

# Post-translational Modifications of bZIP Transcription Factors in Abscisic Acid Signaling and Drought Responses

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**Abstract:** Under drought stress, plants have developed various mechanisms to survive in the reduced water supply, of which the regulation of stress-related gene expression is responsible for several transcription factors. The basic leucine zippers (bZIPs) are one of the largest and most diverse transcription factor families in plants. Among the 10 *Arabidopsis* bZIP groups, group A bZIP transcription factors function as a positive or negative regulator in ABA signal transduction and drought stress response. These bZIP transcription factors, which are involved in the drought response, have also been isolated in various plant species such as rice, pepper, potato, and maize. Recent studies have provided substantial evidence that many bZIP transcription factors undergo the post-translational modifications, through which the regulation of their activity or stability affects plant responses to various intracellular or extracellular stimuli. This review aims to address the modulation of the bZIP proteins in ABA signaling and drought responses through phosphorylation, ubiquitination and sumoylation.

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## 1. INTRODUCTION

As sessile organisms, plants are bombarded by environmental stresses throughout their lives. Among all environmental stresses, drought stress frequently occurs worldwide because of global warming and climate change, causing water deficits that reduce crop productivity. Plants have survived harsh environmental conditions by developing many physiological and molecular adaptive strategies [1-5]. The plant hormone abscisic acid (ABA) is the main modulator that regulates the drought stress response. Under drought conditions, ABA induces stomatal closing to inhibit undesirable transpirational water loss and activates various stress-related genes, including *RD29A*, *RD29B*, and *RD22* to initiate rapid and efficient defense responses [6-11].

Transcriptional control of the expression of stress-responsive genes is crucial for the plant response to a range of environmental stress. Transcription factors positively or negatively regulate stress responses by interacting with *cis*-elements in the promoter regions of various abiotic stress-related genes. Several families of transcription factors such as ethylene-responsive-element-binding factors (ERF), WRKY, and basic leucine zipper (bZIP) have been reported to be involved in plant stress response [12]. Among them, bZIPs are a large family of transcription factors in plants,

and they contain a bZIP domain that consists of basic domain and leucine zipper [13, 14]. Since bZIP protein was identified as a *trans*-acting factor that binds to ABA-responsive element (ABRE; PyACGTGGC), it is an important transcription factor involved in ABA signaling pathway [15]. Plant bZIP proteins can be classified into 10 (A-I and S) or 13 groups (Three groups [J,K and L] was added to the former classification) based on the sequence similarity of basic regions and additional conserved motifs [16, 17]. ABRE-binding transcription factors (AREB/ABFs) belong to group A bZIP protein [18-22]. They function as positive regulators in ABA-mediated drought stress response. However, later studies revealed that bZIP proteins also act as a negative regulator. *CaATBZ1*, a pepper bZIP protein belonging to group A, negatively modulates ABA signaling and drought response [23]. *SlbZIP38* also acts as a negative regulator of ABA-mediated drought response in tomatoes [24]. Overexpression of *CaATBZ1* or *SlbZIP38* resulted in reduced tolerance to drought stress [23, 24]. In addition to stress response, bZIP transcription factors modulate several processes such as hormone signaling, energy metabolism, flowering, senescence, and seedling maturation [16, 25].

In eukaryote, complex signaling networks are tightly regulated through post-translational modifications (PTMs). PTMs diversify and expand protein function beyond those directed by gene transcripts. PTM reactions occur reversibly or irreversibly and can dynamically regulate signaling and physiological responses in eukaryotic cells. Several proteomic and genetic analyses have shown that post-translational modifications are involved in the signal transduction path-

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ways of various phytohormones, including auxin, brassinosteroid (BR), ethylene (ET), cytokinin, gibberellic acid (GA), salicylic acid (SA), jasmonic acid (JA), and ABA [26-31]. In particular, phosphorylation is essential to relay the signal in the core components of ABA signaling pathway [32-34]. Ubiquitination also has a great effect on signal transduction by promoting proteasomal degradation of ABA- or stress-signaling components [35-39]. Sumoylation, which has been studied relatively recently, also affects signal transduction by regulating the activity or stability of target proteins [40-42]. Recent findings suggest that plant bZIP transcription factors are under the control of various post-translational mechanisms that are crucial for regulating their function [43]. In this review, we primarily focused on the regulation of the ABA signaling and drought response *via* phosphorylation, ubiquitination, and sumoylation of bZIP transcription factors.

