

Review

Transcriptional and Post-Translational Regulation of Plant bHLH Transcription Factors during the Response to Environmental Stresses

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Abstract: Over the past decades, extensive research has been conducted to identify and characterize various plant transcription factors involved in abiotic stress responses. Therefore, numerous efforts have been made to improve plant stress tolerance by engineering these transcription factor genes. The plant basic Helix–Loop–Helix (bHLH) transcription factor family represents one of the most prominent gene families and contains a bHLH motif that is highly conserved in eukaryotic organisms. By binding to specific positions in promoters, they activate or repress the transcription of specific response genes and thus affect multiple variables in plant physiology such as the response to abiotic stresses, which include drought, climatic variations, mineral deficiencies, excessive salinity, and water stress. The regulation of bHLH transcription factors is crucial to better control their activity. On the one hand, they are regulated at the transcriptional level by other upstream components; on the other hand, they undergo various modifications such as ubiquitination, phosphorylation, and glycosylation at the post-translational level. Modified bHLH transcription factors can form a complex regulatory network to regulate the expression of stress response genes and thus determine the activation of physiological and metabolic reactions. This review article focuses on the structural characteristics, classification, function, and regulatory mechanism of bHLH transcription factor expression at the transcriptional and post-translational levels during their responses to various abiotic stress conditions.

Keywords: bHLH transcription factors; abiotic stress; transcriptional regulation; post-translational regulation



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1. Introduction

The basic Helix–Loop–Helix (bHLH) Transcription Factors (TF) are a large and diverse family of transcription factors characterized by a highly conserved bHLH domain [1]. The bHLH transcription factor conservatively contains two connected subregions, namely the basic region (b), which is an essential DNA-binding region, and the HLH region, which consists of 40–50 amino acid residues and participates in homodimerization or heterodimerization [2] (Figure 1A,B). The amino acid sequences outside the bHLH region are divergent, even in closely related proteins from the same species. These short conserved amino acid motifs are commonly present in related plant bHLH proteins and are generally conserved within each subfamily [3,4].

The bHLH motif was first discovered in the murine transcription factors E12 and E4 [5]. Since then, several *bHLH* genes have been discovered, providing an initial classification of animals that divided bHLH transcription factors into six subgroups (A to F) based on their protein sequences, differences in bHLH domains, and comparisons of the functions of different family members [6,7]. Furthermore, outside of mammals, multiple

classifications of 15 to 25 subfamilies based on bHLH and non-bHLH motifs have been obtained [3,4,8]. As more species were included, the most recent classification allows them to be divided into 26 subgroups [1], reflecting a deep evolutionary relationship in plants. In addition, phylogenetic analysis of several atypical bHLH proteins extended the number of subfamilies to 32 [8].

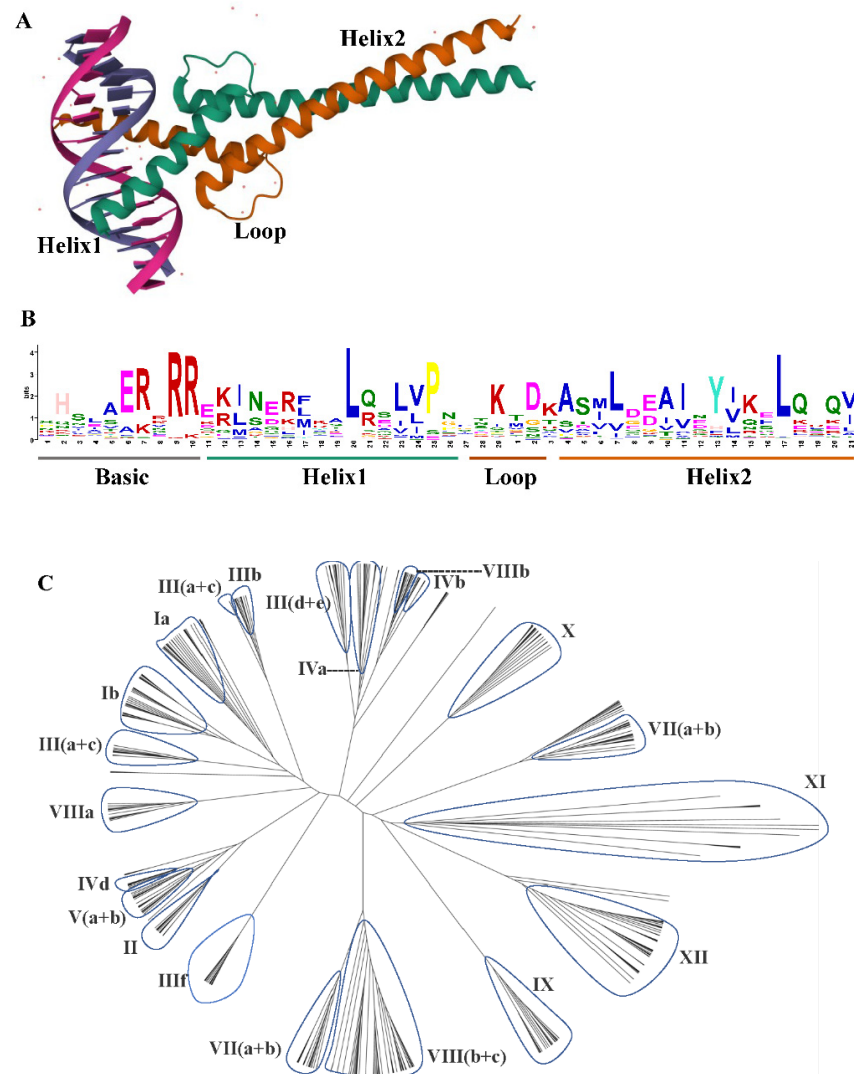


Figure 1. (A) The crystal structure of bHLH domain heterodimer bound to the DNA. (B) The sequence logo of the bHLH domain. The overall height of each stack represents the conservation of the sequence at that position. Each color of the letters represents a type of amino acid residue. (C) The phylogenetic tree analysis of bHLH gene family in *Oryza sativa* [monocot]; *Arabidopsis thaliana* [eudicot]; *Selaginella moellendorffii* [lycophyte]; *Physcomitrella patens* [moss]; *Volvox carteri*; *Chlamydomonas reinhardtii*; *Chlorella vulgaris*; *Ostreococcus tauri*; and *Cyanidioschyzon merolae* was constructed using MEGA7.0 with the JTT method and 1000 replicates. Then, the trees were visualized using Figtree. Group names were marked outside the circle. The protein sequences were downloaded from the report in 2010 [1].

Maize (*Zea mays* L.) was the first plant species in which the bHLH superfamily was first identified. Subsequently, 162 bHLH genes were identified in the model plant *Arabidopsis thaliana* [9], 167 in rice (*Oryza sativa* L.) [4] and 202 bHLH genes in *Poplar* [10]. The number of characterized and identified bHLH genes in plants has increased, showing their extensive and diverse functional involvement; 100 PmbHLH genes were identified in *Prunus mume* [11], 102 bHLH genes in walnut (*Juglans regia* L.) [12], 212 MibHLH genes in mango

(*Mangifera indica* L.) [13], 37 *SsbHLH* genes in sugarcane (*Saccharum spontaneum*) [14], 110 *IbbHLHs* in sweetpotato (*Ipomoea batatas* (L.) Lam.) [15], 118 *bHLH* genes were identified in melon [16], 107 *CabHLHs* were identified in *Capsicum annuum* [17], and 85 *bHLH* proteins (*GbbHLH*) were obtained from *Ginkgo biloba* [18]. *bHLH* gene families are widespread in plants and have demonstrated their essential roles in various biological processes involved in normal plant growth and development [1], flowering [19], and metabolic biosynthesis, including anthocyanin [20]. Therefore, many of them have a role and regulatory function in signal transduction [21,22] and gene expression in response to abiotic stresses such as salinity, drought, low temperature, and nutrient deficiency [23,24].

