcription Factors Involved in Plant Tolerance to Abiotic Stress

4.1. NAC Transcription Factors

NAC (NO APICAL MERISTEM (NAM), ARABIDOPSIS TRANSCRIPTION ACTIVATOR FACTOR 1/2 (ATAF1/2), and CUP-SHAPED COTYLEDON 2 (CUC2)) transcription factors are plant-specific transcription factors [94,95]. Plants contain more than 100 NAC transcription factors, indicating that the NACs constitute one of the largest families of transcriptional regulators in plants. This suggests that NAC-dependent transcription networks are involved in many biological processes in plants [96,97]. NAC transcription factors contain a conserved NAC domain in the N-terminal region and a regulatory domain in the C-terminal region, which are responsible for DNA binding and transcriptional regulation, respectively [98,99]. The expression of many *NACs* is regulated by abiotic stress. For example, Jiang and Deyholos (2006) reported that the expression of 33 *NAC* genes was significantly upregulated by salt stress in *Arabidopsis* [100], and Fang et al. (2008) and Le et al. (2011) reported that the expression of approximately 40 *NACs* was upregulated in response to abiotic stresses, such as drought and salinity, in rice and soybean [101,102]. These studies suggested that stress-responsive NACs are involved in plant abiotic stress responses. Indeed, many studies of stress-responsive NACs including *ANAC019*, *ANAC055*, *ANAC072*, *OsNAC6*, *OsNAC5*, *OsNAC9*, and *OsNAC10*, have demonstrated this [103–107].

EARLY RESPONSIVE TO DEHYDRATION STRESS 1 (*ERD1*), encoding a chloroplast ATP-dependent protease, is involved in the response to abiotic stresses [108]. *ERD1* expression is tightly regulated by abiotic stress, and the stress-responsive expression pattern of *ERD1* largely depends on a CATGTG motif in its promoter. ANAC019, ANAC055, and ANAC072, which interact with the motif, are responsible for the expression of *ERD1* [103], and further characterization of *ANAC019*, *ANAC055*, and *ANAC072* revealed that their expression is induced by diverse abiotic stresses, such as drought and salinity, and by ABA, and overexpression of these NACs significantly increases drought tolerance. In contrast to the overexpressing plants, mutant plants that lack the activity of ANAC019, ANAC055, and ANAC072 displayed reduced tolerance to salt stress compared to wild-type control plants [109]. These findings suggest that stress-responsive NACs play a crucial role in plant tolerance to abiotic stress, and the results of other stress-responsive NACs, such as *RD26* and *ANAC042*, support this [7,110].

The function of stress-responsive NACs is conserved in plants. Heterologous overexpression of *Arabidopsis ANAC042/AtJUB1* improved abiotic stress tolerance in tomato (*Solanum lycopersicum*) and *Arabidopsis* [110,111]. In addition, transgenic *Arabidopsis* plants expressing stress-responsive wheat *TaNAC29* exhibited enhanced tolerance to high salinity by reducing the accumulation of hydrogen peroxide [112]. This suggests that stress-responsive NACs would be good targets for improvement of abiotic stress tolerance in crops. For example, OsNAC6 is a rice NAC transcription factor, and its expression is upregulated by a variety of abiotic stresses [104]. *OsNAC6*-overexpressing transgenic rice showed enhanced tolerance to drought, whereas *OsNAC6* knock-out mutants displayed reduced tolerance compared to wild-type control plants. This indicated that *OsNAC6* positively regulates abiotic stress tolerance [112]. In addition, genome-wide transcription profiling revealed that *OsNAC6* regulates the expression of nicotianamine biosynthesis genes such as *NICOTIANAMINE SYNTHASE 2* (*NAS2*), and overexpression of *NAS2* improved tolerance to drought. These findings suggest that *OsNAC6* modulates plant tolerance to drought by regulating nicotianamine biosynthesis [113].

