Review

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Basic Leucine Zipper (bZIP) Transcription Factors as Biological Macromolecules Responded to Abiotic Stress and Secondary Metabolite Biosynthetic Pathways in Plants: A Comprehensive Review

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Review

Basic Leucine Zipper (bZIP) Transcription Factors as Biological Macromolecules Responded to Abiotic Stress and Secondary Metabolite Biosynthetic Pathways in Plants: A Comprehensive Review

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Abstract

Since abiotic stress is an unfavourable environmental factor that significantly affects plant growth and development, plants have evolved over time to adapt to these stresses, thereby enhancing their survival capabilities. As one of the largest transcription factor families in plants, bZIP transcription factors are involved in plant growth and development, plant hormone signalling transduction, secondary metabolism synthesis pathways, and responses to abiotic stress. Numerous studies have shown that bZIP transcription factors, upon activation by external environmental signals, can either act independently or through interactions with other proteins to bind to the A-box (TACGTA), the C-box (GACGTC), and the G-box (CACGTG) cis-acting elements in the promoter regions of downstream target non-biotic stress genes, thereby regulating the expression of downstream stress response genes and modulating plant tolerance to non-biotic stress as well as secondary metabolic pathways in plants. Additionally, bZIP transcription factors are involved in plant hormone signalling pathways in response to non-biotic stress. For example, abscisic acid, jasmonic acid, brassinosteroids, and salicylic acid. In this review, we discuss the structure, classification, and mechanisms of action of plant bZIP transcription factors, their roles in plant hormone regulation, and the mechanisms by which bZIP transcription factors respond to abiotic stresses such as drought, salt stress, high/low temperatures, nutrient deficiencies, heavy metal stress and light stress. Additionally, we summarise the role of bZIP transcription factors in regulating the biosynthesis of various secondary metabolites, such as flavonoids, terpenoids, alkaloids, phenolic acids and lignans. Finally, the role of bZIP transcription factors and non-coding RNAs (ncRNA) in enhancing tolerance to abiotic stress was discussed. In the future, we will focus on studying bZIP transcription factors as core regulators of downstream gene networks associated with abiotic stress to enhance plant tolerance to abiotic stress and improve crop yields, thereby addressing food security issues.

Keywords: bZIP transcription factor; plant hormone signalling; abiotic stress; plant growth and development; secondary metabolite biosynthetic pathways

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1. Introduction

Transcription factors are proteins that can bind to specific nucleotide sequences upstream of a gene, and these proteins regulate the transcription of these genes and thus have a regulatory effect on plant growth and development, biotic and abiotic stresses, secondary metabolites [1–4]. Transcription factors contain four types of structural domains, such as DNA-binding structural domains, transcriptional regulatory structural domains, oligomerisation sites and nuclear localisation structural domains [5–7]. Transcription factors can regulate the expression of downstream genes by interacting with other transcription factors, or enhance or repress the expression of genes by binding to the promoter sequences of downstream target genes, thus improving the tolerance of plants to stresses and abiotic stresses, and they play important roles in regulating the physiological and biochemical processes of plants and even the whole life activities [8–11] **(Figure 1)**. bZIP (basic region/leucine zipper motif) transcription factors are one of the largest families of transcription factors in plants, and they are induced to be expressed in response to abiotic stresses, such as drought, salt, cold, high temperature, nutrient stress, heavy metal stress, and high light stresses, and induced to be expressed in response to biotic stresses. They also play important roles in regulating plant growth and development and secondary metabolite biosynthetic pathways [12,13]. It has been shown that when activated by external environmental signals, bZIP transcription factors can regulate the transcription level of target genes by interacting with other transcription factors or by directly interacting with cis-acting elements in the promoter regions of the adversity-associated genes [14–16]. bZIP transcription factors can recognize cis-acting elements with the core sequence ACGT, such as CACGTG (G box), GACGTC (C box), TACGTA (A box) and so on. The bZIP transcription factor is involved in regulating the expression of downstream adversity response-related genes through these elements, thereby regulating plant tolerance to abiotic adversity and biotic adversity [17,18]. Nowadays, researchers have identified a large number of bZIP transcription factors in plants, many of which are involved in plant abiotic stress response and regulate plant resistance under abiotic stress, such as *Arabidopsis thaliana* L., *Oryza sativa* L., *Zea mays* L., *Glycine max* L. and so on **(Table 1)**. It has been found that overexpression or silencing of the expression of these transcription factor genes can increase plant resistance to abiotic and biotic stresses [12–14]. Therefore, the study of bZIP transcription factors is crucial for the future improvement of crop survival under stress conditions. In the future, these research results can not only provide a theoretical basis and support for the improvement of crop resistance, but also be utilised as direct genetic resources.

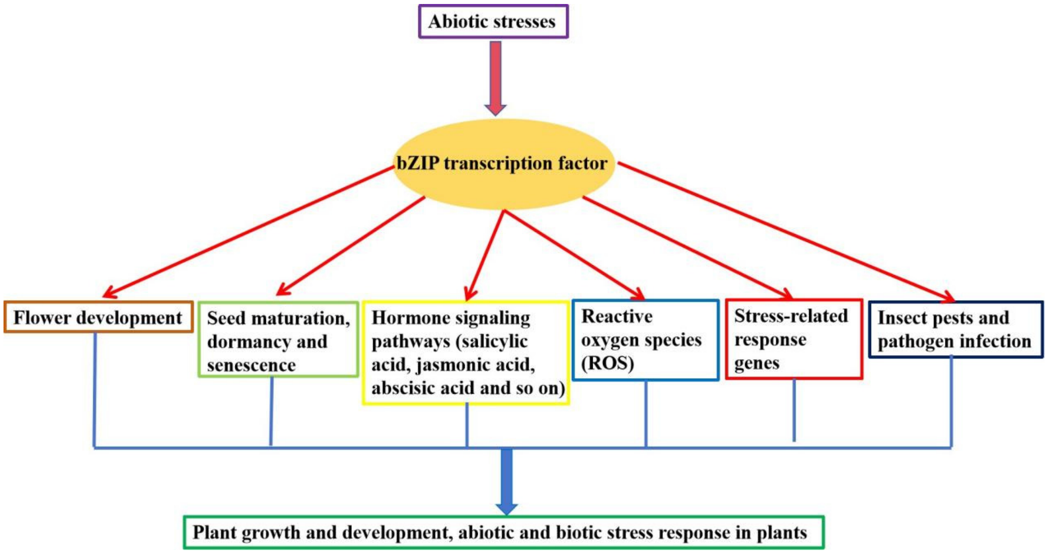

Figure 1. The bZIP transcription factors involved in the regulatory mode in plants growth and development, abiotic and biotic stress response.

Phytohormones not only play an important role in the growth and development of plants, but also play an important role in disease, biotic and abiotic stresses resistance signalling pathways in plants [19,20]. Currently, the resistance-related hormones that have been studied in plants include abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), ethylene (ET), cytokinin (CTK), brassinosteroid (BR), strigolactones (SL) and cytokinin (CTK), among others. There are many genes directly involved in resistance in plants, and the pathways that regulate the expression of these genes are very complex [21–24]. The opening of each resistance signalling pathway requires the concerted efforts of many upstream key regulators. When plants are subjected to external abiotic and biotic stresses, specific signalling molecules such as phytohormones, Ca^{2+} and NO^{-} in their bodies bind to receptor proteins in plant cells, regulating downstream transcription factors to interact with other proteins, and thus activating or repressing the expression of target genes by binding to the promoters of the downstream resistance genes concerned [25–28]. The bZIP transcription factors, a common family of transcription factors in plants, they usually act as positive or negative regulators in the phytohormone-mediated regulation of disease, stress resistance and plant growth and development signalling [29,30]. The bZIP transcription factors are multifunctional in plant, thus they can participate in a wide range of hormone-mediated signalling pathways. Sometimes, bZIP transcription factors also interact with other transcription factors to co-regulate hormone-mediated signalling pathways [31,32].

In recent years, research reviews on bZIP transcription factors have been published, but most of the published reviews focus only on the discovery, structure, classification, functional diversity, and certain adversity regulatory mechanisms of bZIP transcription factors, with a very poor understanding of the bZIP regulatory network and bZIP transcription factors regulate plant responses to abiotic stresses through plant hormones [33,34]. For example, Han et al [12] reviewed the structure, classification, biological functions and regulatory mechanisms of bZIP transcription factors are described, and the molecular mechanisms by which bZIP transcription factors regulate the biosynthesis of flavonoids, terpenoids, alkaloids, phenolic acids and lignin are elaborated. Liu et al [13] reviewed the structural features and functional characterisation of the bZIP transcription factor group, the bZIP transcription factor complex and its molecular regulatory mechanisms associated with salt stress resistance, and the regulation of transcription factors in plant salt stress resistance are summarised and discussed. Guo et al [14] reviewed the latest discussions on the interaction of bZIP with other proteins to regulate abiotic stresses, such as cold, heat, drought, and salt. However, some studies have shown that bZIP transcription factors can indirectly affect plant growth and development and tolerance to abiotic stress by participating in the regulation of plant hormone signal transduction. At the same time, the regulatory effect of exogenous plant growth regulators also requires the participation of bZIP transcription factors [35,36]. Other studies have shown that bZIP transcription factors can interact with non-coding RNAs (ncRNAs) to jointly regulate the expression of downstream genes, thus affecting the tolerance of plants under stress conditions [37,38].

In summary, there is little summary literature on the effects of bZIP transcription factors on plant stress tolerance signalling pathways through the hormonal pathway and the cross-cutting network of bZIP transcription factors and ncRNA that promotes normal plant growth and development and enhances abiotic stress in plants. Therefore, it is highly necessary for us to conduct a more comprehensive review of plant bZIP transcription factors to provide a comprehensive perspective for future in-depth studies of bZIP transcription factors. To fill this knowledge gap, this review firstly introduces the structure, classification and evolution of bZIP transcription factors. Secondly, the roles of bZIP transcription factors involved in plant hormones in plant response to abiotic stresses are summarised. Thirdly, we systematically summarised the molecular mechanisms of bZIP transcription factors involved in plant resistance to various abiotic stresses. Finally, the effects of bZIP transcription factors on the biosynthesis of secondary metabolites in plants as well as the cross-network between bZIP transcription factors and ncRNAs for normal growth and development and enhancement of abiotic stresses are discussed. The current research problems are also presented and their future research directions are envisioned. In this sense, it can serve as an effective reference point for understanding the regulatory network of plant bZIP transcription factors and their related functions, providing valuable insights for stress tolerance breeding applications and theoretical support for future global food security.