Many research studies have paid close attention to regulatory genes, including *bHLH* TFs, which play essential roles in multiple abiotic stress responses by regulating the expression of a wide range of downstream stress-responsive genes by interacting with the specific cis-elements in their promoter region [25]. Therefore, genetically modifying the expression of TFs can strongly affect plant stress tolerance as it mimics or enhances stress signals to simultaneously regulate many downstream stress-responsive genes. In recent years, several mechanisms of regulation and tolerance of *bHLH* TF to abiotic stress in model and non-model plants have been revealed, providing a better and more detailed explanation of their intervention under specific stress conditions. *bHLHs* are involved in various functional gene approaches to significantly enhance stress tolerance in plants. They can be activated under multiple stresses and play an essential role in abiotic stress responses by regulating a wide range of downstream stress-responsive genes [26]. Meanwhile, *bHLH* TFs themselves undergo various modifications at the post-translational level, such as ubiquitination [27], phosphorylation [28], and sumoylation [29], thereby forming a regulatory complex network to modulate the expression of *bHLH* stress-responsive genes.

Both transcriptional and post-translational modifications contribute to this plant stress response regulatory function. In this review, we focused on the structure and gene classification of *bHLH* TFs, as well as recent studies on their expression and the different mechanisms of transcriptional and post-translational regulation under different abiotic stress conditions.

2. Structure and Gene Family of *bHLH* TFs

The *bHLH* TF family, known for its conserved *bHLH* domain [30], is considered the second largest gene family after the MYB family gene and is found in the majority of eukaryotes. With a total of ~60 amino acids, the *bHLH* transcription factor is divided into two functionally distinct regions. On the one hand, there is the primary region, which is located in the N-terminal domain and contains a total of 15 to 20 amino acids, including basic amino acid residues, and is responsible for DNA binding, with certain conserved amino acids responsible for recognition of the E-box, a hexanucleotide consensus sequence in DNA (5-CANNTG-3). Other residues, on the contrary, are specific for a different E-box region in DNA (e.g., the G-box [5-CACGTG-3]) in target genes [25,31]. According to Toledo-Ortiz et al., *bHLH* genes can be divided into E-box or non-E-box binders and DNA-binding or non-DNA-binding proteins. The Helix–Loop–Helix (HLH) region, on the other hand, is found in the C-terminal domain and is composed of hydrophobic residues rearranged into two amphipathic regions connected to a loop region forming a hydrophobic ring (Figure 1B). They are involved in homo- or heterodimerization, as shown in Figure 1A, and thus participate in protein–protein interaction and gene expression control [2]. The dimer structure is stabilized by the hydrophobic amino acids Isoleucine (I), Leucine (L), and Valine (V) in conserved positions in the *bHLH* domain [30].

Outside of the *bHLH* domain, *bHLH* proteins show little to nonexistent conservation [3]. However, some groups of *bHLH* show some conserved domains outside of *bHLH*, most of which have been previously characterized in animals. For example, there is the highly conserved Leucine Zipper (LZ) motif adjacent to the second helix of the *bHLH* domain, which is predicted to adopt a coiled-coil structure, allowing protein dimerization. The PAS domain, the orange domain, the WRPW motif, and the COE domain are other do-

mains also found in bHLH proteins [6,32]. The bHLH motif was first identified by Massari and Murre in 1989. Then, with more identified bHLH proteins, the first classification of different family members of animal bHLH TFs was performed using only the bHLH motif. This classification led to the selection of four distinct groups based on amino-acid patterns and E-box-binding specificity [7]. This classification separated bHLH proteins into classes A, B, C, and D [7].

Using the entire protein sequence and not just the bHLH domain allowed the inclusion of additional domains associated with many other proteins (e.g., Zip, Orange, and PAS) that may play important roles in protein dimerization and DNA binding. Therefore, the classification was extended to include two additional groups (E and F) [6,33]. The characterized bHLH proteins have been restricted to animals. It has been suggested that the ancestral plant bHLH sequence was a group B protein present in early eukaryote evolution, from which bHLHs of different lineages independently evolved [6,7] and function in transcriptional regulation associated with various diverse functions in plants including anthocyanin biosynthesis, phytochrome signaling, globulin expression, fruit dehiscence, and carpel and epidermal development [3]. Furthermore, some studies have aimed to divide the large bHLH family into smaller subgroups based on their sequence homology [1,3,8]. In 2003, Heim et al. compared the genetic structure, number of introns, and conservative motifs of 133 *bHLH* isolates from *Arabidopsis* and rearranged them into 12 subgroups. Since then, Pires and Dolan have divided bHLH into 26 subgroups by phylogenetic analysis, using a total of 544 *bHLH* genes from 9 land plants and algae [1] (Figure 1C). Meanwhile, Carretero-Paulet et al. added 29 to the original 133 *Arabidopsis bHLH* and classified them into 32 subfamilies by phylogenetic analysis, intron pattern, and conservative protein motif structure using 9 plant species [8].

Mainly, members of the same bHLH subfamily generally share similar gene structure and the same non-bHLH conserved motifs, such as a Leucine Zipper (LZ) domain (shared between IVb subfamilies and between IVc subfamilies) [7]. There is also an ACT domain, which is a ligand-binding regulatory domain found in a diverse group of proteins, mainly metabolic enzymes. The occurrence of the ACT domain in some proteins from different bHLH subfamilies suggests that the ACT bHLH association occurred multiple times, possibly through domain shuffling processes, suggesting that domain shuffling processes may play a small role in the evolution of *bHLH* genes in plants [1]. Members of the same plant bHLH subfamily are also often involved in the same biological processes, such as subgroup Va, which is involved in brassinosteroid signaling [34], and the Active Phytochrome Binding (APB) motif, encoded in several proteins of subfamily VII (a + b), which mediate the binding of multiple *A. thaliana* bHLH proteins to phytochrome B [1,35].

Plant bHLH diversity was already present in the early land plants before the moss and vascular plant lineages separated over 440 million years ago. Many current bHLH interactions also occurred in early land plants and were essentially conserved in the major plant groups [1]. The expansion of this family is closely related to plant evolution and diversity, not only in higher plants but also in lower plants such as algae, lichens, and mosses or non-plants such as mycobacteria [1]. The availability of a large number of land plants and algal genomes allowed further analysis of the conserved motifs of the *bHLH* gene family throughout the photosynthetic plant spectrum (Figure 2). Different numbers of members of the *bHLH* gene family have been identified in different species by searching for proteins containing the bHLH domain. The *bHLH* gene family was found to originate from Rhodophyta. The conservation of the bHLH conservative domain in different species was further predicted by MEME (Figure 2). According to the conservative motif, the bHLH domain will evolve to be more complete as species evolve. The evolution of the *bHLH* gene family also provides insights regarding the evolution of green algae into flowering plants through their adaptation to environmental changes [8]. Specifically, the genome-wide analysis of *bHLH* gene families from different species will help us to better understand the biological function, evolutionary origin, and expansion outcome of *bHLH* genes.