## 2. IDENTIFICATION OF BZIP TRANSCRIPTION FACTORS

In the promoter analyses of ABA-regulated genes, conserved *cis*-element designated ABA-responsive element (ABRE) has been identified [44-46]. The bZIP transcription factors had been studied since it was reported that EmBP-1, a DNA binding protein that specifically interacts with ABRE, had a conserved basic and leucine zipper domain found in plant transcription factors [15]. Subsequently, various types of ABRE-like sequences, including the G-box sequence (CACGTG), the coupling element (CGCGTG), CE3, hex3, and motif3, were reported [45, 47-49]. Proteins that contain bZIP domains interacting with these sequences were classified as bZIP transcription factors, which were included in related studies [45, 50].

The bZIP domain consists of two distinct structures, a basic region and a leucine zipper, which are on an adjacent  $\alpha$ -helix. The basic region, which consists of approximately 16 amino acid residues, has a nuclear localization signal, followed by an invariant N-X7-R/K motif binding directly to DNA [13, 14]. In the leucine zipper region, leucine residues are repeatedly located within every seven amino acids and are sometimes replaced with isoleucine, phenylalanine, valine, or methionine [13, 14]. The leucine residues determine the dimerization specificity of bZIP proteins. Therefore, these variant residues represent hallmarks that determine homodimerization and heterodimerization specificity [16, 51, 52]. The bZIP domain has been widely studied in yeast GCN4, mammalian CREB, and Jun/Fos [53, 54]. *Arabidopsis* has about four times as many bZIP genes as yeast, humans, or worms [55]. The bZIP gene family is one of the largest and diverse family in plants and has been characterized based on whole genome sequences of several plants, including *Arabidopsis*, rice, maize, sorghum, grapevine, tomato, and apple [16, 51, 56-60].

## 3. PLANT BZIP TRANSCRIPTION FACTORS INVOLVED IN DROUGHT RESPONSE

Plants are constantly exposed to various abiotic stresses such as drought, cold, salinity, heat, light, and heavy metal

toxicity. Drought stress is fatal to plant survival because it directly reduces water availability. The bZIP transcription factors involved in drought response are widely present in various plant species, and a large number of genes have been reported [61, 62]. Therefore, we will focus on bZIP transcription factors related to the drought stress responses.

### 3.1. Classification of Different bZIP Transcription Factors and their Involvement in Abiotic Stress

In *Arabidopsis*, 75 putative genes encoding bZIP proteins have been identified, and *Arabidopsis* bZIP proteins are clustered into 10 groups [16]. Each group is classified according to sequence and domain similarities, and their biological functions (Fig. 1). Group A bZIP proteins (ABI5, ABF2/AREB1, ABF4/AREB2, AREB3, GBF4, ABF1, and ABF3) are ABRE-binding factors (ABFs) and ABA-responsive element binding proteins (AREBs) that bind to ABRE-containing promoters. To modulate abiotic stress responses, they function as crucial components in ABA signal transduction both in seeds and vegetative tissues, thereby modulating abiotic stress responses such as drought, salt, and cold [18-22]. ABA and abiotic stresses induce the expression of group A bZIP genes and also promote the phosphorylation of AREB1/2. Phosphorylation of AREB1/2 is necessary to induce downstream gene [63, 64]. ABA induces transcriptional and post-translational regulation of the group A bZIP. Thus, group A bZIP plays an integral role in the ABA signaling pathway [16]. In *Arabidopsis*, AREB1, AREB2, and ABF3 are the most well-known bZIP transcription factors and function as core components that cooperatively regulate ABRE-dependent gene expression. Overexpression analyses revealed that AREB1, AREB2, and ABF3 are involved in ABA signaling in response to drought stress [63, 65]. In addition, *areb1/areb2/abf3* triple mutant displayed reduced expression of ABA- and stress-responsive genes, resulting in reduced drought tolerance and decreased sensitivity to ABA [46, 64]. ABF1 is a functional homolog of ABRE1, ABRE2, and ABF3 in *Arabidopsis* and is involved in the regulation of drought response through the same pathway [66]. ABI5 is a bZIP transcription factor that regulates seed germination and early seedling growth. The ABI5 protein accumulates in response to salt and drought stresses, resulting in *abi5-4* embryos being more tolerant to drought stress than wild-type plants [20].