The essential role of stress-responsive OsNACs in stress tolerance was also shown in other studies using *OsNAC5*, *OsNAC9*, and *OsNAC10*. Similar to *OsNAC6*, expression of *OsNAC5*, *OsNAC9*, and *OsNAC10* is activated by abiotic stress, and overexpression of these transcription factors significantly improved drought tolerance [105–107]. Consequently, grain yields of the *OsNACs*-overexpressing transgenic rice plants were higher than that of wild-type control plants under stress conditions. Unlike these NACs, *OsNAC2* negatively regulates plant tolerance to drought stress [114], suggesting that stress-responsive transcription factors including NACs are involved in negative regulation of plant tolerance to abiotic stresses [115]. Previous studies also show that NACs mediate modulation of plant growth and development under stress conditions. For example, overexpression of *OsNAC5*, *OsNAC9*, and *OsNAC10* promoted root growth, suggesting that these stress-responsive NACs are involved in developmental changes under stress conditions [116]. A wheat NAC transcription factor, TaRNAC1, showed a similar function to the rice NACs; overexpression of *TaRNAC1* resulted in enhanced dehydration tolerance, and promoted root growth in wheat [117].

Despite the crucial role of NAC transcription factors in abiotic stress tolerance, the regulatory interactions between NACs and ABA, or NACs and JA remain largely unknown. However, increasing evidence suggests that NACs cooperate with ABA and JA to modulate plant responses and tolerance to abiotic stress. For example, the expression of many *NACs* is regulated by ABA and JA, as well as abiotic stress [103,105–107,118]. Furthermore, the *Arabidopsis* NAC transcription factor ANAC096 directly interacts with ABF2 and 4, which are key transcription factors of ABA signaling, to regulate dehydration and osmotic stress responses, and the *Arabidopsis* NAC transcription factor VASCULAR-RELATED NAC-DOMAIN-INTERACTING 2 (VNI2) integrates ABA signals into leaf senescence [119,120]. In addition, ANAC019 and ANAC055 regulate the JA-signaled defense response, and the rice NAC transcription factor RIM1 functions as a regulator of JA signaling [121,122]. These findings suggest that NACs are fundamentally involved in ABA- and JA-mediated modulation of abiotic stress responses in plants.

4.2. AP2/ERF Transcription Factors

The APETALA 2/ETHYLENE-RESPONSIVE FACTOR (AP2/ERF) transcription factor family comprises a large group of plant-specific transcription factors (122 AP2/ERFs in *Arabidopsis* and 139 in rice) that includes four major subfamilies, AP2, RELATED TO ABSCISIC ACID INSENSITIVE 3/VIVIPAROUS 1 (RAV), ETHYLENE-RESPONSIVE FACTOR (ERF), and DEHYDRATION-RESPONSIVE ELEMENT-BINDING PROTEIN (DREB) [123–125]. Genome-wide transcription profiling studies showed that expression of most *AP2/ERFs* is activated by abiotic stress, and this activation largely depends on the stress or ABA-responsive *cis*-elements of their promoter regions. For example, the *Arabidopsis* AP2/ERF transcription factor DREB2A plays a key role in controlling plant tolerance to abiotic stresses such as drought, and the expression of *DREB2A* is controlled by a direct interaction between stress-signaling proteins, such as ABFs and the ABA-Responsive Element (ABRE) of the *DREB2A* promoter [126,127]. AP2/ERF transcription factors contain an AP2 domain consisting of approximately 60 amino acids in the N-terminal region and a regulatory domain in the C-terminal region, which are responsible for the activity of DNA binding and transcriptional regulation, respectively [125].

AP2/ERFs play an essential role in plant response and tolerance to abiotic stress by regulating the expression of stress-responsive genes. DREB1s/C-REPEAT-BINDING FACTORS (CBFs), belonging to the AP2/ERF transcription factor family, are key regulators of plant response to cold temperature stress [128]. Expression of *DREB1s/CBFs* is strongly upregulated by cold, and overexpression of *DREB1s* enhances plant tolerance to freezing stress in *Arabidopsis*. In contrast to the overexpressing plants, knock-out mutants that lack the activity of DREB1s displayed reduced tolerance to freezing temperatures, indicating a pivotal role of *DREB1s* in cold stress tolerance [129]. Expression of *DREB1s* also affects plant tolerance to drought and salt stress, and it is likely that expression of a common set of stress-responsive gene is involved in this phenomenon [125,130,131]. The crucial role of AP2/ERFs in plant stress tolerance was also shown in other subfamilies of the AP2/ERFs in *Arabidopsis*. AtERF53 is a stress-responsive AP2/ERF transcription factor and its overexpression confers enhanced tolerance to heat stress and drought in *Arabidopsis* [132,133]. Similar to *AtERF53*, transgenic plants overexpressing *AtERF74* displayed enhanced tolerance to drought, whereas *AtERF74* knock-out mutants exhibited reduced tolerance [133]. Furthermore, the peanut (*Arachis hypogaea*) *AP2/ERF* transcription factor *AhDREB1* improved tolerance to osmotic stress in *Arabidopsis* [134]. These studies indicate a crucial role of AP2/ERFs in stress tolerance, and that the function of stress-responsive AP2/ERFs is conserved in plants.