1.1. The Structure of the Plant bZIP Transcription Factors

As one of the largest transcription factor families in plants, bZIP transcription factors are widely present in various eukaryotic organisms. To date, scientists have discovered and identified members of the bZIP gene family in many plants, most of which are involved in plant growth and development, abiotic stress, biotic stress, and the regulation of secondary metabolism in plants [39,40]. The bZIP transcription factors are named after the conserved bZIP structural domain and have a relatively conserved structure consisting of 60-80 amino acids, and the structural domain consists of two specialised structures, including a basic region and a leucine zip region [41,42]. The basic region is usually a nuclear localisation signal consisting of about 16 amino acids followed by an invariant N-X7-R/K sequence, which is responsible for recognising and binding to specific sequences on the promoter to perform biological functions, and it is a highly conserved region [43–46]. As shown in the figure, the bZIP domain is divided into two closely adjacent parts. The first is a highly conserved basic region consisting of approximately 20 amino acid residues, which contains a nuclear localisation signal and an N-X7-R/K motif capable of binding to DNA; the second is a leucine zipper region, where each repeat unit consists of 7 amino acid residues, with leucine or a related hydrophobic amino acid at position 7, and the number of repeat units varies from 3 to 8 **(Figure 2A)**. Each bZIP domain forms a continuous α-helix, and the α-helices of two bZIP proteins interlock due to the hydrophobicity of their side chains, forming a zipper structure **(Figure 2B)** [24,47]. bZIP proteins must form homodimers or heterodimers to function properly.

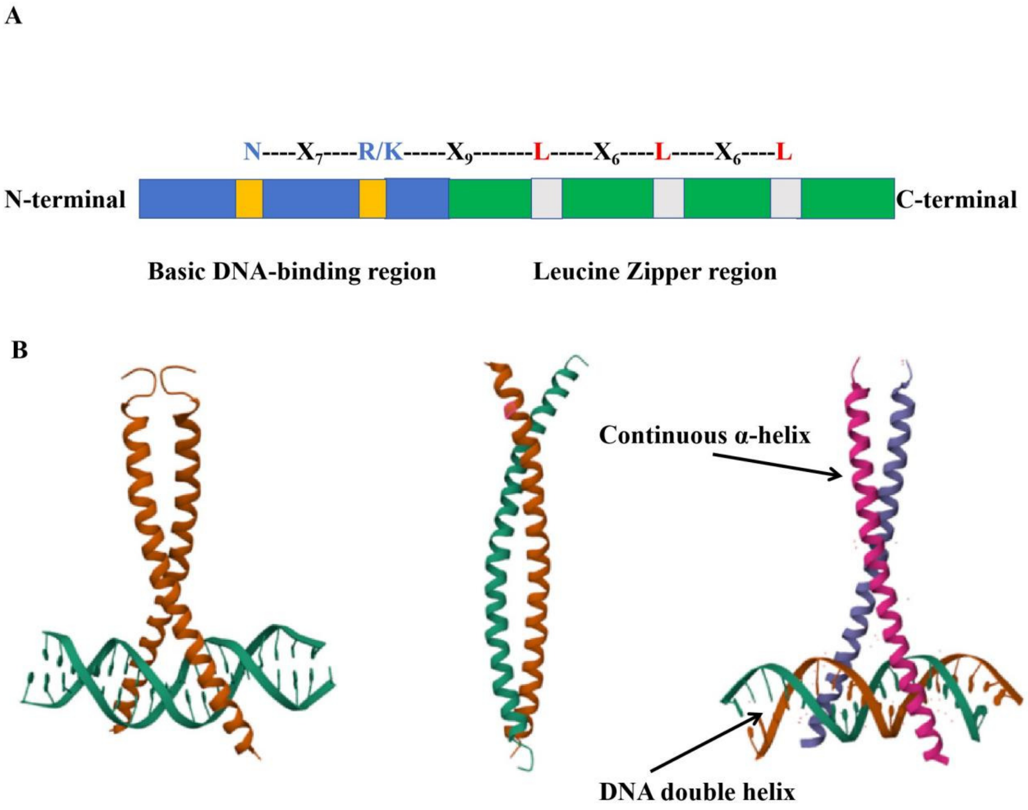

Figure 2. (**A**) Primary structure of the bZIP domain. Schematic representation of the bZIP transcription factors domain, consisting of a basic DNA-binding region (blue) and the leucine zipper region (green) respectively. (**B**) Structural model of a dimer of the bZIP transcription factors domains, which is derived by PDB website (www. rcsb.org). The leucine zip region is composed of one or more repeats containing 7 amino acid residues, where the 7th position of each repeat is leucine, and the rest of the amino acids include isoleucine, methionine, valine, methionine and so on. This region can mediate the formation of homo- or heterodimers of bZIP transcription factor proteins with transcriptional activation or repression functions. Other hydrophobic residues may be

present in positions 3 and 4. The leucine zip region allows the bZIP transcription factor protein to bind to DNA in a dimerised form by forming an amphipathic α-helix structure.

1.2. The Classification of the Plant bZIP Transcription Factors

The classification method of bZIP transcription factor is relatively diverse and varies among different species **(Table 2)**. The number of bZIP members in different species ranges from 9 to 227, and the number of bZIP subfamilies is between 10 and 20, with only a few species having bZIP subfamilies smaller than 10 or larger than 20. The functions of different subfamilies vary greatly, but these bZIP transcription factors play very important roles in plant stress response and growth and development [48–51].

Currently, classification is primarily based on amino acid richness, DNA binding sites, conserved sequences, and phylogenetic relationships. Classification based on specific amino acid richness divides the bZIP family in *Brassica rapa* into 9 groups, each of which is rich in glutamine (Q), aspartic acid (D), proline (P), asparagine (N), serine (S), glycine (G), and those with only a simple domain, no simple domain, or only one transmembrane domain [48]. Based on the amino acid sequences of the bZIP basic structure domain and hinge region, as well as the DNA-binding sites, bZIP genes in rice can be classified into 11 groups, I–XI, with each group containing 7, 3, 6, 22, 3, 14, 16, 3, 11, 3, and 1 OsbZIP genes, respectively [49]. Tomato bZIP genes can be divided into 9 groups, A-I, containing 16, 12, 6, 2, 12, 2, 3, 4, and 12 SlbZIP genes, respectively [52]. Grape (*Vitis vinifera*) bZIP genes can be divided into 11 groups: A-I, J, and U, with each group containing 13, 3, 10, 5, 4, 6, 2, 1, 2, 7, and 2 VvbZIP genes, respectively [53]. According to the specificity of the conserved basic structural region binding to DNA, plant bZIP proteins can be classified into four types, namely, G-box-binding bZIP proteins, C-box-binding bZIP proteins, bZIP proteins binding to both G-box and C-box, and bZIP proteins that do not form dimers with DNA [54].

By selecting *Arabidopsis thaliana* L., *Zea Mays* and other species, a number of amino acid sequences were found in bZIP family transcription factor proteins, and therefore it was hypothesized that these amino acid sequences might be bZIP family transcription factors conserved amino acid sequences. As shown in the Figure S1, amino acid sequences KTLRRLAQNREAARKSRLRKKAYIQNLET is a conserved amino acid sequences of the bZIP family transcription factors **(Supplementary Figure S1)**. To investigate the phylogenetic and evolutionary relationships of bZIP transcription factors in different species, we constructed phylogenetic trees of the amino acid sequences of some bZIP TF in *Arabidopsis thaliana*, *Oryza sativa*, *Glycine max*, *Panicum virgatum*, *Phragmites australis* and *Sorghum bicolor*. using MEGA 11.0 software [55]. Among them, we found that OsbZIP54 and OsbZIP56 and OsbZIP24 were highly related, PvTGAL9-Like isoform X1 and PvTGAL9-Like isoform X4 were highly related, PvLG2 isoform X1 and PvLG2 isoform X2 were highly related, AtTGA9 and AtT27G7.2 were highly related, PvPVAP13 and PvTGAL4-Like isoform X3 were highly related. At the same time, we also found that MYB transcription factors between different species have strong phylogenetic relationships. Such as, PhTGA2.3-Like isoform X1, PhTGA2.3-Like isoform X2 and OsbZIP64 were highly related, SbTGAL4 isoform X5 and MfTGAL4-Like isoform X3 were highly related, it is possible that bZIP TF have similar functions in different species. The bZIP TF are involved in regulating plant growth and development, secondary metabolism and response to abiotic and biotic stress **(Supplementary Figure S2)**.

1.3. The Mechanism of Action of bZIP Transcription Factors

Three of the four core nucleotide flanking bases determine the binding specificity of plant bZIP transcription factor proteins. They recognise the cis-acting element (Abscisic acid responsive elements) ABRE whose core sequence is an ACGT palindrome. bZIP transcription factors are involved in ABA signalling mainly by binding to the promoter regions of genes containing ABRE [56]. The structure of the plant bZIP transcription factor determines its function. bZIP binds preferentially to DNA sequences containing the ACGT core, such as the A-box (TACGTA), the C-box (GACGTC), and the G-box (CACGTG), and is able to promote or repress downstream expression of relevant abiotic stress genes, which enables the plant to survive in complex abiotic environments better [57]. Additionally, some bZIP transcription factors can also bind to non-palindromic DNA sequences. For example, other non-palindromic cis-acting elements such as the PB (TGAAAA) element and the H-box (CCTACC) element [58]. The GmbZIP44 transcription factor in soybeans can specifically bind to the cis-element GLM (GTGAGTCAT) [59].

The bZIP transcription factors can alter their specificity and affinity for DNA binding through phosphorylation modifications, dimerisation, or interactions with other proteins, while also affecting the stability of bZIPs themselves. bZIP can specifically bind to the promoter sequence of target genes through homodimer or heterodimer forms. The binding site is located in the basic region of bZIP, and this specific binding can activate or inhibit the transcription of target genes [60]. The bZIP TF family members respond to abscisic acid (ABA) signals through cis-acting elements in *Arabidopsis*, such as ABRE. When ABA is recognised by specific receptors, protein kinase II or serine/threonine kinase transduces the ABA signal, phosphorylating bZIP transcription factors to induce the expression of downstream genes. Following post-translational modification, bZIP is activated and participates in responses to various stress signals and plant growth and development. The upstream region of bZIP promoters contains cis-acting elements associated with hormone regulation, such as gibberellic acid (GA), ABA, indoleacetic acid (IAA), and methyl jasmonate (MeJA) response elements, indicating that bZIP expression can be regulated by multiple plant hormones [56–60].