Group B bZIP proteins are involved in endoplasmic reticulum (ER) stress responses [67]. AtbZIP17, 28, and 49 belong to group B and are membrane-bound ER-localized bZIP proteins that move to the nucleus under ER stress [68]. Group C bZIP proteins share structural features with a well-characterized family of plant bZIPs of maize Opaque2 and parsley (*Petroselinum crispum*) CPFR2 [16]. The members of this group have an extended leucine zipper with up to nine heptad repeats [69]. However, their exact function in plants has not been discovered.

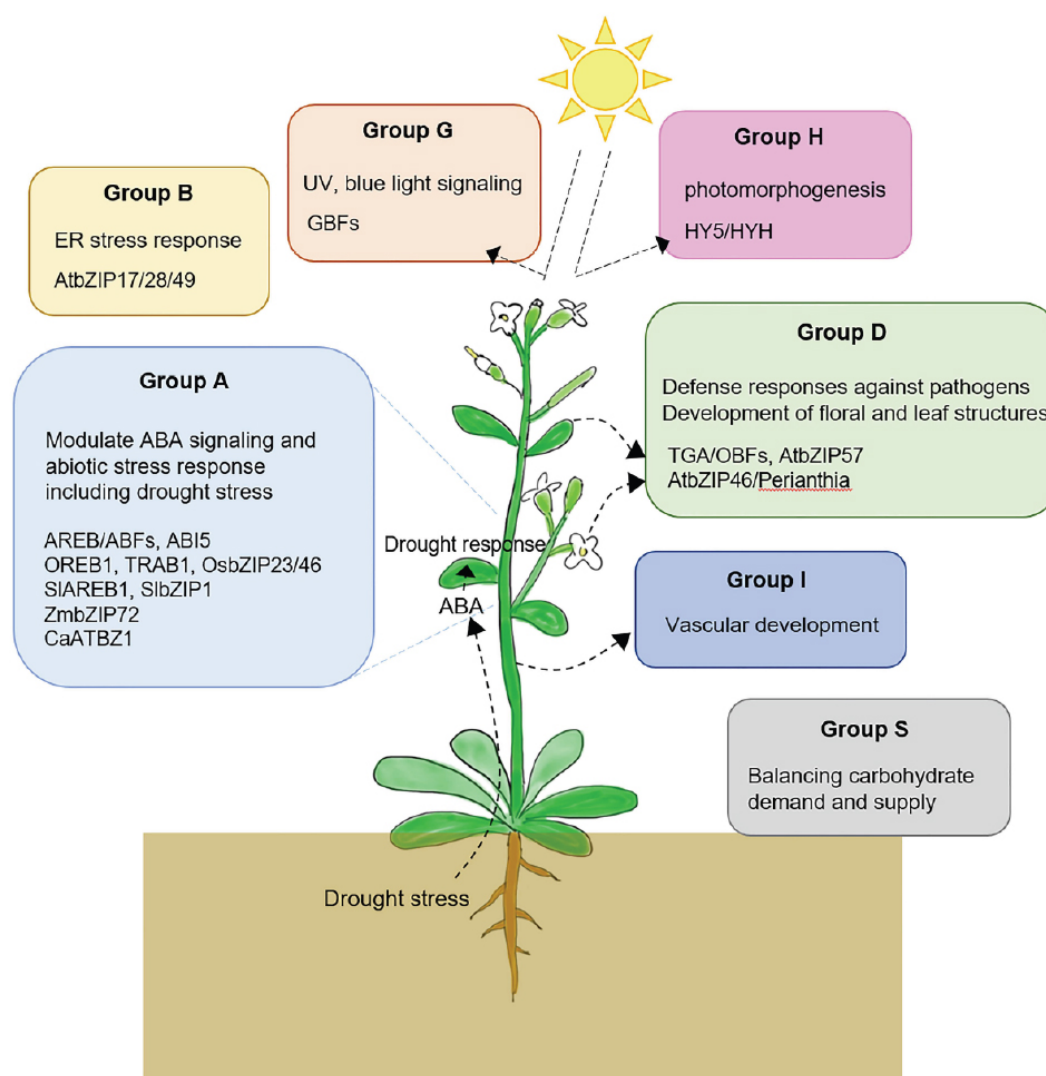
Group D bZIP proteins play important roles in the defense response against pathogens. TGA factors belonging to group D regulate pathogenesis-related (PR) gene expression by interacting with the NPR protein [70]. In addition, At-