Because of the essential role of AP2/ERFs in stress tolerance, many studies have aimed to identify and characterize stress-responsive AP2/ERFs in crops. For example, the rice stress-responsive AP2/ERFs OsDREB1, OsEREBP1, and OsERF71 mediate abiotic stress responses in rice. The expression of *OsDREB1*, *OsEREBP1*, and *OsERF71* is regulated by abiotic stress, and their overexpression improved abiotic stress tolerance in rice by regulating the expression of stress-responsive genes [135–139]. Interestingly, the stress-responsive OsERF71 also regulates lignin biosynthesis by directly regulating the expression of lignin biosynthesis genes such as *CINNAMOYL-COENZYME A REDUCTASE 1* [137]. Lignin biosynthesis affects drought stress because lignin, a key component of plant secondary cell walls, is hydrophobic and inhibits water loss from plant tissues [140]. Indeed, drought-tolerant inbred lines displayed increased levels of lignin compared to drought-sensitive lines in maize [141]. These studies suggest that OsERF71 regulates plant tolerance to drought stress by controlling lignin biosynthesis. Many stress-responsive AP2/ERFs have been identified in other crops besides rice, including soybean ERF3, maize DREB2A, and tomato SlERF5, based on their stress-responsive expression patterns and functions in abiotic stress tolerance [17,142–144]. This further suggests that AP2/ERF transcription factors are critical for meditating plant response and tolerance to abiotic stress.

It has been suggested that DREBs regulate plant response to abiotic stress in an ABA-independent manner [145]. However, increasing evidence suggests that several stress-responsive AP2/ERFs are involved in ABA-dependent stress responses [17,132,134,137,139,146]. Furthermore, a study by Feng et al. (2014) showed that the AP2/ERF transcription factor RAV1 directly interacts with SnRK2s, which are key kinases that determine the activity of ABFs, and regulates ABA sensitivity [147]. This finding supports the idea that some AP2/ERF transcription factors are involved in ABA-dependent stress responses. In addition, a recent study showed that OCTADECANOID-RESPONSIVE AP2/ERF TRANSCRIPTION FACTOR 47 (ORA47) regulates the biosynthesis of JA, suggesting that AP2/ERFs might be involved in modulation of JA -mediated plant responses [17].

4.3. MYB Transcription Factors

MYB transcription factors are named for the conserved MYB domain responsible for DNA binding, and constitute a large family of transcription factors [148]. The MYB domain is composed of approximately 50 amino acids and MYB transcription factors are divided into four subfamilies based on the number and the position of MYB repeats: 1R-, R2R3, R1R2R3-, and 4R-MYB [149]. R2R3-MYBs are plant-specific MYB transcription factors, and it has been suggested that plants have approximately 100 R2R3-MYBs [150,151]. Genome-wide transcription profiling showed that expression of many *MYBs* and genes with MYB-binding elements are regulated by abiotic stresses such as drought [152–155], suggesting that MYBs are involved in plant responses and tolerance to abiotic stress. MYBs tend to interact with other transcription factors, and direct interaction between MYBs and stress-responsive transcription factors, such as MYCs and WRKYs, support the finding that MYBs are involved in plant response and tolerance to abiotic stresses [156–158]. The role of MYBs in abiotic stress response have been further demonstrated by functional characterization studies using overexpression and knock-out systems. For example, *AtMYB44* regulates drought tolerance in *Arabidopsis* [159]. *AtMYB44* is specifically expressed in guard cells, and the expression is activated by abiotic stresses such as drought, cold, and salinity. Furthermore, overexpression of *Arabidopsis AtMYB44* increases ABA sensitivity and ABA-induced stomatal closure, leading to improved tolerance to drought stress. By contrast, *atmyb44* knockout plants displayed increased sensitivity to drought stress, indicating that *AtMYB44* positively regulates drought tolerance by modulating ABA-dependent stomatal closure [159]. *AtMYB96* is also involved in drought tolerance in *Arabidopsis* [160,161]. Expression of *AtMYB96* is induced by drought and ABA, and overexpression of *AtMYB96* enhanced drought resistance by activating cuticular wax biosynthesis, which inhibited water loss through the leaf surface. This result is supported by a study in *Camelina sativa* in which heterologous overexpression of *AtMYB96* resulted in improved drought tolerance via cuticular wax accumulation, similar to *Arabidopsis* [162], suggesting that the function of AtMYB96 in cuticular wax synthesis and drought tolerance is conserved among plants.