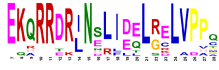
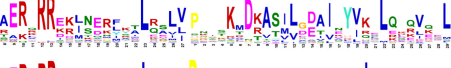
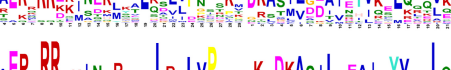
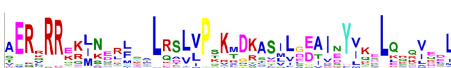
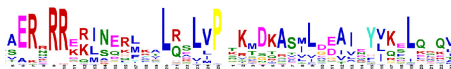
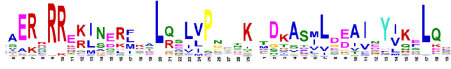
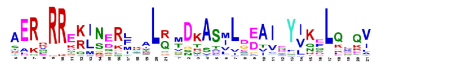
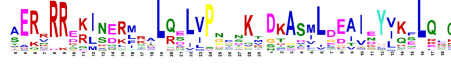
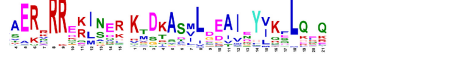
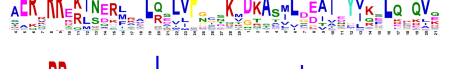
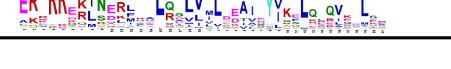
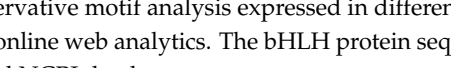
Lineage	Species	bHLH domain
Algae	<i>Chondrus crispus</i>	
Algae	<i>Chara braunii</i>	
Moss	<i>Marchantia polymorpha</i>	
Moss	<i>Physcomitrella patens</i>	
Fern	<i>Selaginella moellendorffii</i>	
Fern	<i>Anthoceros formosae</i>	
Fern	<i>Salvinia cucullata</i>	
Gymnospermae	<i>Picea abies</i>	
Gymnospermae	<i>Gnetum montanum</i>	
Angiosperm	<i>Liriodendron chinense</i>	
Angiosperm	<i>Aristolochia fimbriata</i>	
Eudicots	<i>Arabidopsis thaliana</i>	
Eudicots	<i>Malus domestica</i>	
Eudicots	<i>Populus trichocarpa</i>	
Eudicots	<i>Vitis vinifera</i>	
Eudicots	<i>Cucumis sativus</i>	
Eudicots	<i>Clonorchis sinensis</i>	
Eudicots	<i>Glycine max</i>	
Eudicots	<i>Nicotiana tabacum</i>	
Monocots	<i>Oryza sativa</i>	
Monocots	<i>Zea mays</i>	
Monocots	<i>Triticum aestivum</i>	

Figure 2. The bHLH domain conservative motif analysis expressed in different plants. Conservative domain motifs are used in MEME online web analytics. The bHLH protein sequences of these species were downloaded from the JGI and NCBI databases.

3. Regulation of bHLH TFs in Plant Stress Response

Previous research has revealed that the bHLH TF family can participate in the regulation of abiotic stresses such as drought, high salinity, low temperature, and nutrient deficiencies through transcriptional and post-translational modifications [36–41]. Transcriptome is commonly used in abiotic stress studies. Transcriptome technology can be used to identify key nodes or genes for stress resistance at the transcriptional regulatory level for subsequent research. In order to reveal the potential roles of bHLH members in various stress responses in different species, most functional signaling pathways of bHLH TF regulations were identified (Table 1 and Figure 3).

Table 1. bHLH transcription factors involved in plant response to abiotic stress.

Original Plant	Nomenclature	Stress Response	Regulation Type	Refs.
<i>Ipomoea batatas</i> (L.) Lam.	IbbHLH79	Cold	Positive regulation	[15]
<i>Arabidopsis thaliana</i> L.	rd22BP1/AtMYC2/ AtbHLH006	Drought	Positive regulation	[21]
<i>Arachis hypogaea</i> L.	AhbHLH112	Drought/salt	Positive regulation	[42]
<i>Oryza sativa</i>	OsWIH2/OsbHLH130	Drought	Positive regulation	[43]
<i>Fagopyrum tataricum</i>	FtbHLH3	Drought/oxidative	Unknown	[44]
<i>Solanum lycopersicum</i>	SlbHLH22	Drought	Positive regulation	[45]
<i>Zea mays</i> L.	ZmPIF1	Drought	Positive regulation	[46]
<i>Malus × domestica</i> Borkh.	MdCIB1	Drought	Positive regulation	[47]
<i>Arabidopsis thaliana</i> L.	AtbHLH68	Drought	Unknown	[48]
<i>Populus euphratica</i>	PebHLH35	Drought	Positive regulation	[49]
<i>Arabidopsis thaliana</i> L.	AtbHLH122	Drought/salt	Positive regulation	[50]
<i>Oryza sativa</i>	OsbHLH148	Drought	Positive regulation	[51]
<i>Oriza rufipogon</i>	OrbHLH001	Salt/cold	Positive regulation	[52]
<i>Oryza sativa</i>	BEAR1/OsbHLH014	Salt	Positive regulation	[53]
<i>Oryza sativa</i>	OsbHLH062	Salt	Unknown	[54]
<i>Eleusine coracana</i> L.	EcbHLH57	Salt/oxidative/drought	Positive regulation	[55]
<i>Beta vulgaris</i> L.	BvbHLH93	Salt	Positive regulation	[56]
<i>Selaginella lepidophylla</i>	SlbHLHopt	Salt	Positive regulation	[57]
<i>Arabidopsis thaliana</i> L.	AtbHLH112	Drought/salt	Positive regulation	[58]
<i>Oryza sativa</i>	OsbHLH035	Salt	Unknown	[59]
<i>Oriza rufipogon</i>	OrbHLH2	Salt/osmotic	Positive regulation	[60]
<i>Panax ginseng</i> C.A. Meyer	PgbHLH102	Salt	Unknown	[61]
<i>Arabidopsis thaliana</i> L.	AtICE1/AtbHLH116	Cold	Positive regulation	[62]
<i>Arabidopsis thaliana</i> L.	ICE2	Cold	Positive regulation	[63]
<i>Malus × domestica</i> Borkh.	MdCIBHLH1	Cold	Positive regulation	[64]
<i>Pyrus ussuriensis</i>	PuICE1	Cold	Positive regulation	[65]
<i>Oryza sativa</i>	OsbHLH1	Cold	Positive regulation	[66]
<i>Nicotiana tabacum</i> L.	NtbHLH123	Cold/salt	Positive regulation	[67]
<i>Zoysia japonica</i>	ZjbHLH76/ZjICE1	Cold	Positive regulation	[68,69]
<i>Vitis amurens</i>	VaICE1/VaICE2	Cold	Positive regulation	[70]
<i>Dimocarpus longan</i> Lour.	DIICE1	Cold	Positive regulation	[71]
<i>Citrus sinensis</i>	CsbHLH18	Cold/salt	Positive regulation	[72]
<i>Poncirus trifoliata</i>	PtrbHLH	Cold/oxidative	Positive regulation	[73,74]
<i>Rosa multiflora</i>	RmICE1	Cold/salt	Positive regulation	[75]
<i>Prunus avium</i> L.	PavbHLHs	Cold	Unknown	[76]
<i>Arabidopsis thaliana</i> L.	FIT/AtbHLH29	Fe deficiency	Unknown	[77]
<i>Arabidopsis thaliana</i> L.	AtbHLH38	Fe deficiency	Positive regulation	[78]
<i>Arabidopsis thaliana</i> L.	AtbHLH39	Fe deficiency	Positive regulation	[78]
<i>Arabidopsis thaliana</i> L.	AtbHLH100	Fe deficiency	Positive regulation	[79]
<i>Arabidopsis thaliana</i> L.	AtbHLH101	Fe deficiency	Positive regulation	[79]
<i>Arabidopsis thaliana</i> L.	PYE/AtbHLH47	Fe deficiency	Unknown	[80]

Table 1. Cont.