bZIP57/TGA4/OBF4 interacts with AtEBP, which binds to the ethylene response element in many PR gene promoters [71]. Other group D genes are involved in the development of floral or leaf structures. *AtbZIP46/Perianthia* regulates floral organ number in *Arabidopsis* and *Liguleless2* establishes the blade-sheath boundary in maize [72, 73]. Interestingly, recent studies have found that the pepper bZIP transcription factors belonging to group D also play a role in ABA signaling and drought response [74, 75]. CaDILZ1 and CaAIBZ1 function as positive and negative modulators, respectively, in the ABA-mediated drought stress response [23, 74].

GBFs (G-box binding factor) of group G bZIP proteins are mainly involved in ultraviolet and blue light signal transductions and regulate light-responsive promoters [76, 77]. HY5 (ELONGATED HYPOCOTYL 5) of group H plays a

role in promoting photomorphogenesis. HY5 directly regulates the expression of several light-inducible genes by binding to G-boxes [78]. Group I proteins have a characteristic lysine residue in the basic domain that substitutes the highly conserved arginine (N-X7-R to N-X7-K). Members of group I bZIP proteins might play a role in vascular development [79]. Group S is the largest bZIP group in *Arabidopsis* and these proteins might be involved in balancing carbohydrate demand and supply [80].

Rice bZIP transcription factors are also involved in the drought response. Among the 13 rice bZIP transcription factor groups, not only group A but also group C and S are known to be involved in abiotic stress signaling [17, 56]. Like *Arabidopsis*, most of group A bZIP transcription factors in rice are related to ABA and stress signaling [17, 18, 56]. OsbZIP23 is a key player in ABA sensitivity, salinity,



**Fig. (1).** Biological functions of bZIP transcription factors for each group. The plant bZIP proteins function in the various cellular processes of stress responses and development. Functional characteristics and representative bZIP proteins were shown for each group. (A higher resolution / colour version of this figure is available in the electronic copy of the article).

and drought tolerance [81]. OsbZIP16 and OsbZIP71, which belong to the group S bZIP transcription factors, have been found to positively regulate drought tolerance and ABA signaling [82, 83]. In rice, OsbZIP72, which is another ABRE-binding factor, also has a positive role in drought tolerance *via* ABA signaling [84]. OsbZIP66, OsbZIP42, and OsbZIP46 also function as positive regulators in drought tolerance [85-87]. However, OsbZIP52/RISBZ5 functions as a negative regulator in the drought stress response [88].

bZIP transcription factors of maize, ZmbZIP72 and ABP9, function as positive modulators of abiotic stress tolerance, especially drought stress [89, 90]. bZIPs of tomato, SlbZIP1 and SlbZIP38, play positive and negative roles in drought tolerance, respectively [24, 91]. TaAREB3 and TabZIP60 (wheat) [92, 93], GhABF2 (cotton) [94], GmFDL19 (soybean) [95], VlbZIP36 (grape) [96], and BnaABF2 (rapeseed) [97] have been identified as positive regulators of drought tolerance.

### 3.2. Role of bZIP Transcription Factors in Biotic Stress

In biotic stress conditions, the SA signaling pathway acts mainly during biotrophic and hemibiotrophic pathogen attack and determine the establishment of systemic acquired resistance [98]. JA and ET signaling usually respond to necrotrophic pathogens, insects, and herbivores [99]. As mentioned earlier, TGA factors belonging to group D are linked to biotic stress responses *via* SA defense signaling pathway [12, 70]. In *Arabidopsis*, TGA transcription factors and bZIP10 regulate pathogen defense responses [100-103]. CabZIP1, a bZIP transcription factor of pepper, is also involved in resistance to pathogen infection [104]. In the natural environment, plants often encounter abiotic and biotic stresses simultaneously. By interacting with the SA and JA signaling pathways, ABA functions as a major phytohormone regulating stress responses [105]. Therefore, some bZIP transcription factors are involved in both abiotic and biotic stresses. VvbZIP23 (bZIP from grapevine), SlAREB1 (tomato), GmbZIP19 (soybean) modulate both abiotic and biotic stress responses [106-108].