MYBs are also involved in salt stress. Expression of *AtMYB20* is upregulated by salt stress, and transgenic plants overexpressing *AtMYB20* showed improved tolerance to salt stress [163]. By contrast, suppression of *AtMYB20* resulted in hypersensitivity to salt stress, indicating that *AtMYB20* positively regulates plant tolerance to salt stress. Similar to *Arabidopsis*, many stress-responsive MYBs have been identified in crops, including rice and soybean, based on their expression patterns and functions in abiotic stress tolerance. For example, *OsMYB4*, *OsMYB6*, *OsMYB48-1*, and *OsMYB91* were identified in rice, and *GmMYB76*, *GmMYB92*, and *GmMYB177* in soybean [164–168]. The interaction between MYBs and ABA is largely unknown, but several studies showing that the expression of many stress-responsive *MYBs* is also regulated by ABA and JA suggest that MYBs are involved in modulation of ABA- and JA-dependent stress responses. This is partially supported by studies showing that *AtMYB20* suppresses the expression of *PP2Cs*, which encode negative regulators of ABA signaling, and AtMYB21 and 24 directly interact with the JA signaling repressors JAZs [169].

4.4. WRKY Transcription Factors

WRKY transcription factors contain a highly conserved WRKYGQK motif in their N-terminal region and a novel zinc-finger-like motif at their C-terminal region [170]. WRKY transcription factors constitute a large family in plants. For example, the *Arabidopsis*, rice, and soybean genomes are predicted to have approximately 74, 103, and 197 WRKYs, respectively [170–172]. Stress-responsive expression patterns of *WRKYs* have suggested their involvement in plant response to abiotic stress. For example, a microarray analysis showed that the expression of 18 *WRKYs* (among 35 *WRKYs* tested) is induced by salt stress [100]. The involvement of WRKYs in plant stress responses has been demonstrated through functional characterization using knock-out or overexpression systems. In Arabidopsis, heat stress affects the expression of *AtWRKY25*, *26*, and *33* [173]. In normal growth conditions, germination and growth of *wrky25 wrky26* and *wrky25 wrky33* double mutants and the *wrky25 wrky26 wrky33* triple mutant were similar to those of wild-type control plants. However, these mutants were hypersensitive to heat stress, and their survival rate was significantly decreased. By contrast, transgenic plants overexpressing *WRKY25*, *WRKY26*, and *WRKY33* displayed enhanced tolerance to heat stress, providing evidence that *WRKY25*, *WRKY26*, and *WRKY33* positively regulate plant tolerance to heat stress. Similarly, heat stress-responsive *WRKY39* also positively regulates heat stress tolerance [174]. In addition, increasing evidence suggests that WRKYs are involved in modulating development under stress conditions, similar to NACs and AP2/ERFs. For example, stress-responsive *WRKY46* modulates the development of lateral roots under abiotic stress conditions, and *WRKY22* mediates dark-induced senescence [175,176]. Despite the crucial role of WRKYs, the interaction between WRKYs and ABA in abiotic stress response remains largely unknown; however, findings that the expression of *WRKYs*, such as *AtWRKY18*, *AtWRKY40*, *AtWRKY60*, *AtWRKY63*, and *GhWRKY17*, affects the ABA response suggest that *WRKYs* are involved in ABA-mediated abiotic stress signaling [177–179].