Original Plant	Nomenclature	Stress Response	Regulation Type	Refs.
<i>Arabidopsis thaliana</i> L.	ILR3/AtbHLH105	Fe deficiency	Positive regulation/Negative regulation	[81]
<i>Arabidopsis thaliana</i> L.	AtbHLH104	Fe deficiency	Positive regulation	[82]
<i>Arabidopsis thaliana</i> L.	AtbHLH18	Fe deficiency	Negative regulation	[83]
<i>Arabidopsis thaliana</i> L.	AtbHLH19	Fe deficiency	Negative regulation	[83]
<i>Arabidopsis thaliana</i> L.	AtbHLH20	Fe deficiency	Negative regulation	[83]
<i>Arabidopsis thaliana</i> L.	AtbHLH25	Fe deficiency	Negative regulation	[83]
<i>Chrysanthemum morifolium</i>	CmbHLH1	Fe deficiency	Unknown	[84]
<i>Oryza sativa</i>	OsIRO3/OsbHLH2	Fe deficiency	Positive regulation	[85]
<i>Oryza sativa</i>	OsIRO2/OsbHLH056	Fe deficiency	Positive regulation	[86]
<i>Oryza sativa</i>	OsbHLH156	Fe deficiency	Positive regulation	[87]
<i>Triticum aestivum</i> L.	TabHLH1	Pi and N deficiency	Positive regulation	[88]
<i>Chlamydomonas reinhardtii</i>	NRI1	N starvation	Positive regulation	[89]
<i>Oryza sativa</i>	OsPTF1	Pi starvation	Positive regulation	[90]
<i>Nicotiana tabacum</i> L.	NtbHLH1	Fe deficiency	Positive regulation	[91]
<i>Zea mays</i> L.	ZmICE1	Cold	Positive regulation	[92]
<i>Oryza sativa</i>	OsPRI2/OsbHLH058	Fe deficiency	Positive regulation	[93]
	OsPRI3/OsbHLH059			
<i>Solanum lycopersicum</i>	SlICE1	Cold/salinity	Positive regulation	[94]
<i>Cucumis sativus</i> L.	CsbHLH041	Salt	Positive regulation	[95]
<i>Nicotiana tabacum</i> L.	NtbHLH86	Drought	Positive regulation	[96]
<i>Malus × domestica</i> Borkh.	MdbHLH3	Cold	Positive regulation	[97]
<i>Malus × domestica</i> Borkh.	MdbHLH106L	Salt	Positive regulation	[98]
<i>Malus × domestica</i> Borkh.	MdbHLH130	Salt	Positive regulation	[99]
<i>Pyrus ussuriensis</i>	PubHLH1	Cold	Positive regulation	[100]
<i>Arabidopsis thaliana</i> L.	AtbHLH92	Salt/osmotic stress	Unknown	[101]
<i>Arabidopsis thaliana</i> L.	AtAIB/AtbHLH17	Drought/salt	Positive regulation	[102]
<i>Fagopyrum tataricum</i>	FtbHLH2	Cold	Positive regulation	[103]
<i>Solanum tuberosum</i>	StbHLH45	Drought	Unknown	[104]
<i>Eucalyptus camaldulensis</i>	EcaICE1	Cold	Positive regulation	[105]
<i>Triticum aestivum</i> L.	TabHLH39	Osmotic	Unknown	[106]
<i>Arabidopsis thaliana</i> L.	AtNIG1/AtbHLH028	Salt	Positive regulation	[107]
<i>Glycine Max</i> (L.) Merrill	GmbHLH57	Fe deficiency	Unknown	[108]
<i>Glycine Max</i> (L.) Merrill	GmbHLH300	Fe deficiency	Unknown	[108]
<i>Zea mays</i> L.	ZmPIF3	Drought	Positive regulation	[109]
<i>Oryza sativa</i>	OsbHLH133	Fe deficiency	Negative regulation	[110]
<i>Oryza sativa</i>	OsPRI1/OsbHLH115	Fe deficiency	Positive regulation	[111]
<i>Arabidopsis thaliana</i> L.	AtbHLH121	Fe deficiency	Unknown	[112]
			Positive regulation/Negative regulation	
<i>Arabidopsis thaliana</i> L.	AtbHLH106	Salt	regulation/Negative regulation	[113]
<i>Arabidopsis thaliana</i> L.	AtbHLH11	Fe deficiency	Negative regulation	[114]
<i>Oryza sativa</i>	OsbHLH006	Drought	Unknown	[115]
<i>Oryza sativa</i>	OsbHLH068	Salt	Positive regulation	[116]
<i>Vitis vinifera</i>	VvbHLH1	Drought/salt/cold	Positive regulation	[117]

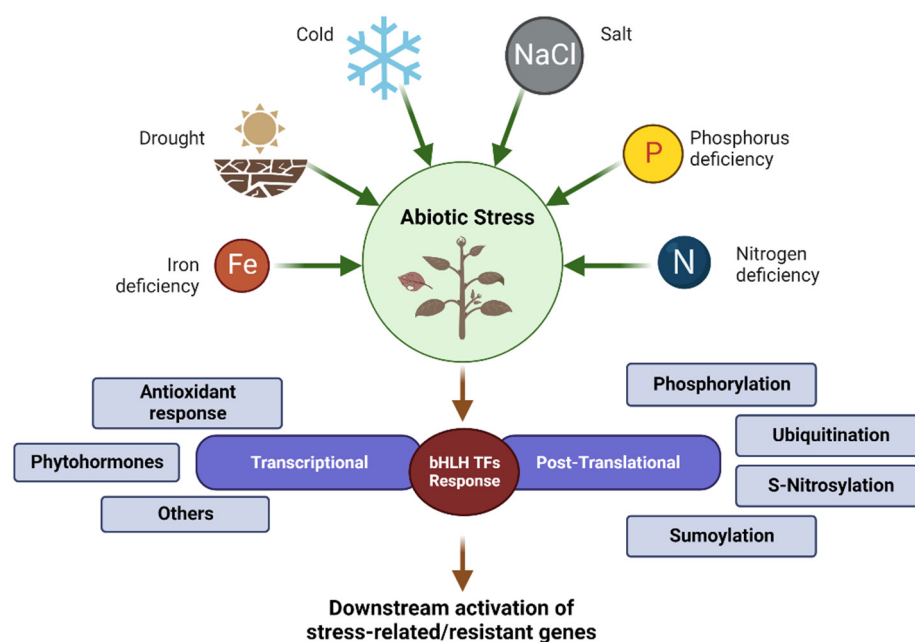


Figure 3. Summary of the different types of bHLH TFs responses to abiotic stresses in plants.

4. Drought Stress Response

One of the major environmental issues that reduces plant growth and development is drought. Drought-induced yield declines have been reported for many crop species, which depend on the severity and duration of the stress period and are associated with a decline in crop yield productivity [118]. Absciscic acid (ABA) is an important phytohormone that plays an important role in abiotic stress tolerance, whose main function appears to be the regulation of plant water balance and osmotic stress tolerance. Plant bHLH transcription factors generally respond to drought stress through both ABA-dependent and ABA-independent regulatory systems [119–121].