## 4. POST-TRANSLATIONAL MODIFICATION OF BZIP TRANSCRIPTION FACTORS INVOLVED IN ABA SIGNALING AND DROUGHT RESPONSE

Many studies have identified the biological influences of several types of PTMs [109-112]. Among them, phosphorylation, ubiquitination, and sumoylation appear to be critically involved in ABA signal transduction by modulating the activity and stability of transcription factors and the enzymatic activity of protein kinase.

### 4.1. Phosphorylation

ABA-activated kinases of the SNF1-related protein kinase 2 (SnRK2) family, SnRK2.2, SnRK2.3, and SnRK2.6/OST1, are an essential component in the ABA signaling pathway [9, 32, 113, 114]. Regulation of plant responses to ABA through these SnRKs requires direct phosphorylation of several downstream targets, including transcription

factors. AREB/ABFs have been reported to be a major positive regulator of ABA- or stress-signaling [66, 113]. Genome-wide transcriptome analyses have found that four AREB/ABF transcription factors (AREB1, AREB2, ABF3, and ABF1) and ABI5 act downstream of the three SnRK2s in *Arabidopsis* [32, 66]. For example, the transcriptional activity of AREB1 is activated when the Ser/Thr residue of the R-X-X-S/T sites in the conserved regions of AREB1 is phosphorylated by ABA-activated SnRK2-type protein kinase [63]. Interestingly, it has been shown that transcription factors are not only activated but also stabilized through phosphorylation. ABA-activated SnRK2.6/OST1 phosphorylates Thr451 of ABF3, which enhances ABF3 stability by interacting with 14-3-3 proteins [115].

Similarly, rice TRAB1, a homolog of ABF, is phosphorylated and activated by the ABA-activated SnRK2 protein kinases *i.e.* SAPK8, SAPK9, and SAPK10 [114]. As another bZIP transcription factor in rice, OREB1 is phosphorylated by OSRK1, a dehydration-inducible member of the rice SnRK2 family [116] and OsbZIP23 is activated *via* phosphorylation by SAPK2, a homolog of the SnRK2 protein kinase [117].

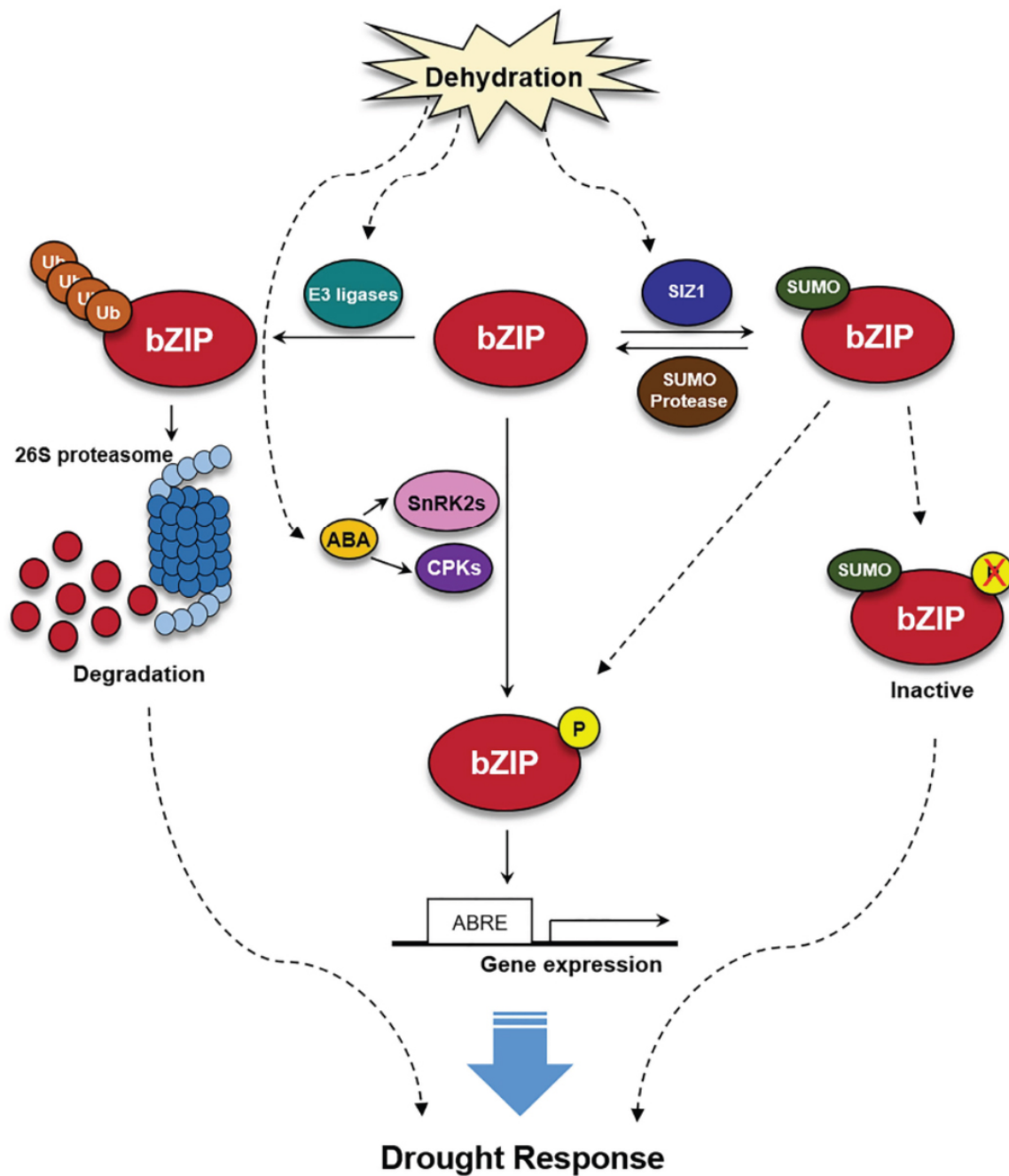
In addition to SnRK2-type protein kinases, calcium-dependent protein kinases can phosphorylate the bZIP transcription factor. CPK11 has been reported to phosphorylate and activate bZIP transcription factors belonging to the ABF/AREB clade (ABF1, ABF3, ABI5) [118, 119]. AtCPK32 interacts with the Ser-110 residue of ABF4 to induce the phosphorylation and increase the transcriptional activity of ABF4 [120]. StABF1, a stress-responsive bZIP transcription factor of potato, is phosphorylated by StCDPK2 and StCDPK3 [121, 122]. In maize, the CK2 protein kinase phosphorylates two bZIP transcription factors (EmBP-2 and ZmBZ-1), thereby regulates the expression of ABA-responsive genes such as *rab28* [123]. These studies suggest that the bZIP transcription factors of the ABF/AREB clade can be phosphorylated by CPK as well as SnRK2-type kinase [118].