Phosphorylation is an important regulatory mechanism of bZIP transcription factors and plays an important role in the ABA pathway and stress response in plants. The negative charge generated by phosphorylation can modify the conformation of proteins and their repulsive and attractive forces [60–62]. When abiotic or biotic stress signals are detected by plants, bZIP transcription factors can be activated by sucrose non-fermenting 1-related protein kinase (SnRK), mitogen-activated protein kinase (MAPK), and calmodulin-domain protein kinases (CDPK), thereby participating in plant stress responses and growth regulation **(Figure 3)**.

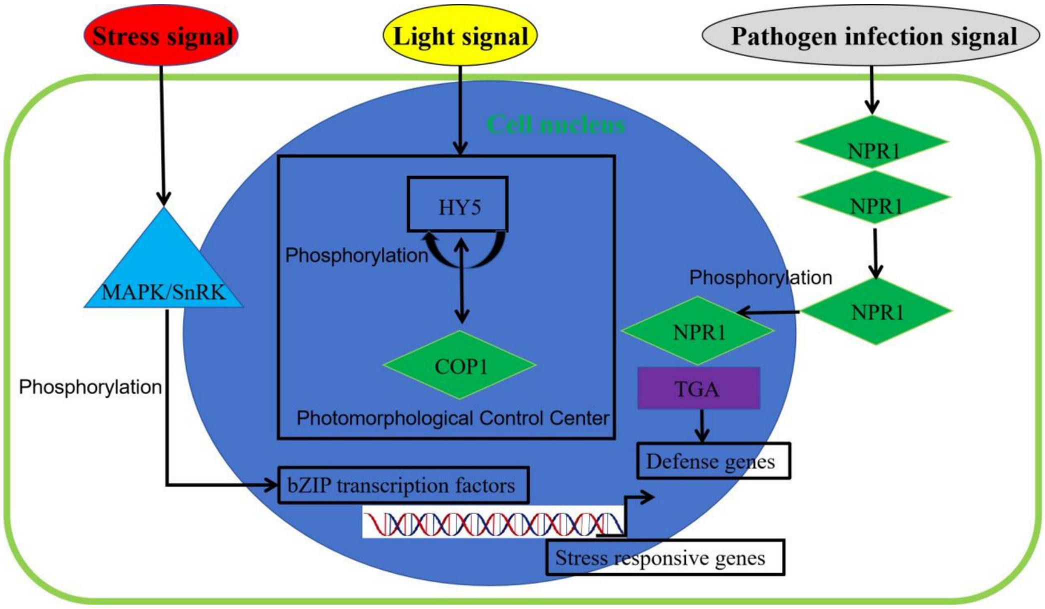

Figure 3. The bZIP transcription factor regulatory mechanism. The arrows in the figure indicate the route of action.

Ubiquitination, one of the post-translational modifications of bZIP transcription factors, is also an important mechanism for bZIP biological activity. The degradation of bZIP is mediated by the ubiquitin-26S proteasome. The MdbZIP44 transcription factor is degraded by the ubiquitin-26S proteasome system in *Malus domestica*, thereby inhibiting the anthocyanin biosynthesis regulated by MdbZIP44 [63]. The bZIP transcription factor can interact with other transcription factors or proteins to regulate downstream gene expression, thereby regulating plant stress resistance by enhancing or inhibiting gene expression. OsbZIP23 can be activated by *OsSAPK2* phosphorylation, while *OsPP2C49* can inhibit OsbZIP23 transcription, indicating that bZIP transcription factor interacts with these two enzymes to regulate the rice ABA signalling pathway and stress resistance [64]. Zhang et al. reported the ThbZIP1 transcription factor of binds to the cis-elements C-box, G-box, and A-box of stress response gene promoters under ABA, salt, and drought stress, thereby regulating the expression of downstream genes in *Tamarix hispida* [65].

2. Role of bZIP Transcription Factors Involved Phytohormone in Plant Response to Abiotic Stresses

Phytohormones have an important impact on plant growth and development and on the regulation of plant tolerance to abiotic stresses. It was found that bZIP can indirectly affect plant growth and development as well as abiotic stress by participating in the regulation of phytohormone signalling. Expression of bZIP transcription factor genes is altered in the presence of exogenous phytohormones such as salicylic acid (SA), abscisic acid (ABA), jasmonic acid (JA), cytokinin (6-BA), gibberellin (GA) and ethylene (ET) [16,66–68]. Zhang et al. found Expression of the wheat *TabZIP1* gene was up-regulated after exogenous JA and ET treatments, whereas there was no significant change in the expression of this gene under the influence of exogenous SA [69]. Han et al. identified 66 putative bZIP transcription factor genes in the genome of *Glycyrrhiza uralensis*, and quantified the gene expression levels of the 66 bZIP family members under abiotic stress treatments using qRT-PCR, which is responsive to ABA stress, was also found to have a regulatory role in the synthesis of secondary metabolites by *Glycyrrhiza uralensis* [70]. Wang et al. reported a SAPK10-bZIP72-AOC pathway, through which ABA promotes JA biosynthesis to synergistically inhibit rice seed germination. SAPK10-dependent phosphorylation enhances the stability of the bZIP72 protein as well as its binding ability to the AOC promoter, increasing the transcription of AOC and the concentration of endogenous JA. Blocking JA biosynthesis significantly reduced the sensitivity of ABA to rice seed germination [71,72]. Wang et al. identified some bZIP transcription factor genes from whole genome sequences of *V. radiata* and *V. angularis*, respectively. A number of cis-acting regulatory elements (CARE) involved in abiotic stress and phytohormone responses were detected in the putative promoter region of the bZIP genes. To analysis of bZIP genes expression profiles under drought, salt and ABA stress using quantitative real-time PCR revealed that most of the bZIP genes had altered expression [73]. Zhang et al. identified a novel *TabZIP14-B* gene involved as a positive regulator in mediating abiotic stress response in wheat. TabZIP14-B is transcriptionally activated and binds to the ABA response element (ABRE) in yeast. *TabZIP14-B* was expressed in roots, stems, leaves, and young spikes and was up-regulated by treatments with exogenous ABA, salt, freezing temperature, and polyethylene glycol (PEG) stress. Overexpressing *TabZIP14-B* showed enhanced tolerance to salt, freezing stress, and ABA sensitivity in *Arabidopsis* [74]. Zhou et al. Identified 66 bZIP family members in *Bletilla striata*. Some of the *BsbZIPs* were highly expressed under low temperature, injury, oxidative stress and GA treatment. In addition, BsbZIP13 was located in the nucleus. Yeast two-hybrid (Y2H) and bimolecular fluorescence complementation (BiFC) experiments showed that BsbZIP13 could interact with multiple BsSnRK2 [75]. A total of eight gene family members were identified in cucumber (*Cucumis sativus* L.) by Lu et al. All eight *CsABF/AREB* genes were responsive to ABA and JA, with *CsABF7* showing the highest expression under ABA and Me-JA treatments. Drought and salt stress significantly induced the expression of *CsABF1*, *CsABF2*, *CsABF7* and *CsABF8*. Drought and NaCl stress significantly induced the expression of *CsABF1*, *CsABF2*, *CsABF7* and *CsABF8* [76]. Chai et al. identified a soybean bZIP gene *GmbZIP60*. GmbZIP60 is located in the nucleus. *GmbZIP60* is induced by salt stress, drought stress, and various phytohormone treatments, including ABA, ET, and JA. Overexpression of *GmbZIP60* in transgenic soybean and rice enhanced their tolerance to salt stress and drought stress. Chromatin immunoprecipitation-qPCR (ChIP-qPCR) analysis further confirmed that GmbZIP60 could directly bind to the promoters of abiotic stress-related genes induced by ABA, ET, JA and SA [77]. He et al.

isolated a bZIP gene *GmbZIP19* from soybean, and the expression of *GmbZIP19* was significantly induced by ABA, JA, and SA, but decreased under salt and drought stress conditions. By constructing a soybean transient *GmbZIP19* overexpression line and performing chromatin immunoprecipitation experiments, and found that GmbZIP19 was able to bind to the promoters of marker genes induced by ABA, JA, ET and SA in soybeans [78]. In conclusion, bZIP TF genes expression are altered under the regulation of plant hormone, such as SA, ABA, JA, 6-BA and ET.

3. Role of bZIP Transcription Factors in Response to Abiotic Stresses

Abiotic stress has a significant impact on plant growth, development, and yield. These stresses disrupt plant physiological and biochemical processes, leading to growth inhibition, metabolic disorders, and even cellular damage and death [79,80]. To cope with abiotic stress, plants have evolved a series of complex adaptive mechanisms, including osmotic regulation, reactive oxygen species (ROS) scavenging, hormone regulation, and gene expression regulation [81]. Therefore, to understand the mechanisms of abiotic stress is of great importance for protecting crop yields. With the continuous improvement of whole-genome sequencing technology, bZIP transcription factors have been found to play an important role in abiotic stress in many higher plants, such as *Oryza sativa*, *Zea mays*, and *Glycine max* **(Figure 4) (Table 3).**