In peanuts (*Arachis hypogaea*), AhbHLH112 responds to drought stress by regulating antioxidant gene-mediated reactive oxidative species (ROS) scavenging or ABA-dependent pathways as, under drought stress, ABA accumulates, and blocks Ca^{2+} influx and membrane proton pumps, resulting in plasma membrane depolarization and stomatal closure, which is required to reduce water loss and maintain high water potential. Under drought stress, AhbHLH112 is induced and could activate antioxidant genes and promote ROS scavenging (POD) [42]. *MfHHLH38* also acts positively on plant defenses via the ABA-dependent signaling pathway and enhances the ROS scavenging system, thereby reducing oxidative damage under stress [40]. Drought stress can also induce the accumulation of OsbHLH130, which activates *OsWIH2* expression, and the latter improves rice drought tolerance by reducing the water loss rate and ROS accumulation [43]. *FtbHLH3* responds to drought stress by increasing photosynthetic efficiency and upregulating the expression of critical genes in the ABA signaling pathway, the proline biosynthetic pathway, the ROS scavenging system, and the drought-responsive pathway [44]. *SlbHLH22* also improved tomato plant stress resistance by inducing the expression of genes involved in flavonoid biosynthesis. Flavonoids can enhance plant tolerance to drought and salt stress due to their ability to scavenge superoxides, peroxides, and free radicals generated during stress through ABA biosynthesis and the ROS scavenging pathway, leading to stomatal closure, increased proline content, and enhanced CAT, POD, and SOD activities with reduced ROS accumulation, resulting in an improved tolerance under abiotic stress [45]. ZmPIF1 is a positive regulator of root development, ABA synthesis, signaling pathways, and drought tolerance. It was found that ZmPIF1 binds to the G-box element in the promoters of NCED, CBF4, ATAF2/NAC081, NAC30, and other transcription factors and positively regulates their expression [46]. Cryptochrome-interacting bHLH1 (MdCIB1), through ABA-dependent

and ABA-independent signaling pathways, regulates ABA signal transduction, antioxidant system, osmotic balance, and expression levels of stress-related genes [47]. AtbHLH68 may positively respond to drought stress through ABA signaling and by regulating ABA homeostasis in *Arabidopsis* [48]. *PebHLH35* in transgenic *Arabidopsis* confers drought tolerance by reducing stomatal density, opening, transpiration rate, and water loss, and increasing the chlorophyll content and photosynthesis rate [49]. AtMYC2 (AtbHLH006) is a transcriptional activator in ABA-inducible gene expression under drought stress in plants as it regulates the expression of *rd22* [21]. The *rd22* gene is a dehydration-responsive gene that is activated in *Arabidopsis* plants by exogenous ABA [122]. *AtbHLH122* responds to drought stress via an ABA-independent pathway as it represses CYP707A3, an important ABA 8'-hydroxylase [123], increasing ABA content, and then expressing ABA-inducible genes. It functions as a positive regulator in drought, salt and osmotic signaling [50]. OsbHLH148 also responds to drought stress via a jasmonate signaling pathway. Jasmonates (JAs) are a class of oxygen-containing lipid derivatives (oxylipins) that are considered plant hormones necessary for plant growth and environmental adaptation [124]. In the absence of stress and JA, OsbHLH148 is repressed through its interaction with OsJAZ. Upon exposure to drought stress, JA increases, leading to the degradation of OsJAZ proteins. The released OsbHLH148 activates drought tolerance genes, including *OsDREB1s*, leading to drought tolerance [51] (Figure 4A).

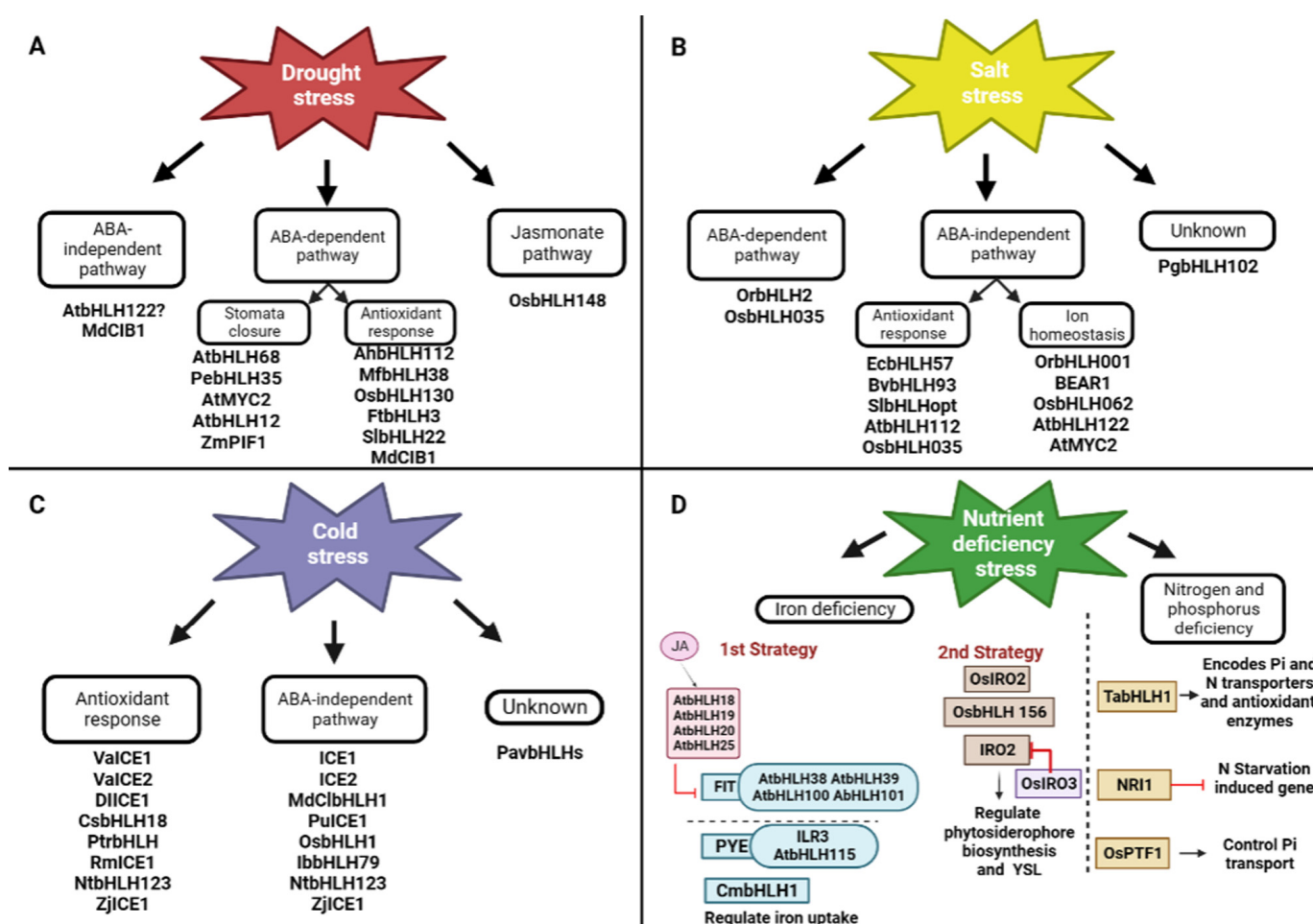


Figure 4. Transcriptional regulations of bHLH TF under abiotic stresses. (A) For drought stress; (B) for salt stress; (C) for cold stress; and (D) for nutrient deficiency stress.

Under drought and salt stress, the overexpression of CgbHLH001 can confer stress tolerance. Regulated by phosphorylation by a protein kinase such as calcium-dependent

protein kinase (CDPK), CgbHLH001 acts as a positive regulator in controlling downstream relevant genes, thereby reducing ROS production and enhancing ROS scavenging ability and improving physiological performance [18] (Figure 5D).