### 4.2. Ubiquitination

Ubiquitination is a eukaryotic-specific post-translational modification that is primarily associated with the determination of protein stability. The covalent attachment of ubiquitin to a target protein is facilitated through sequential reactions catalyzed by the ubiquitin-activating enzyme (E1), the ubiquitin conjugation enzyme (E2), and ubiquitin ligase (E3) [124]. Polyubiquitinated target proteins are cognized and degraded by 26S proteasomes. In eukaryotes, most transcription factors, including bZIPs, are degraded *via* the ubiquitin-26S proteasome pathway. Among the various bZIP transcription factors of *Arabidopsis*, ABI5 is the key regulator of the ABA signaling pathway, and ABI5 is frequently modulated by ubiquitination [125]. The Really Interesting New Gene (RING)-type E3 ligase KEEP ON GOING (KEG) is a negative regulator of ABA signaling that is associated with ubiquitination and degradation of ABI5, maintaining a low level of ABI5 [126, 127]. In keg mutant plants,

ABI5 protein accumulation is high, making this protein hypersensitive to ABA in a fashion similar to phenotypes of *ABI5*-overexpressing plants [126, 127]. KEG also interacts

with ABF1 and ABF3 and ubiquitinates them *in vitro*. ABF1 and ABF3 are similar to ABI5 in that KEG substrates, and the degradation of ABF1 and ABF3, are inhibited in *keg* knock-out mutant seedlings [128].



**Fig. (2).** Simplified overview of post-translational modifications that regulate bZIP protein activity and stability to modulate ABA signaling and drought stress response. In response to dehydration stress, ABA is biosynthesized, and E3 ligases and SUMO E3 ligase SIZ1 are influenced. ABA-activated SnRK2-type kinases and CPKs phosphorylate bZIP protein to activate transcriptional function. E3 ligase ubiquitinates bZIP protein and polyubiquitinated bZIP is degraded by 26S proteasome. SIZ1 sumoylates bZIP protein and sumoylated bZIP is stabilized. The activation of bZIP protein can be increased as much as sumoylated protein is accumulated, but SUMO conjugation can inactivate bZIP protein by preventing phosphorylation. SUMO protease desumoylates bZIP protein. (A higher resolution / colour version of this figure is available in the electronic copy of the article).