Several *WRKYs* have been identified in crops and functionally characterized through gain-of-function studies. Overexpression of the stress-induced rice *OsWRKY11* and *OsWRKY45* enhanced drought tolerance, and heterologous overexpression of wheat *TaWRKY1* and *TaWRKY33* also improved drought tolerance in *Arabidopsis* [180–182]. These studies suggest that the function of stress-responsive WRKYs is conserved in plants, and also propose that stress-responsive WRKYs may be promising target genes for improving abiotic stress tolerance in crops. The transcription factors described in this review were summarized in Table 1.

Table 1. Transcription factors that mediate plants tolerance to abiotic stress.

Family	Gene	Species	Abiotic tolerance	Reference
bZIP	*ABF3*	*Arabidopsis thaliana*	Drought	[36]
	ABF4	*Arabidopsis thaliana*	Drought	[36]
	FtbZIP5	*Fagopyrum tataricum*	Drought, salinity, oxidative	[39]
	PtrABF	*Poncirus trifoliate*	Drought	[40]
	OsbZIP23	*Oryza sativa*	Drought, salinity	[41]
	OsbZIP12	*Oryza sativa*	Drought	[42]
	OsbZIP71	*Oryza sativa*	Drought, salinity	[45]
	OsbZIP46	*Oryza sativa*	Drought	[43]
	OsbZIP72	*Oryza sativa*	Drought	[44]
	ZmbZIP4	*Zea mays*	Salinity	[47]
bHLH	*MYC2*	*Arabidopsis thaliana*	Oxidative	[69]
	AtbHLH17	*Arabidopsis thaliana*	Salinity, oxidative	[80]
	AtbHLH68	*Arabidopsis thaliana*	Drought	[81]
	AtbHLH122	*Arabidopsis thaliana*	Salinity	[83]
	FtbHLH2	*Fagopyrum tataricum*	Freezing	[84]
	FtbHLH3	*Fagopyrum tataricum*	Drought, oxidative	[82]
	PebHLH35	*Populus euphratica*	Drought	[85]
	OsbHLH148	*Oryza sativa*	Drought	[86]
NAC	*ANAC019*	*Arabidopsis thaliana*	Drought	[103]
	ANAC055	*Arabidopsis thaliana*	Drought	[103]
	ANAC072	*Arabidopsis thaliana*	Drought	[103]
	ANAC042	*Arabidopsis thaliana*	Heat	[110]
	TaNAC29	*Triticum aestivum*	Salinity	[113]
	OsNAC6	*Oryza sativa*	Drought	[112]
	OsNAC5	*Oryza sativa*	Drought	[105]
	OsNAC9	*Oryza sativa*	Drought	[106]
	OsNAC10	*Oryza sativa*	Drought	[107]
	TaRNAC1	*Triticum aestivum*	Drought	[117]

Table 1. *Cont.*

Family	Gene	Species	Abiotic tolerance	Reference
AP2/ERF	*CBF1*	*Arabidopsis thaliana*	Freezing, salinity	[128,129]
	CBF2	*Arabidopsis thaliana*	Freezing, salinity	[128,129]
	CBF3	*Arabidopsis thaliana*	Freezing, salinity	[128,129]
	AtERF53	*Arabidopsis thaliana*	Heat	[132]
	AtERF74	*Arabidopsis thaliana*	Drought	[133]
	AhDREB1	*Arachis hypogaea*	Osmosis	[134]
	OsDREB1	*Oryza sativa*	Drought, salinity, freezing	[135]
	OsEREBP1	*Oryza sativa*	Drought, submergence	[136]
	OsERF71	*Oryza sativa*	Drought	[137–139]
	GmERF3	*Glycine max*	Salinity, drought, heat stress	[142]
	ZmDREB2A	*Zea mays*	Drought, heat	[143]
	SlERF5	*Solanum lycopersicum*	Drought, salinity	[144]
MYB	*AtMYB44*	*Arabidopsis thaliana*	Drought	[159]
	AtMYB96	*Arabidopsis thaliana*	Drought	[160–162]
	AtMYB20	*Arabidopsis thaliana*	Salinity	[163]
	OsMYB4	*Oryza sativa*	Freezing	[164]
	OsMYB6	*Oryza sativa*	Drought, salinity	[165]
	OsMYB48-1	*Oryza sativa*	Drought, salinity	[166]
	OsMYB91	*Oryza sativa*	Salinity	[167]
	GmMYB76	*Glycine max*	Salinity, freezing	[168]
	GmMYB92	*Glycine max*	Salinity, freezing	[168]
	GmMYB177	*Glycine max*	Salinity, freezing	[168]
WRKY	*AtWRKY25*	*Arabidopsis thaliana*	Heat	[173]
	AtWRKY26	*Arabidopsis thaliana*	Heat	[173]
	AtWRKY33	*Arabidopsis thaliana*	Heat	[173]
	AtWRKY39	*Arabidopsis thaliana*	Heat	[174]
	OsWRKY11	*Oryza sativa*	Drought	[180]
	OsWRKY45	*Oryza sativa*	Drought	[181]
	TaWRKY1	*Triticum aestivum*	Drought	[182]
	TaWRKY33	*Triticum aestivum*	Drought	[182]