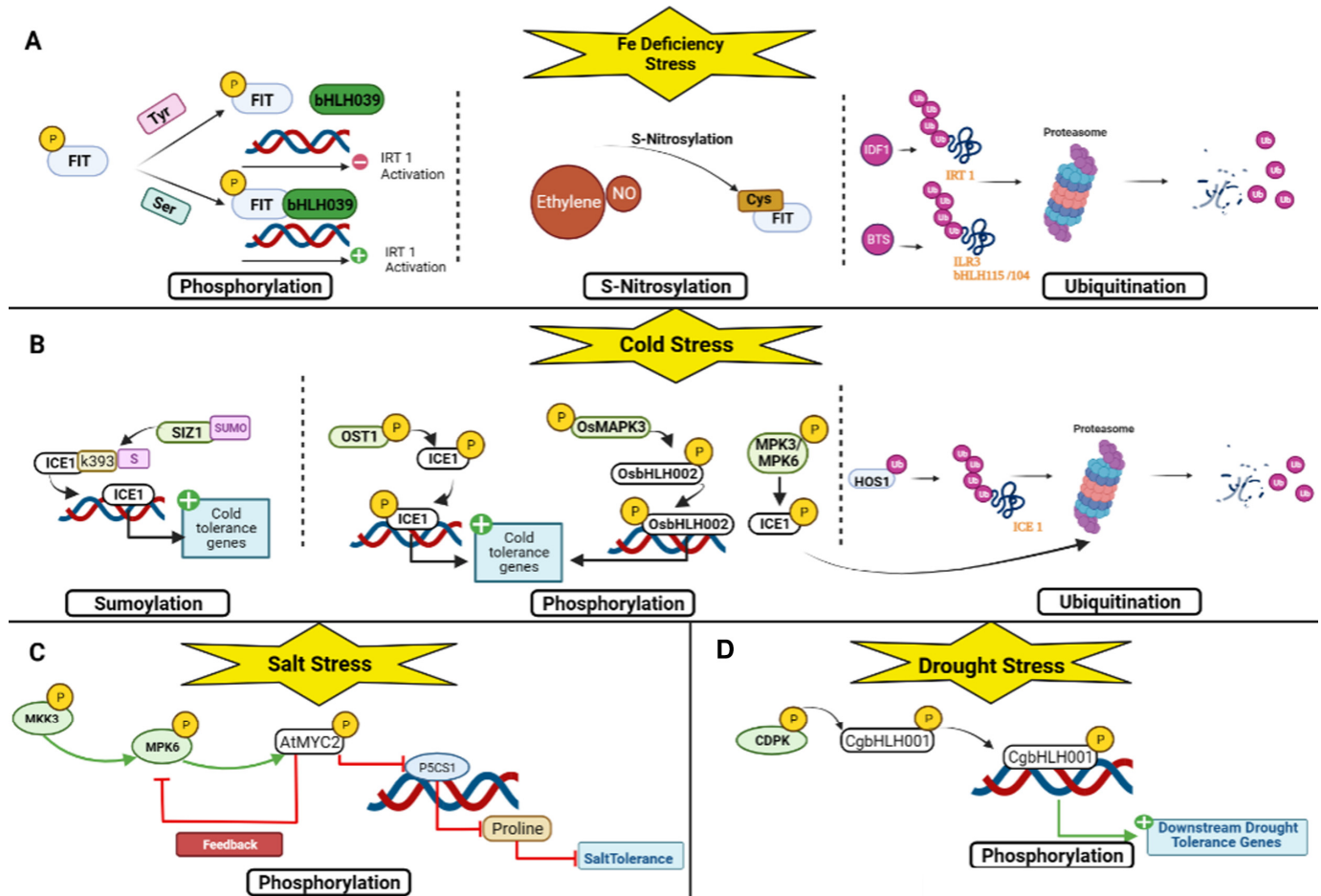


Figure 5. Post-translational regulations of bHLH TF under abiotic stresses. (A) For drought stress; (B) for salt stress; (C) for cold stress; and (D) for nutrient deficiency stress.

5. Salt Stress Response

Salinity has two main effects on plants. It either induces osmotic stress or induces the instability of ions. Several bHLH transcription factors have been characterized in rice. There is *OrbHLH001*, a homologue of *ICE1* (*AtbHLH116*), which activates *OsAKT1*, which enhances Na^+ efflux and K^+ uptake, thus controlling the Na^+/K^+ ratio in salt stress to confer salt stress tolerance [52]. BEAR1 (*OsbHLH014*), a bHLH transcription factor, plays a vital role in rice salt stress response. After receiving the salt stress signal, the BEAR1 protein as a transcriptional activator induces two pathways. On the one hand, it controls the gene expression level of the salt response signaling cascade. On the other hand, it regulates the Na^+/K^+ balance and membrane stabilization genes and thus induces salt stress tolerance [53]. *OsbHLH062* is involved in a jasmonate-dependent transcription regulatory module complex: *Osbhlh062*-JAZ9-*OsNINJA*. *OsJAZ9* represents a transcriptional regulator and an essential element that modulates salt stress tolerance by binding *OsbHLH062*, a transcriptional activator, to *OsNINJA*, an essential repressor of basal jasmonate (JA) signaling. Under salt stress, JA levels increase. The JAZ protein *OsJAZ9* is recruited by SCFCO1 for ubiquitination by the 26S proteasome, leading to its degradation, releasing *OsNINJA*, and allowing *OsbHLH062* to bind to the E-box and activate target genes. *OsbHLH062* can bind to the E-box cis-element and the promoter of *OsHAK21*, including some of the ion transporters, thereby conferring salt stress tolerance [54]. *AtbHLH122*

inhibits *CYP707A3* gene expression under NaCl stress [50]. In addition, Krishnamurthy et al. (2019) identified AtMYC2 and *AtbHLH122* as upstream regulators of ABA-mediated *AtNHX1* and *AtNHX6*, both Na⁺/H⁺ exchangers. In addition, the overexpression of *EcbHLH57* enhanced tobacco resistance to salt stress by increasing the expression of stress-responsive genes such as *LEA14*, *rd29A*, *rd29B*, *SOD*, *APX*, *ADH1*, *HSP70*, and *PP2C* [55]. *BvbHLH93* regulates salt stress tolerance by enhancing antioxidant activity and reducing ROS production, thereby maintaining ion homeostasis, but it needs further investigation at the transcriptional level [56]. *SlbHLHopt* is an essential regulator of water deficit and NaCl stress in transgenic *Arabidopsis* since it increases flavonoid content [57]. In *Arabidopsis*, *AtbHLH112* regulates the expression of genes involved in abiotic stress tolerance by increasing proline levels and reducing ROS accumulation and water loss through the expression of *Proline Dehydrogenase 1 (ProDH)* [58]. *OsbHLH035* responds to salt stress through an ABA-independent pathway by indirectly mediating the expression of *OsHKT1s* such as *OsHKT1;3* and *OsHKT1;5*, which are sodium transporters that transfer Na⁺ from the xylem into xylem parenchyma cells, thus preventing the accumulation of Na⁺ in aerial tissues, since a higher concentration of Na⁺ in the roots causes osmotic stress [59]. *OrbHLH2* in transgenic *Arabidopsis* improved salt tolerance through an ABA-independent pathway by increasing expression levels of *DREB1A/CBF* to confer improved plant tolerance to salt stress; however, more research is needed to determine its mode of action [60]. *PgbHLH102* could respond to salt stress and higher salt concentrations, but its mode of action needs further investigation [61] (Figure 4B). Through an MKK3-MPK6-MYC2 cascade, AtMYC2 (*AtbHLH006*) also functions as a negative regulator of salt tolerance in *A. thaliana*. In brief, the MKK3-MPK6 module phosphorylates and hence activates AtMYC2 in response to salt stress. AtMYC2 binds to *P5CS1*, which is the main contributor to proline accumulation induced by stress [125], and regulates salt tolerance in *Arabidopsis thaliana* by inhibiting the synthesis of *P5CS1* and proline [126] (Figure 5C).