**Table 1.** PTMs of bZIP transcription factors involved in ABA signaling and drought response.

PTM	Species	bZIP TF	Regulating Enzyme	References
Phosphorylation	<i>Arabidopsis thaliana</i>	AREB1	SnRK2.2/2.3/2.6	Furihata <i>et al.</i> 2006 [63]
		AREB2/ABF1	SnRK2.2/2.3/2.6	Yoshida <i>et al.</i> 2015 [66]
		ABF3	SnRK2.2/2.3/2.6	Sirichandra <i>et al.</i> 2010 [115]
		ABI5	SnRK2.2/2.3/2.6	Nakashima <i>et al.</i> 2009 [32]
		ABF4	CPK11	Fujii <i>et al.</i> 2007 [119]
		ABF1/ABF3	CPK11	Lynch <i>et al.</i> 2012 [118]
		ABF4	CPK32	Choi <i>et al.</i> 2005 [120]
	<i>Oryza sativa</i>	TRAB1	SAPK8/9/10	Kobayashi <i>et al.</i> 2005 [114]
		OREB1	OSRK1	Chae <i>et al.</i> 2007 [116]
		OsbZIP23	SAPK2	Zong <i>et al.</i> 2016 [117]
	<i>Solanum tuberosum</i>	StABF1	StCDPK2	Muñiz García <i>et al.</i> 2012 [122]
StABF1		StCDPK3	Grandellis <i>et al.</i> 2016 [121]	
<i>Zea mays</i>	EmBP-2/ZmBZ-1	CK2	Nieva <i>et al.</i> 2005 [123]	
Ubiquitination	<i>Arabidopsis thaliana</i>	ABI5	KEG	Liu and Stone 2013 [127]
		ABF1/ABF3	KEG	Chen <i>et al.</i> 2013 [128]
		ABI5	DWA1/2	Lee <i>et al.</i> 2010 [36]
		ABI5	ABD1	Seo <i>et al.</i> 2014 [129]
	<i>Oryza sativa</i>	OsbZIP46	OsPUB70	Tang <i>et al.</i> 2016 [130]
	<i>Capsicum annuum</i>	CaDILZ1	CaDSR1	Lim <i>et al.</i> 2018 [74]
		CaAIBZ1	CaASRF1	Joo <i>et al.</i> 2019a [23]
		CaATBZ1	CaASRF1	Joo <i>et al.</i> 2019b [75]
CaATBZ1		CaATIR1	Joo <i>et al.</i> 2020 [131]	
Sumoylation	<i>Arabidopsis thaliana</i>	ABI5	SIZ1	Miura <i>et al.</i> 2009 [41]
Desumoylation	<i>Oryza sativa</i>	OsbZIP23	OsOTS1	Srivastava <i>et al.</i> 2017 [142]

Two DWD (DDB1-binding WD40) genes, DWA1 and DWA2 (DWD hypersensitive to ABA1 and ABA2), act as negative regulators in ABA signal transduction by encoding the substrate receptors of CULLIN4-RING E3 ligase [36]. Both DWA1 and DWA2 interact with ABI5 and DDB1, which is an integral member of the Cullin4/Damaged DNA Binding Protein 1 (CUL4/DDB1) E3 ligase complex. These act as substrate receptors for CUL4 E3 ligase and promote ABI5 degradation. In addition to DWA1/2, ABA-hypersensitive DCAF1 (ABD1), another substrate receptor of CULLIN4-based E3 ubiquitin ligase, interacts with DDB1 *in vitro* and *in vivo* and negatively regulates ABA signaling by promoting ABI5 degradation in the nucleus [129]. Rice MODD (Mediator of OsbZIP46 deactivation and degradation), which is homologous to the *Arabidopsis* ABI5-binding protein AFP, interacts with OsbZIP46 and recruits the E3 ligase OsPUB70 to promote OsbZIP46 protein degradation [130].