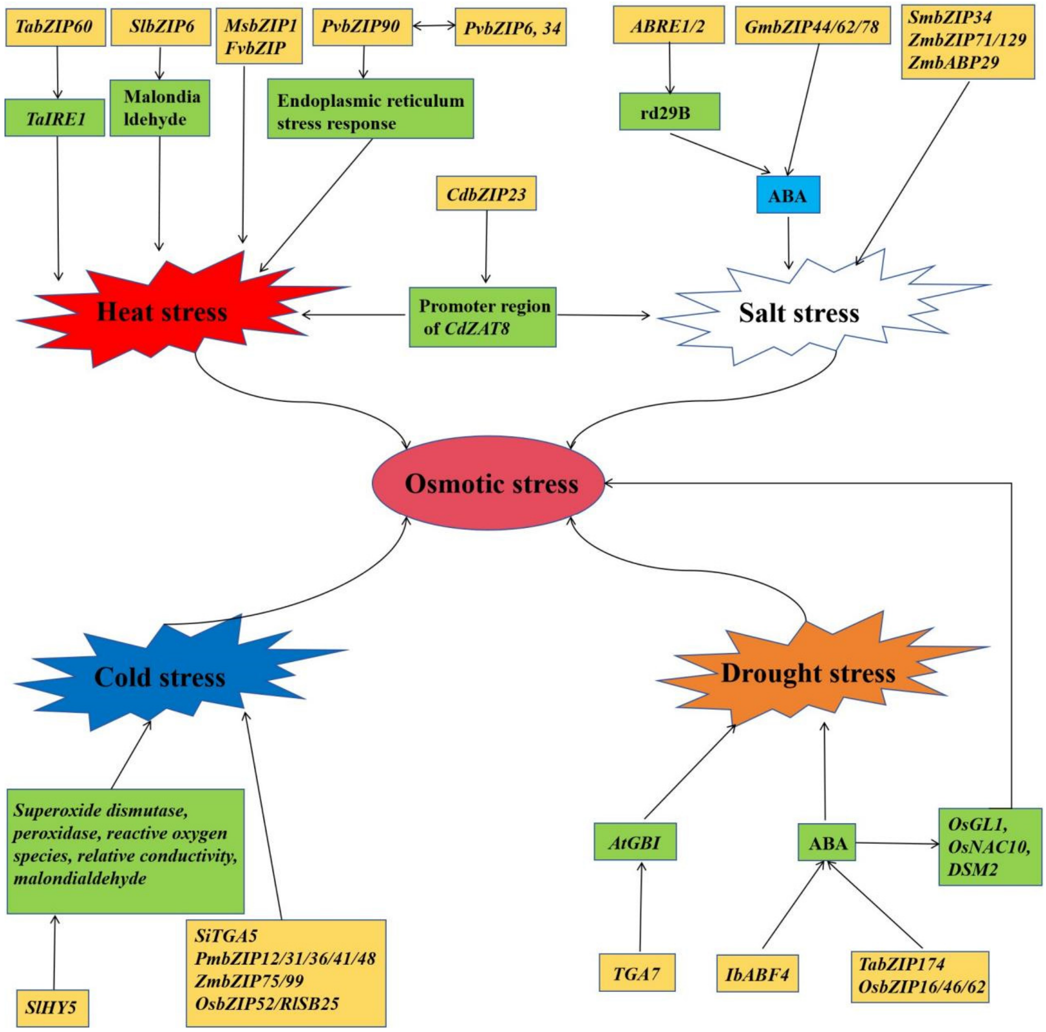

Figure 4. Regulatory function of bZIP transcription factors under abiotic stress in plants. Multiple members of the bZIP transcription factor family enhance plant resistance to abiotic stresses such as high temperature, low

temperature, salt, and drought by participating in osmotic regulation, reactive oxygen species scavenging and redox balance, hormone signal transduction, and other pathways.

3.1. bZIP Transcription Factors in Response to Drought Stress

Drought has a huge impact on plants. It can hinder plant growth, reduce yields, and affect physiological processes such as photosynthesis and water metabolism. In addition, drought can alter soil microbial communities, affecting interactions between plants and microorganisms, increasing plant mortality and the risk of ecosystem fires [82,83]. Pan et al. isolated the bZIP family gene SlbZIP38 from tomato (*Solanum lycopersicum* cv. Ailsa Craig). SlbZIP38 is differentially expressed in different organs of tomato plants and is downregulated by drought, salt stress, and ABA. Overexpression of *SlbZIP38* plants significantly reduces tomato tolerance to drought and salt stress. Overexpression of *SlbZIP38* plants reduces chlorophyll and free proline content in leaves but increases malondialdehyde content [84]. Li et al. identified the soybean bZIP gene *GmTRAB1*, whose transcripts are upregulated under drought, ABA, and oxidative stress conditions. Overexpression of *GmTRAB1* enhanced the tolerance of transgenic *Arabidopsis* and soybean root hairs to osmotic stress. However, RNAi of *GmTRAB1* expression in soybean root hairs increased their drought sensitivity. GmTRAB1 also enhances the sensitivity of transgenic plants to ABA and regulates ABA-mediated stomatal closure under drought stress. Additionally, GmTRAB1 stimulates the transcriptional accumulation of drought, ABA and antioxidant-related genes in response to drought stress [85]**.** Wang et al. identified a bZIP transcription factor named CmbZIP9 from the leaf transcriptome of *Chrysanthemum mongolicum* and found that overexpressing *CmbZIP9* in tobacco reduced malondialdehyde (MDA) content under drought stress, increased peroxidase (POD) and superoxide dismutase (SOD) activity, and elevated the expression levels of stress-related genes, thereby enhancing the drought tolerance of the transgenic tobacco lines [86]**.** Wu et al. identified a bZIP transcription factor named EDT1 from *Oryza sativa.* The EDT1 protein contains a bZIP domain, a putative nuclear localization signal (NLS), and six conserved phosphorylation sites. Overexpressing *EDT1* rice plants exhibited significantly enhanced drought tolerance and the expression of stress-related genes such as *OsbZIP12, SNAC1, OsLEA3, OsbZIP16, OsbZIP10* and *OsABI2* was upregulated in *EDT1*-overexpressing rice lines. These results indicate that EDT1 plays a positive role in rice drought tolerance [82]**.**

3.2. Molecular Mechanisms of bZIP Transcription Factors Associated with Salt Stress

The visible symptoms of salt damage are chlorosis of leaf tips, followed by leaf scorching, browning, and leaf death. This leads to slow plant growth, poor root development, sterility, and reduced seed yield. Excessive salt content causes physiological disorders in plants and can even lead to death **(Figure 5)** [10,87]. He et al. cloned a new F-bZIP transcription factor ZmbZIP76 from the maize inbred line *He344*. The expression of *ZmbZIP76* in maize is significantly induced by high salt, osmotic stress and ABA. Overexpression of *ZmbZIP76* enhances the tolerance of transgenic plants to salt and osmotic stress. ZmbZIP76 upregulates the expression of a series of non-biotic stress response genes by binding to ACGT elements, thereby enhancing ROS scavenging capacity, increasing abscisic acid levels, proline content, K^+/Na^+ ratios, reducing water loss rates, and minimizing membrane damage, thereby enhancing plant salt tolerance [88]. Wei et al. found that *JrbZIP40* is strongly induced under both drought and salt stress. JrbZIP40 is localized to the cell nucleus and possesses transcriptional activation activity. Overexpression of *JrbZIP40* in transgenic *Arabidopsis* seedlings significantly enhanced their resistance to salt and drought stress. JrbZIP40 can bind to the promoters of *JrHB7* and *JrATG8G* and activate their expression, thereby enhancing the plant's resistance to salt and drought stress. The results elucidate the regulatory network and biological functions of JrbZIP40 in drought and salt tolerance [89]. Wang et al. identified and analyzed 49 bZIP transcription factor genes in the potato genome, several of which are induced under different stress conditions. The expression of *StbZIP25*, which is homologous to the AtbZIP36/ABF2 gene in *Arabidopsis*, was significantly upregulated under salt stress treatment. The StbZIP25 protein is localized in the cell nucleus and functions as a transcription activator. Overexpression of *StbZIP25* enhances the salt tolerance of *Arabidopsis* [90]. Liu et al. identified an OsbZIP71 transcription factor from rice. OsbZIP71 can bind to the G-box motif but lacks transcriptional activity. Drought, polyethylene glycol (PEG), and ABA treatments strongly induced the expression of *OsbZIP71*, while salt treatment inhibited its expression. Overexpressing-*OsbZIP71* plants showed significantly enhanced tolerance to drought, salt, and PEG osmotic stress. RNAi knockdown *Osbzip71* lines had the opposite effect. Some abiotic stress-related genes *OsVHA-B*, *OsNHX1*, *COR413-TM1* and *OsMYB4* were upregulated in the overexpressed *OsbZIP71* lines but downregulated in the *Osbzip71* lines. OsbZIP71 can directly bind to the promoters of *OsNHX1* and *COR413-TM1* in vivo. These results suggest that OsbZIP71 may play an important role in rice drought and salt tolerance [91].

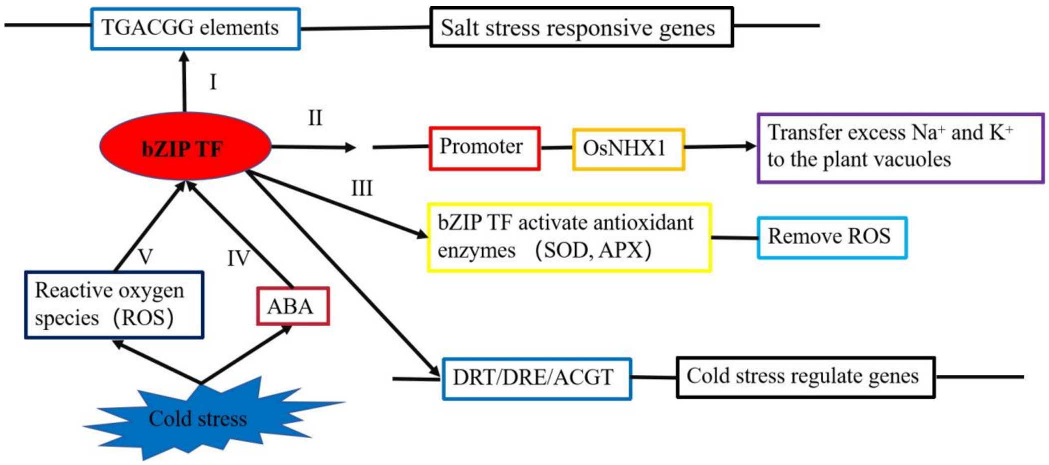

Figure 5. The bZIP transcription factors involved in abiotic stress response pathways. The bZIP transcription factors participate in pathways related to salt stress and low temperature stress in plants. **(Ⅰ).** The bZIP TF specifically binds to the TGACGG element to regulate the expression of downstream salt stress response genes; **(Ⅰ Ⅰ).** The bZIP TF binds to the promoter of the OsNHX1 anti-transporter gene, transporting Na^+ and K^+; **(Ⅰ Ⅱ).** The bZIP TF activates the activity of antioxidant enzymes (such as SOD and APX) and removes ROS from plants; **(Ⅳ).** bZIP TF respond to ABA signal transduction; bZIP transcription factors recognise the ACGT sequence in the promoter region of ABA-induced genes, thereby regulating downstream COR genes. **(V).** Under low-temperature conditions, oxidative stress occurs, and ethylene response factors (ethylene response factor, AP2/ERF) regulate downstream low-temperature-related genes by activating bZIP transcription factors.