6. Cold Stress Response

Cold stress, including chilling, adversely affects plant growth and development, limits the geographical distribution of plant species, and reduces crop yields worldwide [127]. For acclimation to cold stress, cold tolerance requires a downstream cascade of transcriptional regulation of target genes. Cold-responsive genes contain DRE/CRT cis-elements with a core sequence CCGAC [25,128]. C-repeat Binding Factors (CBFs) (*CBF1*, *CBF2*, and *CBF3*; also known as *DREB1b*, *DREB1c*, and *DREB1a*, respectively) are known genes that bind to these elements, triggering transcription of cold-responsive genes [129]. Since CBFs are only induced after 15 min of cold exposure, the intervention of another TF present in the cell is required [130]. In *Arabidopsis*, the most well-defined pathway is the *ICE 1 (AtbHLH116)* transcription factor, an ABA-independent pathway that binds to the CBF promoter and activates transcription of *CBF1/3*, which in turn induces the *CRT/BRE* genes responsible for cold tolerance [62]. *ICE2 (BAC42644)*, a homologue of *ICE1 (AtbHLH116)*, mediates the same ABA-independent pathway in cold tolerance [63]. *MdCibHLH1* also interferes with the CBF pathway by activating the transcription of *CBF 1* and *2* [64]. *PuICE1* demonstrates a CBF/DREB pathway that requires cold-induced protein-protein interactions with the Heptahelical protein 1 (PuHHP1), which acts as a positive regulator of ABA-mediated stomatal closure in response to cold stress, thus increasing the levels of PuDREBa transcripts and positively regulating cold stress; however, more research is needed to experimentally clarify the physiological mechanism between PuHHP1 and *PuICE1*. [65,131]. In rice, *OsbHLH1* expression is significant for cold tolerance as it might also regulate CBF/DREB1 gene expression [66]. The *IbbHLH79* protein, an *ICE1*-like gene, can activate the CBF pathway and *IbbHLH79*-overexpressing transgenic plants show enhanced cold tolerance [15]. Using the *NtCBFs* signaling pathways, cold-activated *NtbHLH123* and *ZjbHLH76/ZjICE1* regulate the expression of their target genes or regulate stress-responsive genes such as CBFs associated with ROS scavenging, resulting in improved tolerance to cold stress [67–69]. *ValICE1* and *ValICE2* ICE-like TF play a positive role in freezing tolerance and influence

cold stress-related factors such as electrolyte leakage and proline and malondialdehyde (MDA) levels, thereby reducing ROS damage and improving osmotic protection [70]. The overexpression of *DIICE1* in transgenic *Arabidopsis thaliana* enhances cold tolerance by increasing proline content, reducing ion leakage and accumulation of MDA and ROS [71]. *CsbHLH18* mediates a cold response by regulating antioxidant genes by binding to and activating the *CsPOD* promoter, thereby inducing ROS scavenging [72]. *PtrbHLH* also responds to cold stress by modulating POD and CAT [73,74]. *RmICE1* also responds to cold stress by regulating antioxidant genes [75]. Several *PavbHLH* also demonstrated a cold response regulatory mechanism, but the molecular details require further studies [76] (Figure 4C). HOS1 encodes a ring finger protein with E3 ligase activity that reduces *ICE1* (*AtbHLH116*) activity via the ubiquitination/proteasome pathway [132,133]. In addition, OST1 phosphorylates *ICE1* (*AtbHLH116*) and inhibits HOS1-mediated degradation of *ICE1*, since the OST1 protein competes with HOS1 for binding to *ICE1*, thereby releasing *ICE1* from the HOS1–*ICE1* complex. The dual role of OST1 helps enhance *ICE1* stability to increase *CBF* expression and freeze tolerance [134]. MKK2 is also activated by cold stress in plants and consequently activates MPK4 and MPK6 [135]. In brief, MPK3/6-mediated phosphorylation promotes *ICE1* (*AtbHLH116*) degradation, with Ser94, Thr366, and Ser403 being important sites for phosphorylation-dependent degradation [28]. Subsequently, when *ICE1* (*AtbHLH116*) levels accumulate, it is phosphorylated by MPK3/MPK6 and consequently cleared via the 26S proteasome pathway, which inhibits *CBF*-dependent cold signaling [136]. Another positive regulation is found in SUMO conjugation, which enhances *ICE1* (*AtbHLH116*) activity. SIZ1 (SAP and Miz) encodes a SUMO-E3 ligase that is necessary for freezing tolerance, facilitates sumoylation of *ICE1* (*AtbHLH116*), and recognizes K393 as the SUMO conjugation residue in the protein. SIZ-mediated SUMO1 conjugation to K393 affects the activity of *ICE1* (*AtbHLH116*) to control *CBF3/DREB1A* expression and prevents access to the ubiquitination complex. A K393R mutation blocks *ICE1* (*AtbHLH116*) sumoylation, represses expression of *CBF3/DREB1A* and its regulon genes, and reduces cold tolerance [29]. Under cold stress, active OsMAPK3 phosphorylates OsbHLH002, accumulating phospho-OsbHLH002, promoting trehalose-6-phosphate phosphatase 1 (OsTPP1) expression, and increasing trehalose content and resistance to chilling damage [137] (Figure 5B).

7. Iron Deficiency Response

Iron (Fe) is an essential element for plant survival and development as it is involved in several vital processes: photosynthesis, DNA synthesis, respiration, and chlorophyll synthesis. In *Arabidopsis*, FIT (*AtbHLH029*) is a well-known TF that plays a crucial role in Fe uptake via the first strategy [77], which consists of the acidification of the external environment mediated by membrane proton pumps, the *Autoinhibited Plasma Membrane H⁺/ATPases* (*AHA2*) [138], to release and solubilize the iron. It is then reduced from ferric iron to ferrous iron by *Ferric Reduction Oxidase 2* (*FRO2*) [139] and transported through specific channels within the *Iron-Regulated Transporter 1* (*IRT1*) in the plant [140]. It binds to the fer uptake genes *FRO2* and *IRT1*. Since it cannot function alone, it forms heterodimers with the four bHLH TFs *AtbHLH38*, *AtbHLH39*, *AtbHLH100*, and *AtbHLH101* [78,79,141,142]. There is also another protein, POPEYE (PYE) (*AtbHLH47*), that responds to Fe deficiency by using a network independent of FIT [80]. The dimers of ILR3 (*AtbHLH105*) and *AtbHLH104* or ILR3 (*AtbHLH105*) and *AtbHLH34* regulate PYE (*AtbHLH47*), which interacts with two bHLH transcription factors, ILR3 (*AtbHLH105*) and *AtbHLH115* [81,82,143]. Four other bHLH partners of FIT (*AtbHLH029*) (*AtbHLH18*, *AtbHLH19*, *AtbHLH20*, and *AtbHLH25*) promote its degradation in response to JA induction, thereby antagonizing the activity of *AtbHLH38*, *AtbHLH39*, *AtbHLH100*, and *AtbHLH101* and limiting Fe uptake [83]. At the transcriptional level, the active and inactive states are distinguished by specific covalent modifications. Suppose the transition from the inactive state to the active state is bottlenecked. In that case, this could be achieved by limiting the enzymes that can confer or remove covalent modifications to “activate” FIT (*AtbHLH029*). FIT (*AtbHLH029*) could