CaDILZ1, induced by ABA and drought conditions, is a pepper bZIP protein that positively regulates drought tolerance by interacting with the RING-type E3 ligase CaDSR1 [74]. CaDSR1 functions as a negative regulator of the drought response by promoting the degradation of CaDILZ1 via the ubiquitin-26S proteasome system [74]. In contrast to CaDILZ1, CaAIBZ1 is a bZIP protein that negatively affects the drought response and is degraded by RING-type E3 ligase CaASRF1 [75]. CaASRF1 ubiquitinates and degrades

another bZIP protein CaATBZ1, as well as CaAIBZ1 [23]. Moreover, CaATBZ1 interacts with CaATIR1, another RING-type E3 ligase that positively regulates the ABA-mediated drought response by promoting the degradation of CaATBZ1 [131].

### 4.3. Sumoylation

Small Ubiquitin-like Modifier (SUMO) conjugation of substrate proteins influences protein stability, activity, and localization [132-136]. Like ubiquitination, sumoylation is accomplished by three enzymes: E1 activating enzyme, E2 conjugating enzyme, and E3 SUMO ligase [137]. Protein sumoylation in plants affects stress signal transduction and defense responses [138, 139]. Under drought conditions, SUMO-protein conjugates increase, and SUMO E3 ligases such as SIZ1 and MMS21 positively regulate drought tolerance [40, 140, 141]. *Arabidopsis* SUMO E3 ligase SIZ1 induces SUMO protein binding to the K (lysine) 391 residues of ABI5, leading to the inactivation of ABI5 [41]. SIZ1-mediated sumoylation of ABI5 prevents ABI5 protein degradation by AFP and KEG. Since sumoylation and desumoylation are reversible mechanisms, ABI5 can be de-sumoylated when needed without first biosynthesizing the protein. Thus, the ABI5-mediated ABA response is precisely and rapidly regulated [41]. Rice SUMO protease Overly Tolerant to Salt1 (OsOTS1) induces the desumoylation of OsbZIP23, a drought-responsive transcription factor, and reduces OsbZIP23 stabil-

ity [142]. In contrast to the inactivity of SUMO-conjugated ABI5, sumoylation of OsbZIP23 does not influence activity and increases stability. Since sumoylation of OsbZIP23 improves drought tolerance, OsOTS1 acts as a negative regulator of drought response [142].

## CONCLUSION AND PERSPECTIVE

The synthesis, modification, intercellular localization, and degradation of the bZIP protein are necessary for plant growth and survival in stressful environments. Therefore, post-translational modifications of bZIP protein are associated with plant stress responses. In this review, we focused on the regulation of the activity and stability of bZIP transcription factors *via* post-translational modifications (Fig. 2). In addition, this provided various examples regarding the modulation of ABA signaling and drought responses by phosphorylation, ubiquitination, and sumoylation of bZIP proteins (Table 1). The following mechanisms contribute to fine-tuning the regulation of the plant stress response and drought tolerance: (i) different post-translational modifications to a bZIP protein can occur sequentially in the same pathway or simultaneously in the different pathway; (ii) the activation and abundance of proteins are important for protein functionality. However, sometimes, the protein state is more important than the amount; hence, (iii) crosstalk can be observed in proteins where ubiquitination, sumoylation, and phosphorylation can occur together [143]; and (iv) deubiquitinating enzymes and SUMO protease may play an important role in the mechanisms modulating bZIP transcription factors. As a well-known bZIP transcription factor, the ABI5 protein is activated by phosphorylation, degraded by ubiquitination, and stabilized by sumoylation. These three post-translational modifications act cooperatively or antagonistically to regulate the activity and stability of ABI5 [41, 144]. The involvement of many ABA signaling and drought stress-related bZIP transcription factors in the post-translational modifications remains to be explained. Studying the fine regulations of stress-related bZIP proteins by post-translational modification can provide an understanding of how plants rapidly adapt to stress conditions and might contribute to the development of drought-tolerant crops by manipulating related genes.

## LIST OF ABBREVIATIONS

ABF	=	ABRE-Binding Factors
ABRE	=	ABA-regulated genes identified the conserved cis-element-designated ABA-responsive element
AREB	=	ABA-Responsive Element-Binding
AtEBP	=	<i>Arabidopsis thaliana</i> ethylene-responsive element binding protein
ER	=	Endoplasmic Reticulum
GA	=	Gibberellic Acid
JA	=	Jasmonic Acid

PR	=	Pathogenesis-Related
SA	=	Salicylic Acid
SUMO	=	Small Ubiquitin-like Modifier

## CONSENT FOR PUBLICATION

Not applicable.

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## CONFLICT OF INTEREST

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

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