3.3. bZIP Transcription Factors Involved in Plant Response to Temperature Stress

Temperature is a major environmental factor affecting plant growth and development and fruit quality after harvest. Suitable temperatures are conducive to plant growth. Both high and low temperatures can cause varying degrees of stress on plants, affecting physiological processes such as photosynthesis, respiration, and water metabolism, which in turn impact plant growth, flowering, fruiting and yield [92–94].

3.3.1. bZIP Transcription Factors and High-Temperature Stress

When temperatures exceed the optimal temperature, the enzyme systems involved in physiological and biochemical reactions are impaired, metabolic activity is hindered, and this in turn affects normal plant growth and development [95]. Shen et al. reported that the bZIP family member CabZIP63 regulates the expression of *CaWRKY40* in *Capsicum annuum*. Silencing the *CabZIP63* gene in pepper plants significantly reduced their resistance to ralstonia solanacearum inoculation (RSI) and tolerance to high temperature-high humidity (HTHH), accompanied by downregulation of immunity or heat-related genes *CaPR1*, *CaNPR1*, *CaDEF1* and *CaHSP24*. Overexpression of *CabZIP63* plants induced allergen-mediated cell death and increased the expression of the detected immunity and heat-tolerance-related marker genes. In conclusion, CabZIP63 is involved in plant immunity or heat-tolerance biological processes [96]. Chen et al. identified OsbZIP33 is significantly upregulated under drought, high salinity, H_2O_2 and high-temperature stress conditions in *Oryza sativa* L.. Overexpressing-*OsbZIP33* plants exhibited significantly enhanced drought tolerance. Under drought conditions, the expression levels of representative downstream drought-induced genes in transgenic rice plants were significantly higher than those in wild-type plants. Studies indicate that OsbZIP33 is induced by exogenous ABA. Overexpression of *OsbZIP33* increases the sensitivity of transgenic plants to ABA compared to wild-type plants. In summary, the results indicate that OsbZIP33 regulates rice drought tolerance and plant tolerance under high-temperature conditions [97]. Qiu et al. found that OsbZIP14 is a key heat-responsive transcription factor gene. After knocking out *Osbzip14* gene in the rice (ZH-11), the knockout mutant exhibited dwarfism and reduced tillering during the grain filling stage. Under high-temperature treatment, the expression of *OsbZIP58*, a key gene regulating the accumulation of rice seed storage proteins (SSPs), was upregulated in *Osbzip14* mutants. Additionally, OsbZIP14 directly can interact with OsbZIP58. The results indicate that under high-temperature stress, OsbZIP14 regulates plant tolerance to high temperatures through synergistic interactions with OsbZIP58 and OsbZIP14 [98]. Jiang et al. demonstrated that the nuclear-localized proteins BdibZIP44 and BdibZIP53 are involved in heat tolerance mechanisms. These proteins exhibit inducible expression under heat stress conditions in *Brachypodium distachyon*. Overexpression *BdibZIP44* and *BdibZIP53* plants enhanced antioxidant enzyme activity including catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD), reinforcing their positive regulatory role in adapting to high-temperature stress. These antioxidants collectively enhance the removal of harmful ROS. In summary, BdibZIP44 and BdibZIP53 play a crucial role in regulating the robust defense mechanisms that enable plants to withstand high-temperature stress [99].

3.3.2. bZIP Transcription Factors and Low-Temperature Stress

When environmental temperatures are between the minimum and optimal temperatures, physiological and biochemical reactions within plants accelerate as temperatures rise, metabolic activity increases, thereby accelerating growth and development **(Figure 5)** [100,101]. A bZIP transcription factor named *CsbZIP18* was found to be strongly induced under cold conditions by Yao et al. Compared with wild-type, overexpressing-*CsbZIP18* plants showed reduced sensitivity to ABA, increased relative electrolyte leakage (REL), and decreased maximum quantum efficiency of photosystem II (Fv/Fm) under freezing conditions in *Arabidopsis*. Under cold stress, the expression of ABA homeostasis and signal transduction-related genes, as well as the abiotic stress-induced genes *RD22*, *RD26* and *RAB18*, are suppressed in the overexpression lines. These results suggest that CsbZIP18 negatively regulates plant freezing tolerance via an ABA-dependent pathway [102]. Liang et al. identified the TabZIP transcription factor TaABI5 in wheat, whose ectopic expression upregulated the expression of multiple cold-response genes in *Arabidopsis*. TaABI5 can enhance the plant's cold tolerance. TaABI5 is located in the cell nucleus and TaABI5 interacted with the cold-tolerance transcription factor TaICE1 in a yeast two-hybrid system. In summary, this study demonstrates that the TaABI5 influences the cold tolerance of plants [103]. Liu et al. isolated a member of the bZIP transcription factor family OsbZIP52/RISBZ5 from *Oryza sativa*. The expression of *OsbZIP52* gene is strongly induced by low temperatures. OsbZIP52 is a nuclear-localized protein. OsbZIP52 functions as a transcription activator and can specifically bind to the G-box promoter motif. Overexpression of *OsbZIP52* plants exhibit significantly enhanced sensitivity to cold and drought stress. Several abiotic stress-related genes, including *OsLEA3*, *OsTPP1*, *Rab25*, are downregulated in *OsbZIP52*-overexpressing lines. In conclusion, OsbZIP52/RISBZ5 may play a negative regulatory role under cold and drought stress conditions [104]. A cold-induced transcription factor, ABF1 was identified in the bZIP family by Shu et al. Knockout of *abf1* resulted in reduced cold tolerance, increased ion leakage, and decreased proline content in rice, while *ABF1*-overexpressing lines exhibited the opposite trend. The SnRK2 protein kinase SAPK10 can phosphorylate ABF1, enhancing its DNA-binding ability to the G-box cis-element of the *TPS2* promoter, thereby increasing TPS2 transcription levels and endogenous trehalose content. Exogenous trehalose application also enhances the cold tolerance of *abf1* mutant lines. In summary, a new pathway "SAPK10-ABF1-TPS2" regulates trehalose homeostasis to improve rice cold tolerance [105].

3.4. Role of bZIP Transcription Factors in Response to Nutritional Element Stress

Plant growth and health depend on adequate and balanced nutrition. Nutrition affects plants in many ways, including growth, development, disease resistance, yield and quality. Nutritional deficiencies can lead to stunted growth, discoloured leaves, reduced fruit production, and even plant death. Excessive nutrition can also be harmful to plants, affecting their normal growth and development [106,107]. Zinc has a significant impact on plants. It indirectly influences the synthesis of auxin within crops. When crops are deficient in zinc, the auxin content in stems and buds decreases, growth stagnates, and plants become stunted. Additionally, zinc acts as an activator for many enzymes, exerting a broad influence on plant carbon and nitrogen metabolism, thereby aiding photosynthesis. Furthermore, zinc enhances plants stress tolerance. Increases seed weight and alters the seed-to-stem ratio [108,109]. Assunção et al. identified the bZIP transcription factor genes bZIP19 and bZIP23 in *Arabidopsis*, which regulate plant adaptation to low zinc supply. bZIP19 and bZIP23 are associated with the promoter regions of the *ZIP4* gene, which belongs to the zinc-responsive transporter ZIP family induced by zinc deficiency. The *bzip19/bzip23* double mutant is highly sensitive to zinc deficiency. This is because the *bzip19/bzip23* mutant cannot induce the expression of a small group of genes that constitute the primary response to zinc deficiency, including additional ZIP metal transporter genes. In summary, the AtbZIP19 and AtbZIP23 transcription factors are involved in zinc regulation in higher plants [110]. Lilay et al. discovered that the bZIP19 and bZIP23 transcription factors are central regulatory factors in the zinc deficiency response in *Arabidopsis*. Their targets include members of the ZIP (Zrt/Irt-like protein) transporter family, which are involved in cellular zinc absorption and are upregulated in response to zinc deficiency. The zinc deficiency-sensitive phenotype of *bzip19/bzip23* double mutants indicates that the zinc-dependent activity of bZIP19 and bZIP23 is regulated by zinc at the protein level in the nucleus, while adequate intracellular zinc suppresses their activity. Additionally, bZIP19 and bZIP23 transcription factors exhibit significant functional redundancy [111].

Iron is an essential trace element for plant growth and participates in many important physiological processes in plants, including chlorophyll synthesis, photosynthesis, respiration, and enzyme activity. Iron has poor mobility within plants, and iron deficiency can cause symptoms such as leaf yellowing and shoot death [112]. Mankotia et al. reported that the bZIP transcription factor family member HY5 (Elongated Hypocotyl 5) plays an important role in the iron deficiency signaling pathway of *Arabidopsis*. *hy5* mutants fail to produce an optimal iron deficiency response and exhibit root growth defects under iron-deficient conditions. Compared to WT plants under iron-deficient conditions, the induction of genes involved in the iron absorption pathway (*FIT-FER-LIKE IRON DEFICIENCY-INDUCED TRANSCRIPTION FACTOR*, *FRO2-FERRIC REDUCTION OXIDASE 2*, and *IRT1-IRON-REGULATED TRANSPORTER1*) is reduced in *hy5* mutants. These results indicate that bZIP transcription factor HY5 plays an important role in regulating the iron deficiency response in *Arabidopsis* [113].