be in a negative feedback loop, limiting its abundance. In the context of Fe regulation, the rapid switching off of FIT (AtbHLH029) could be to prevent Fe toxicity symptoms [39]. A study by Zhao et al. showed that *chrysanthemum* CmbHLH1 promoted iron absorption through H⁺-ATPase-mediated rhizosphere acidification. The second strategy is not based on the reduction of iron [84]. Nonetheless, it is chelated by phytosiderophores (PS) [144] and then transported by a specific transporter, the oligopeptide transporter YS1. This strategy led to the discovery of the transcription factors IDEF1 and IDEF2 in rice, which control the expression of phytosiderophore biosynthesis and YSL2 [145,146]. IRO2 in rice is a close homologue of bHLH39 and positively regulates phytosiderophore biosynthesis and YSL15 [41]. In rice, the iron-related transcription factor 3 (*OsIRO3*) (*OsbHLH063*), which belongs to the bHLH gene family, plays a critical role in maintaining iron homeostasis in an iron-deficient environment, as it negatively controls transcript levels of *OsIRO2* (*OsbHLH056*) [85–87]. Ogo et al. (2007) found that the overexpression of *OsIRO2/OsbHLH056* promotes iron uptake in rice following the 2nd strategy; however, its mode of action still needs further studies. Wang et al. studied the role of a new rice bHLH-type transcription factor, *OsbHLH156*, in iron homeostasis and found that *OsbHLH156* greatly increased iron deficiency. They concluded that *OsbHLH156* is required for a strategy II uptake mechanism in rice (Figure 4D). Ethylene (ET) and Nitric Oxide (NO) are required for complete upregulation of Fe-deficiency gene expression and FIT (AtbHLH029) protein abundance as they increase the accumulation of FIT by inhibiting proteasomal FIT (AtbHLH029) and thereby prevent its degradation. Therefore, they stabilize FIT (AtbHLH029) expression by nitrosylation of Cys residues present in FIT [147]. Therefore, this finding requires further elucidation. To limit Fe accumulation in plants, a RING-type E3 ubiquitin ligase called Degradation Factor 1 (IDF1) (AT4G30370) is directly involved in the degradation of *IRT1* through ubiquitination [148,149]. To limit the excess of Fe, which can be toxic to plants, there is BRUTUS (BTS) (AT3G18290), a RING-type E3 ubiquitin ligase that plays a role as a negative regulator since it is induced in Fe deficiency and has been shown to target the bHLH transcription factors ILR3 (AtbHLH105) and bHLH115/104 for degradation via the 26S proteasome by its RING domain (E3 ligase), thus inhibiting the formation of heterodimer complexes of PYE/PYEL (AtbHLH47). This includes disrupting the activation of Fe-deficiency genes regulated by PYE (AtbHLH47). BTS (AT3G18290) contains a hemerythrin-like domain that can bind Fe. Fe binding to the hemerythrin-like domain of BTS is involved in its destabilization and subsequent degradation [27,150]. On the one hand, it has been shown that the phosphorylation of Ser 221 and Ser 272 in FIT (AtbHLH029) positively regulates FIT accumulation in the nucleus, enabling its dimerization to AtbHLH039 and its activation of *IRT1* promoters [39]. On the other hand, phosphorylation of Tyr238 and Tyr278 reduces and inhibits heterodimerization of FIT (AtbHLH029) with AtbHLH039 and expression of *IRT1* promoters, rendering FIT (AtbHLH029) inactive [41] (Figure 5A).

8. Phosphorus and Nitrogen Deprivation Stress Response

Phosphorus (P) and Nitrogen (N) are both indispensable macronutrients for plant growth and crop productivity. *TabHLH1* is sensitive to external Pi and N deficiency stress. It confers enhanced tolerance to both Pi and N deficiency through the transcriptional modulation of a panel of genes encoding *Phosphate Transporter* (PT), *Nitrate Transporter* (NRT), and antioxidant enzymes [88]. *NRI1*, previously named *Nitrogen Starvation-Induced Gene 17* (*NSG17*) (BAD44756.1), a basic Helix–Loop–Helix (bHLH) TF, represses the transcriptional activators of N starvation-induced genes to regulate N starvation-specific responses when sufficient N is supplied to *C. reinhardtii* [89]. *OsPTF1* (AAO73566), responsible for tolerance to Pi starvation in rice, controls the Pi transport system in plants. *OsPTF1* is an essential element involved in higher root growth and consequently higher uptake rates of Pi, and it is also involved in the efficient use of Pi in plants. Therefore, *OsPTF1* has potential in engineering plants with higher Pi utilization efficiency [90] (Figure 4D).

9. Conclusions and Future Perspectives

To withstand environmental stresses, plants have evolved interdependent regulatory pathways that allow them to respond and adapt to the environment in a timely manner. Abiotic stress conditions affect many aspects of plant physiology and cause widespread changes in cellular processes. Research into plant defense mechanisms after abiotic stress is of great importance for subsequent breeding. As one of the most abundant transcription factor families in eukaryotes, members of the bHLH family have complex structures, large numbers, and diverse functions. Many studies have shown that bHLHs can regulate plant resistance to a variety of abiotic stresses. This review summarized the roles of the bHLH transcription factor family in the corresponding abiotic stresses in plants from two aspects. First, bHLH transcription factors show evolutionary differences in the conservative domain. Previous studies have shown that members of the same subfamily may regulate the synthesis of the same plant hormones [151]. Thus, there is reasonable speculation that members of the same subfamily may have evolved through genetic replication from the same ancestor. However, these assumptions still need to be verified. Second, we discussed how the bHLH transcription factor specifically regulates plant tolerance to abiotic stresses through transcriptional and post-translational modification pathways. Furthermore, with the development of transcriptome sequencing, transcriptome technology has been widely used in the study of plant stress tolerance. RNA-seq can quickly screen important functional genes by looking for genes with significant differences through samples, in order to find key nodes or genes for stress resistance at the transcriptional level for subsequent research. This naturally raises an interesting question: can bHLHs regulate plant tolerance to stress by controlling the synthesis of plant hormones or compounds via transcriptional or post-translational modification pathways?

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Abbreviations

ACT domain, small regulatory domains initially found in AK, chorismate mutase, and TyrA (prephenate dehydrogenase); TFs, transcription factors; ACE, ACTIVATOR FOR CELL ELONGATION; AIF, ATBS1 (ACTIVATION-TAGGED BRI1 SUPPRESSOR 1)-INTERACTING FACTOR; ARF, AUXIN RESPONSE FACTOR; BEE, BR ENHANCED EXPRESSION; BEH, BES1-HOMOLOGUE; BES1, BRI1 EMS-SUPPRESSOR 1; bHLH, basic helix–loop–helix; BIM, BES1-INTERACTING MYC-LIKE; BR, brassinosteroid; BRZ, brassinazole; CES, CESTA; CIB, CRYPTOCHROME INTERACTING bHLH; CIL, CIB1-LIKE PROTEIN; HOS1, high expression of osmotically responsive gene 1; NCED, 9-cis-epoxycarotenoid dioxygenase; CBF4, C-repeat-binding factor; GA, gibberellin; HBI1, HOMOLOGUE OF BEE2 INTERACTING WITH IBH1; HFR1, LONG HYPOCOTYL IN FAR-RED 1; IBH1, ILI1 BINDING BHLH 1; IBL1, IBH1-LIKE 1; KDR, KIDARI; PAR, PHYTOCHROME RAPIDLY REGULATED; phy, phytochrome; PIF, PHYTOCHROME INTERACTING FACTOR; PIL1, PIF3-LIKE 1; PRE, PACLOBUTRAZOL RESISTANCE; YSL, an iron-phytosiderophore transporter; ABA, abscisic acid; JA, jasmonic acid; P5CS1, pyrroline-5-carboxylate synthetase 1; FIT, FER-LIKE IRON DEFICIENCY-INDUCED TRANSCRIPTION FACTOR.

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