5. Future Perspectives

ABA and JA are key hormones that mediate plant response and tolerance to abiotic stress. However, increasing evidence suggests that other phytohormones, such as auxin, cytokinin, brassinosteroid, salicylic acid and ethylene, are also involved in plant response to abiotic stress [183–185]. At present, a large number of phytohormone-derived growth regulators are used commercially in agriculture to improve plant tolerance to abiotic stresses [186–193], suggesting that identification and characterization of genetic components such as transcription factors, which mediate hormonal response, provide important clues to understand the molecular mechanisms underlying plant response and tolerance to abiotic stress, and to develop crops with improved stress tolerance. In this review, we summarized the function of stress-responsive transcription factors in modulating plant response and tolerance to abiotic stress, focusing on bZIPs, bHLHs, NACs, AP2/ERFs, MYBs, and WRKYs. However, other families of transcription factors, such as HD-ZIP and Zinc Finger transcription factors, whose expressions are regulated by abiotic stress, are also involved in plant response and tolerance to abiotic stress [194–197]. Although many of the questions about the molecular mechanisms underlying transcriptional and translational interaction between multiple transcription factors remain largely unanswered, these suggest that modulation or manipulation of transcription involved in plant stress response factors would be a good strategy to enhance tolerance to abiotic stress in crops. Numerous studies have identified and characterized the roles of stress-responsive transcription factors in plant response and tolerance to abiotic stress, but most of these studies were performed in laboratory conditions.

Functional validation under field conditions will expand potential applications of stress-responsive transcription factors for improvement of abiotic stress tolerance in crops.

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Abbreviations

ABA	Abscisic acid
JA	Jasmonic acid
bZIP	Basic leucine zipper
ABF	ABA-responsive element binding factor
bHLH	Basic helix-loop-helix
NCED	9-cis-epoxycartotenoid dioxygenase
AAO	Abscisic aldehyde oxidase
SDR	Short-chain dehydrogenase/reductase
MCSU	Molybdenum cofactor sulfurase
UGT	UDP glucosyltransferase
CYP707A	Cytochrome P450 monooxygenase 707A
PYR1	Pyrabactin resistance 1
PYL	Pyr-like
RCAR	Regulatory component of aba receptor
PP2C	Protein phosphatase type 2C
SnRK2	SNF1-related protein kinases type 2
ABRE	ABA-responsive element
ABI	ABA-insensitive1
SOC1	Suppressor of overexpression of constans 1
LOX	lipoxygenase
AOC	Allene oxide cyclase
ERF	Ethylene-responsive factor
OPR	12-oxo-PDA reductase
JA-Ile	JA-isoleucine conjugate
MeJA	Methyl jasmonate
JAR1	Jasmonate-amido synthetase 1
JMT	Jasmonate methyl transferase
COI1	Coronatine insensitive 1
JAZ	Jasmonate zim-domain
ROS	Reactive oxygen species
DREB	Dehydration-responsive element-binding protein
ICE	Inducer of CBF expression
NAM	No apical meristem
ATAF1/2	Arabidopsis transcription activator factor 1/2
CUC2	Cup-shaped cotyledon 2
ERD1	Early responsive to dehydration stress 1
NAS2	Nicotianamine synthase 2

VNI2	Vascular-related NAC-domain-interacting 2
AP2/ERF	Apetala 2/ethylene-responsive factor
RAV	Related to abscisic acid insensitive3/viviparous 1
CBF	C-repeat-binding factor
ORA47	Octadecanoid-responsive AP2/ERF transcription factor 47
AOS	Allene oxide synthase

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