3.5. bZIP Transcription Factors Involved in Plant Response to Heavy Metals Stress

The effects of heavy metals on plants are mainly reflected in their physiological and biochemical activities, growth and development, and ultimately their yield and quality [114]. Under heavy metal stress, plants undergo a series of physiological and biochemical reactions, including reduced antioxidant enzyme activity, membrane lipid peroxidation, and cell apoptosis. These reactions affect plant growth and metabolism, leading to symptoms such as stunted growth, leaf chlorosis, and dwarfism, and may even result in plant death [115]. A bZIP gene *BnbZIP2* was cloned from ramie by Huang et al. The BnbZIP2 protein is localized in both the nucleus and cytoplasm. *BnbZIP2* expression is significantly higher in female and male flowers, and its expression is induced by drought, high salt and ABA treatment. Transgenic overexpressing-*BnbZIP2 Arabidopsis* plants exhibit higher sensitivity to drought and cadmium stress during seed germination, while their tolerance to high salt stress during seed germination and plant development is higher than that of WT plants. Therefore, the BnbZIP2 can be involved in plant regulation of cadmium [116]. *Sedum plumbizincicola* is a cadmium (Cd)/zinc (Zn)/lead (Pb) hyperaccumulator native to southeastern China, with potential application value in plant-based remediation of heavy metal-contaminated soils. Lu et al. identified hormone-responsive, abiotic and biotic stress-responsive, and plant development-related cis-acting elements in the *SpbZIP* promoter sequences, and most *SpbZIP* genes showed upregulated expression levels under cadmium stress conditions. SpbZIP60 is localised in the cell nucleus. Overexpression of *SpbZIP60* enhances the cadmium tolerance of transgenic *Arabidopsis* by inhibiting ROS accumulation, protecting photosynthetic organs, and reducing cadmium content [117]. Chai et al. identified a bZIP transcription factor gene GmbZIP152, which is significantly induced in soybeans under stress conditions such as *Sclerotinia sclerotiorum*, plant hormones, salt, drought, and heavy metal stress. Overexpression of *GmbZIP152* enhances soybean resistance to *Sclerotinia sclerotiorum* and tolerance to salt, drought, and heavy metal stress in *Arabidopsis*. Compared to the WT, the antioxidant enzyme-related genes *AtCAT1*, *AtSOD* and *AtPOD1* and their enzymatic activities in *OE-GmbZIP152* are induced by *Sclerotinia sclerotiorum*, salt, drought and heavy metal stress. In conclusion, GmbZIP152 plays a crucial role in soybean response to heavy metal stress [118]. Hou et al. identified four single nucleotide polymorphisms (SNPs) and 30 candidate genes associated with Pb tolerance in maize seedlings. The ZmbZIP107 transcription factor was identified as a key gene controlling Pb tolerance in maize. Two 5'UTR variants of *ZmbZIP107* affect its expression levels and Pb tolerance across different maize varieties. The ZmbZIP107 protein is specifically localized to the cell nucleus and *ZmbZIP107* mRNA expression is highest in the root system of maize seedlings. Heterologous expression of *ZmbZIP107* enhances rice tolerance to lead stress and reduces lead absorption by the root system [119]. These data indicates that bZIP transcription factor can suppress ROS accumulation in the heavy metal stress response of plants, reduce intracellular heavy metal content and alleviate the damage caused by heavy metals to plants.

3.6. bZIP Transcription Factors Involved in Plant Response to High Light Stress

High light has a dual effect on plants. On the one hand, light is the basis for photosynthesis in plants, providing them with energy and promoting growth. On the other hand, excessive or inappropriate light can damage plants, such as leaf scorching and sunburn on fruits, and even inhibit their growth and development [120,121]. Liu et al. identified 56 mulberry bZIP transcription factors and classified them into 12 groups through phylogenetic analysis. Numerous stress response elements were identified in the promoter regions of bZIP genes. Additionally, by analyzing the expression profiles of RNA sequencing data, MabZIP43 and MabZIP24 were identified as responding to high temperature, saline-alkali, and strong light stress, respectively. The results indicate that the bZIP gene family plays a significant role in stress responses [122]. Stracke et al. have discovered that the bZIP transcription factor ELONGATED HYPOCOTYL5 (HY5) is essential for the transcriptional activation of the PRODUCTION OF FLAVONOL GLYCOSIDES（PFG）*PFG1/MYB12* and *PFG3/MYB111* genes under ultraviolet (UV)-B and visible light conditions. A synthetic protein composed of HY5 and the VP16 activation domain is sufficient to activate the expression of *PFG1/MYB12* in plants. However, despite the significant reduction in CHS levels in the *myb11/myb12/myb111* triple mutant under dark and constant light conditions, leading to reduced UV-B tolerance, overexpression of *PFG1/MYB12* enhances tolerance [123]. AtbZIP16 and AthZIP68 are two putative G-group bZIP transcription factors in *Arabidopsis*, and the other three members of the G-group bZIPs are GBF1-3, which can bind to G-boxes. Shen et al. reports that AtbZIP16 and AthZIP68 can bind to cis-elements containing the ACGT core sequence. Additionally, AtbZIP16 and AtbZIP68 can form homodimers and also form heterodimers with other members of the G group. AtbZIP16 and AthZIP68 are localized to the nuclei of onion epidermal cells. In *Arabidopsis*, AthZIP16 and AthZIP68 may also be involved in the light-responsive processes mediated by GBF1-3 [124]. In summary, these results indicate that bZIP transcription factors can regulate plant responses to light stress either independently or in interaction with other proteins, with the aim of improving plant tolerance to light stress.

4. bZIP Transcription Factors Mediated Control of the Plant Secondary Metabolite Biosynthetic Pathways

The bZIP family transcription factors not only play important roles in regulating plant growth and development and abiotic stress response, but also participate in the regulation of plant primary and secondary metabolites, such as flavonoids, terpenoids, alkaloid, phenolic acids and lignans [125–129]. Plant secondary metabolites are diverse in type and structure, and can generally be classified into three major categories: terpenoids, phenolics (such as flavonoids), and nitrogen-containing compounds (such as alkaloids) [130,131]. Secondary metabolites perform various complex biological functions, playing crucial roles in plants responses to environmental stress, interspecific competition and coevolution, attracting insects for pollination, and defending against predator attacks [132]. We will discuss in detail the research progress on the biosynthesis of these secondary metabolites regulated by bZIP transcription factors **(Table 4).**

4.1. bZIP Transcription Factors Are Involved in Flavonoids Biosynthesis in Plants

Flavonoids play a significant role in the prevention and treatment of cardiovascular and cerebrovascular diseases. Many studies have shown that bZIP transcription factors can participate in the biosynthesis pathway of flavonoids **(Figure 6)** [133]. Han et al. isolated and identified the *GbbZIP08* gene in *Ginkgo biloba*. GbbZIP08 is localized in the plant cell nucleus. The total flavonoid, kaempferol, and anthocyanin content in transgenic tobacco was significantly higher than that in the WT. The expression of structural genes in the flavonoid biosynthetic pathway was significantly upregulated. In summary, GbbZIP08 overexpression promotes flavonoid accumulation in plants and increases the transcriptional levels of genes related to flavonoid synthesis [134]**.** Zhou et al. identified 62 *DcbZIP* genes in *Dendrobium catenatum*, grouped into 13 subfamilies. Among these, the expression of *DcbZIP3*, *DcbZIP6*, *DcbZIP28* was induced by low temperatures in both leaves and stems. DcbZIP3, DcbZIP6, DcbZIP28 contains the bZIP conserved domain and is localized to the cell nucleus. DcbZIP6 shows a significant negative correlation with *PAL2* (palmitoyl-CoA), which is involved in flavonoid metabolism. Additionally, DcbZIP28 shows a significant negative correlation with multiple metabolism-related genes in the polysaccharide metabolism pathway, including 6-phosphofructokinase *PFKA1*, aldose-6-phosphate reductase *ALDO2* and fructose kinase *SCRK5*. These results suggest that DcbZIP6 and DcbZIP28 primarily participate in flavonoid or polysaccharide metabolism [135]. Han et al. screened the genome-wide distribution of bZIP transcription factors from the *Ginkgo biloba* L. database, identifying a total of 40 bZIP genes, which were classified into 10 subclasses. *GbbZIP08* and *GbbZIP15* exhibited the highest expression levels in mature leaves, while *GbbZIP13* showed high expression levels in all eight tissues. Correlation analysis and phylogenetic tree analysis indicated that GbbZIP08 and GbbZIP15 are involved in flavonoid biosynthesis. Among them, *GbbZIP08* showed significantly up-regulated expression at 4°C. In summary, GbbZIP08 and GbbZIP15 are involved in regulating flavonoid biosynthesis and abiotic stress responses [136]. Zhang et al. cloned and functionally characterized the receptor-like kinase OsRLCK160 and the bZIP transcription factor OsbZIP48, which positively regulate the accumulation of flavonoids, through a metabolite-based genome-wide association study. OsRLCK160 phosphorylates OsbZIP48, thereby regulating flavonoid accumulation and participating in rice UV-B tolerance. These studies indicate that OsRLCK160 and OsbZIP48 play a significant role in regulating flavonoid accumulation in rice [137].

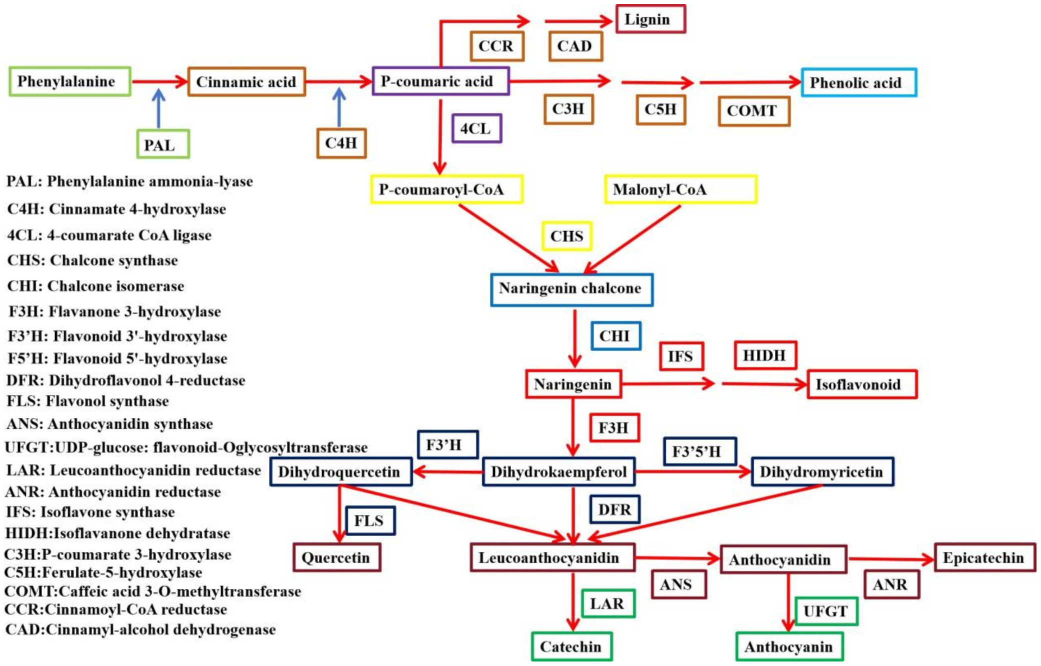

Figure 6. Schematic diagram of the bZIP transcription factors participate in flavonoid biosynthetic pathway in plants.

4.2. bZIP Transcription Factors Are Involved in Terpenoids Biosynthesis in Plants

Terpenoids are essential components for plant growth and development and also play a role in plants adaptation to and defense against environmental stress [138]. Terpenoids, such as monoterpenes and diterpenes, play a crucial role in plants responses to abiotic stressors like drought, salinity, and pest infestations. For example, some terpenoids act as signaling molecules, attracting natural enemies to prey on insects that feed on plants, thereby protecting the plants themselves [139]. Michael et al. demonstrated that the elongated hypocotyl (HY5) acts as a bZIP transcription factor and plays a key role in the light-mediated transcriptional regulation of the terpene synthase *AtTPS03*. Expression analysis of the *hy5-215* mutant and *HY5* overexpression lines revealed that HY5 functions as a positive regulator of *AtTPS03*. Electrophoresis mobility shift assay (EMSA) studies showed that HY5 can bind to the promoter of *AtTPS03*. In summary, HY5 is essential for light-mediated transcriptional regulation of *AtTPS03* in *Arabidopsis* to achieve terpenoid biosynthesis [140]. Xu et al. found that after treatment with the plant hormones MeJA and ABA, the expression level of a TF in *Tanacetum cinerariifolium* significantly increased, and it was named *TcbZIP60*. TcbZIP60 is localized in the cell nucleus and can directly bind to the E-box/G-box motifs on the promoters of the pyrethrin synthesis genes *TcCHS* and *TcAOC*, thereby activating their expression. The transient overexpression of *TcbZIP60* increased the expression levels of the pyrethrin synthesis genes, leading to a significant accumulation of pyrethrin. Silencing *Tcbzip60* significantly downregulates pyrethrin accumulation and the expression of its related genes. In summary, TcbZIP60 regulates the terpenoid and MeJA pathways involved in pyrethrin synthesis [141]. Wu et al. identified 105 *SrbZIP* genes at the whole-genome level and classified them into 12 subfamilies using bioinformatics methods in *Stevia rebaudiana* Bertoni. Three major cis-acting elements were identified in the *SrbZIP* promoter region, including development-related elements, defense and stress response elements. Additionally, qRT-PCR analysis was performed to assess the expression levels of 15 *SrbZIP* genes under various treatments, including light exposure, abiotic stress, plant hormones and different tissues. Among these, three SrbZIP genes *SrbZIP54*, *SrbZIP63* and *SrbZIP32* were predicted to be associated with the synthesis of terpenoid compounds involved in stress responses in *Stevia rebaudiana*. In conclusion, the bZIP TF SrbZIP54, SrbZIP63, and SrbZIP32 can play important regulatory roles in terpenoid compound synthesis [142].

Artemisinin, a secondary metabolite accumulated in *Artemisia annua*, is a sesquiterpene compound that can treat *malaria*. Zhang et al. identified six members of the a subfamily from 64 bZIP transcription factors highly expressed in glandular hairs, named AabZIP1 to AabZIP6. When these transcription factors and the *ADS* and *CYP71AV1* genes were transformed into tobacco leaves, it was found that AabZIP1 could directly bind to the ABRE promoter element of the *ADS* and *CYP71AV1* genes and activate the expression of the two key enzyme genes [143]. Overexpression of *AabZIP1* significantly increases artemisinin content, indicating that the transcription factor AabZIP1 positively regulates artemisinin synthesis. Dual luciferase assay results showed that ABA enhances AabZIP1's transcriptional activity on the *ADS* and *CYP71AV1* promoters. The ABA receptor protein AaPLY9 was isolated from *Artemisia annua* plants where *AabZIP1* was overexpressed and artemisinin content was significantly increased, indicating that AabZIP1 plays a key role in ABA-induced artemisinin synthesis **(Figure 7)** [143,144].

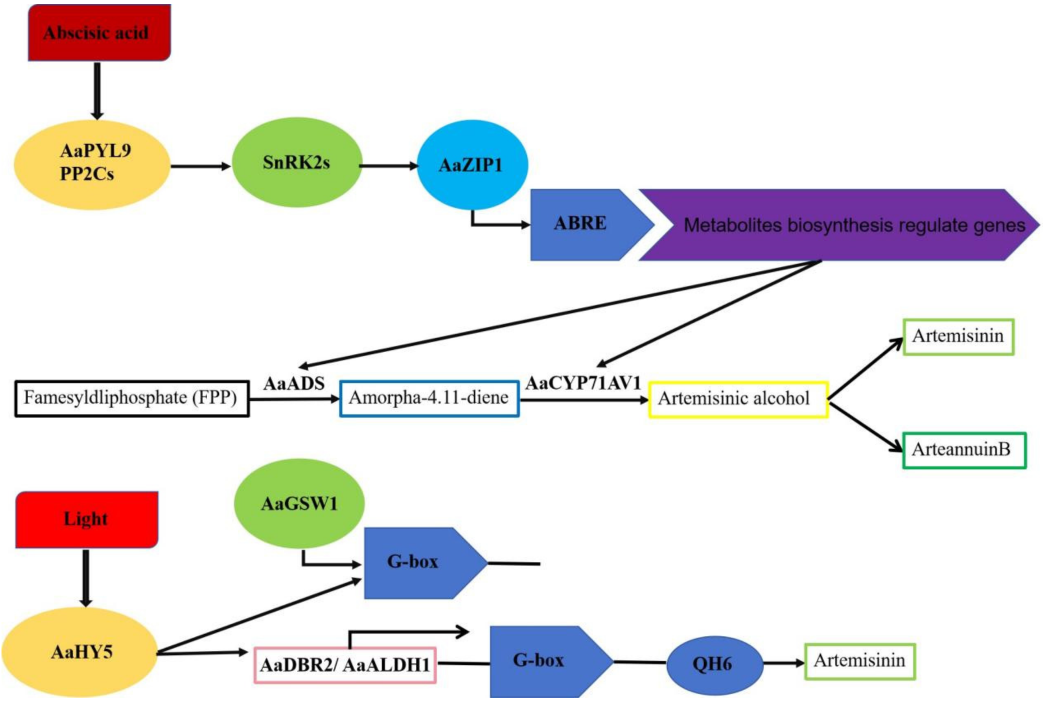

Figure 7. The bZIP transcription factors participate in the ABA-mediated regulation mechanism of artemisinin biosynthesis. ABA binds to the receptor protein AaPLY9, causing a conformational change and forming a complex with the 2C-type serine/threonine residue protein phosphatase (PP2C), thereby inhibiting the phosphatase activity of PP2C and activating the activity of the sucrose non-glycolytic protein kinase (SnRK2). SnRK2 activates the downstream transcription factor AabZIP1 through protein phosphorylation. AabZIP1 binds to the cis-acting element ABRE to activate the expression of the *ADS* and *CYP71AV1* genes. Through a series of intermediate products, artemisinin is ultimately synthesised.

4.3. bZIP Transcription Factors Are Involved in Alkaloid Biosynthesis in Plants

Alkaloids are an important class of secondary metabolites produced by plants during long-term evolution. They have multiple physiological and ecological functions for plants, including regulating cell proliferation and differentiation, influencing plant morphogenesis, responding to environmental stress, and defending against pests and diseases [145,146]. A total of 65 IibZIP genes were identified in the *Isatis indigotica* genome, distributed across seven chromosomes with high conservation and classified into 11 subgroups. Among these, 17 *IibZIP* genes were co-expressed with 79 transcription factors, with most of these genes associated with plant responses to abiotic stress and hormone signaling. The 17 *IibZIP* genes are associated with the regulation of 110 metabolites. Additionally, *IibZIP23*, *IibZIP38* and *IibZIP51* are closely associated with six metabolites, including three alkaloids (quinoline alkaloid Stylopine, indole alkaloid Tabersonine, and indole-3-acetic acid), the flavonoid myricetin 3-O-galactoside, and two major metabolites, 2-hydroxy-6-aminopurine and 3-dehydroquinic acid [147]. Overexpression of *CrMYC2* induces the expression of the bZIP transcription factor *CrGBF* and reduces the accumulation of alkaloids in the hairy roots of *Catharanthus roseus*. Meanwhile, CrGBF1 and CrGBF2 form homodimers and heterodimers, thereby inhibiting the transcriptional activity of key terpenoid indole alkaloids (TIA) pathway gene promoters. The reason is that CrGBFs may antagonize the transcriptional activation of CrMYC2 by competitively binding to the T/G box in the target promoter and/or by forming non-DNA-binding complexes through protein-protein interactions, thereby preventing CrMYC2 from binding to its target promoter [148]. In summary, bZIP transcription factors can regulate the biosynthesis of terpenoid compounds, laying the foundation for future research on secondary metabolism genetic engineering in medicinal plants.

4.4. bZIP Transcription Factors Are Involved in Phenolic Acids in Plants

Phenolic acids have multiple effects on plants, including antioxidant properties, defense mechanisms, UV protection, structural support and allelochemical effects. They can influence plant growth, development, and resistance to adverse conditions. Phenolic acids may also affect the distribution of soil microorganisms, thereby impacting soil quality and ecosystem health [149–151]. ABA can effectively increase the content of phenolic acids and tanshinones in *Salvia miltiorrhiza*, but its regulatory mechanism remains unclear. Shi et al. conducted a deep transcriptomic analysis of ABA-treated *Salvia miltiorrhiza* root hairs. The expression levels of single genes encoding key enzymes such as *PAL*, *TAT*, *C4H*, *RAS*, *CYP98A14* and *GGPPS* were significantly higher than those in the control group. Candidate laccases with expression patterns similar to *RAS* and *CYP98A14* in phenolic acid biosynthesis, as well as potential *P450* single genes involved in tanshinones biosynthesis, were identified. Additionally, they identified 1,250 TFs representing 35 families, with MYB, AP2/ERF, bHLH, and bZIP being the most abundant. Therefore, transcription factors from these families can participate in the regulation of phenolic acid and tanshinones compounds [152]**.** Ibáñez et al. analyzed the *Prunus salicina* Lindl. reference genome and identified 60 genes encoding bZIP proteins. Based on the predicted amino acid sequences, *PsabZIP* genes were distributed across 12 groups. RNA sequencing analysis of fruits from two *Prunus salicina*. varieties at different developmental stages detected 53 expressed bZIP-encoding genes, indicating their role in fruit development. Through correlation analysis of bZIP transcription factor expression with nine phenolic compounds, 29 genes were found to be significantly associated with the biosynthesis of these compounds, suggesting that bZIP transcription factors may act as regulatory factors in the biosynthesis of phenolic compounds in *Prunus salicina* Lindl [153].

4.5. bZIP Transcription Factors Are Involved in Lignin in Plants

Lignin is widely present in the cells of woody plants, herbaceous plants, and all vascular plants, playing a role in strengthening plant tissues. Lignin is the second most abundant plant-based natural substance in nature, following cellulose. Lignin is typically found in the highest concentrations in the trunks of trees, where it serves as an important substance for enhancing plant resilience and keeping trees upright and stable [154–156]. Lignin plays a crucial role in defending against drought stress. Tu et al. demonstrated that VlbZIP30 mediates drought tolerance by activating the expression of lignin biosynthesis genes and increasing lignin deposition in grapevine. Overexpressing *VlbZIP30* grape plants exhibited lignin deposition under control conditions, which was attributed to the upregulation of *VvPRX4* and *VvPRX72* expression. Overexpression of *VlbZIP30* enhanced drought tolerance, characterized by reduced leaf water loss rate under drought conditions, maintained effective photosynthetic rate, and increased lignin content in leaves. VlbZIP30 directly binds to the G-box cis-elements in the promoters of the lignin biosynthesis gene *VvPRX N1* and the drought response gene *VvNAC17*, thereby regulating their expression. In summary, VlbZIP30 is associated with lignin synthesis and drought tolerance in grapevine [157]. Juice sac granulation (a physiological disorder) causes significant postharvest losses in *Citrus maxima.* Juice sac granulation is closely associated with lignin accumulation. The results of Li et al.'s study indicate that lignin content in NC (near the seed) and FC (far from the seed) juice sacs generally increases from 157 DPA after flowering to 212 DPA, reaching a maximum at 212 DPA. Additionally, lignin content in NC juice sacs was higher than in FC juice sacs. Following data assembly and bioinformatics analysis, 11 DEGs were identified as hub genes for lignin biosynthesis. Among these, *PAL* (phenylalanine ammonia-lyase), *HCT* (hydroxycinnamoyl-CoA shikimate/quinic acid hydroxycinnamoyltransferase), *4CL2* (4-coumaroyl: CoA ligase), *C4H* (cinnamic acid 4-hydroxylase), *C3'H* (p-coumaric acid 3-hydroxylase), and *CCoAOMT1* (caffeoyl-CoA 3-oxomethyltransferase) were the most differentially expressed DEGs in granulated juice sacs. Co-expression analysis revealed that the expression patterns of transcription factors such as bHLH130 are highly correlated with lignin formation, indicating that bHLH130 can regulate lignin accumulation in plants [158].

5. bZIP Transcription Factors Interact with ncRNAs to Regulate of Abiotic Stress in Plants

Non-coding RNAs (ncRNAs) are RNAs that do not code for proteins, including rRNAs, tRNAs, snRNAs, snoRNAs, LncRNAs, microRNAs (miRNAs) and so on [159,160]. ncRNAs are RNAs with known functions that share the common characteristic of being transcribed from the genome but are not translated into proteins, and are able to carry out their biological functions at the RNA level [161,162]. Baruah et al. identified 12807 *Long Non-coding RNAs* (*lncRNAs*) in *Capsicum annuum* tissues under abiotic stress conditions. 30 lncRNAs were found to act as precursors for 10 miRNAs in *Capsicum annuum*, and 1807 lncRNAs interacted with 194 miRNAs targeting 621 *Capsicum annuum* mRNAs. The expected role of LncRNAs under different abiotic stress conditions by interacting with miRNAs and regulating stress-responsive bZIP transcription factors in *Capsicum annuum* [163]. Baloglu et al. identified 64 genes encoding bZIP transcription factors in the cucumber genome. genome-wide expression analysis of the *bZIP* transcription factors genes showed that the 64 *CsbZIP* genes were differentially expressed in at least one of the ten sampled tissues. A total of four *CsbZIP* genes showed high expression values in leaf, flower and root tissues. Computerised miRNA and target transcript analyses revealed that a total of 21 CsbZIP transcription factors were targeted by 38 plant *miRNAs*. CsbZIP20 and CsbZIP22 were the most frequently targeted genes by *miR165* and *miR166* family members, respectively. The expression of ten *CsbZIP* transcription factors genes in drought-stressed cucumber root and leaf tissues was also analysed by quantitative RT-PCR. The expression of these genes was found to be increased in root tissues at 24 h after PEG treatment [164]. Neysanian et al. evaluated the effectiveness of foliar sprays of selenates and selenium nanoparticles (SeNPs) on tomato plants to study the mitigation of risks associated with water deficit conditions. Tomato plants were treated with SeNPs at concentrations of 0 and 4 mg L^{-1}; after the third spray, the plants were exposed to water deficit conditions. Foliar sprays of SeNPs not only improved growth, yield, and developmental transition to flowering but also mitigated the deleterious risks associated with water deficit conditions. Under normal irrigation conditions, *miR172* expression was slightly increased in SeNP-treated plants, whereas *miR172* showed a down-regulation under drought stress. The bZIP transcription factor and *CRTISO* gene were up-regulated after SeNP and drought treatments. Drought stress significantly increased H_2O_2 accumulation, which was alleviated by SeNPs. Foliar sprays of Se or SeNPs had a similar tendency to alleviate the negative effects of drought stress on membrane integrity [165]. Two small RNA libraries were generated from micropropagated 'Hamburg muscadine grape' (*V. vinifera*) plants under normal and low temperature conditions by Sun et al. Forty-four cold-induced *miRNAs* were identified by differential expression *miRNAs* (DEMs) analysis, of which 13 belonged to up-regulated DEMs and 31 to down-regulated DEMs. Prediction of the target genes of DEMs indicated that miRNAs may regulate bZIP transcription factors under cold stress [166]. In summary, the bZIP transcription factor is capable of interacting with ncRNAs and plays an important role in abiotic stress response.

6. Conclusion and Prospects

The bZIP transcription factor is one of the largest transcription factor families in plants. It plays a key role in the response of plants to abiotic stress, plant secondary metabolism and plant growth and development. At present, scientists are mainly focusing on the response of bZIP transcription factors to common abiotic stresses such as drought, cold, heat, salt, heavy metals, nutritional stress and light stress. The structure, classification and function of bZIP transcription factors have been studied extensively. The bZIP transcription factors of different species have been mined and identified using bioinformatics methods, and the evolutionary relationship and functional correlation between bZIP transcription factors of different species have been analysed. A number of important results have been obtained. At the same time, there has been a more detailed understanding of the downstream target genes which are under their control. However, there are several shortcomings in studying the bZIP family transcription factors in plants. For example, there has been little research on the homology and evolution of bZIP transcription factors between different crops, such as *Oryza sativa*, *Glycine max* and so on. Therefore, some important bZIP transcription factor genes may be overlooked. The second point is that the current family classification based on the number of bZIP transcription factor structural domains is crude. It lacks a brief description of their functions. In the future, the functional classification should be based on the functional differences of different family members and on the combination of structural and functional classification. This will help to understand the known bZIP transcription factor genes faster and at the same time predict the unknown bZIP genes so that more functions of bZIP transcription factor genes can be discovered. The third point is that, at present, the focus of researchers is only on the function of bZIP transcription factor genes, and in the future, the functional verification of bZIP transcription factor genes will be more important. At present, researchers are only focusing on the function of bZIP transcription factor genes. The future is to combine the functional verification of bZIP transcription factor genes with the actual use of breeding, to apply them to production practice, to improve the resistance of plants, and ultimately to achieve the purpose of high yield.

Up to now, research on MYB transcription factors has been conducted for more than 30 years, but most of the research results are still in the stage of theoretical research. Advanced biotechnological means should be used to conduct in-depth research on the mechanism of bZIP transcription factors regulating the production of plant secondary metabolites, so as to comprehensively improve the resilience of the crop and the economic value of the potential, which will be of great significance to the agricultural economy. Moreover, most of the research on bZIP transcription factors nowadays focuses on agricultural crops as well as fruits and vegetables, while there are relatively few relevant studies in the field of medicinal plants. The slow development of traditional Chinese medicine is largely due to its unclear mechanism of action. If we can form a specific and clear understanding of the mechanism of bZIP transcription factors, it is equivalent to a fundamental understanding of the microscopic composition of traditional Chinese medicine, which will play an important role in the further study of bZIP transcription factors in medicinal plants, and will make the study of its structure, function, and metabolic pathway much easier.

In conclusion, plant growth and development and the regulation of plant responses to abiotic stresses are controlled by the bZIP family of transcription factors, and bZIP transcription factors also can regulate secondary metabolism biosynthetic pathways in plants. In the future, in order to improve plant traits and provide the theoretical basis and germplasm resources for breeding superior varieties, we will pay more attention to controlling the expression of bZIP family transcription factor genes through molecular breeding. Traditional breeding methods to improve plant traits are time-consuming, labour-intensive and uncertain. They cannot meet the needs of modern plant breeding. In addition to being involved in the regulation of plant growth and development, bZIP transcription factors also play an important role in plant response to and tolerance of abiotic stress, and the study of bZIP transcription factors provides an important theoretical basis for breeding varieties that are resistant to stress, thereby maintaining stable crop yields and providing a solid foundation for global food security in the future.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org, **Figure S1** Conserved amino acid structural domains of bZIP transcription factors in *Arabidopsis thaliana*, soybean and other species. The red boxes indicate possible conserved structural domains in the figure. **Figure S2** Phylogenetic tree bZIPs family transcription factor proteins in *Arabidopsis thaliana*, *Oryza sativa*, *Glycine max* and so on. Phylogenetic tree of bZIPs transcription factors proteins in selected angiosperms. The bZIPs family gene sequences of plants were retrieved using the NCBI (https://www.ncbi.nlm.nih.gov/) and China National Rice Data Center (https://www.ricedata.cn/). The phylogenetic tree was constructed using MEGA version 11.0 with the bootstrap method based on full amino acid sequences. Numbers next to the branches show the percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates).

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