Regulation mechanisms of bZIP transcription factors in plant grown on drought, salt and cold soils

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Abstract

The bZIP family is one of the most widely distributed and conserved transcription factor categories in eukaryotes. They are widely involved in processes of plant abiotic stress responses, such as improving the ability of plants to adapt to drought, salinity and cold. To comprehensively understand how plant bZIPs regulating these tolerances, this article will have an overview of their distributions on different species, characteristics of protein architecture, regulation mechanisms for target genes' transcriptional expression, and relevant research progresses in recent years. Specially, we will discuss the possible roles of flavonoids, whose synthesis could be regulated by bZIPs, in abovementioned plant tolerant responses.

INTRODUCTION

In the process of growth and development, plants are exposed to various abiotic stress such as salinity, drought, low temperature, which limit crop yield and quality. During evolution, plants acquire series of resistances to these environmental stresses and survive through physiological, biochemical and molecular responses. These responses are usually originated by regulating the expression of relevant genes. bZIP (basic leucine zipper) transcription factors, as one of the largest transcription factor regulatory families, play very important roles in the response to these abiotic stresses. bZIP TFs could be activated by drought, high salt and chilling damage. By binding specifically to*cis* -elements in the promoter region of stress related genes, they can regulate the transcriptional expressions of target genes, thereby regulating stress resistance of plants. This article comprehensively reviews the structural characteristics of bZIPs and their regulation mechanisms on target genes.

DISTRIBUTION AND CLASSIFICATION OF BZIP TRANSCRIPTION FACTORS

Currently, there are at least 64 families of transcription factors have been found in plants (Pérez-Rodriguez et al., 2010). According to their differences in DNA-binding domains, transcription factors can be defined as different families, such as bZIP, NAC, MYB, EREBP/AP2, Zinc-finger, etc. Among which, bZIPs (basic region/leucine zipper motifs) are widely found in humans, animals and plants, insects and microorganisms. To date, a large number of bZIP transcription factors have been identified in almost all eukaryotes. There are 77, 89, 247, 92, 89, 69, 125, 64, 55, 114 bZIP transcription factors been found in *Arabidopsis thaliana* ,*Oryza sativa* , *Glycine max* , *Sorghum bicolor* ,*Hordeum vulgare L* , *Solanum lycopersicum* , *Zea mays* ,*Cucumis sativus* , *Vitis vinifera* and *Malus domestica* , respectively (Baloglu et al., 2014; Corrêa et al., 2008; Li et al., 2015, 2016; Liu et al., 2014b; Nijhawan et al., 2008; Pourabed et al., 2015; Wang et al. 2011; Wei et al., 2012; Zhang et al. 2018). Only 25, 21 and 21 bZIP transcription factors were found in yeast, nematode, and fruit fly (Riechmann et al., 2000). Compared to other eukaryotes, plants have more bZIP homologous proteins and more conserved amino acid sequences in these homologies (Ali et al., 2016). Studies have shown that the structures of bZIP protein are closely related to its biological function. Jakoby

et al. (2002) used MEME (multiple em for motif elicitation) to analyze a large number of bZIP transcription factors in *Arabidopsis thaliana* . Based on the characteristics of both the bZIP and other conserved motifs, the 75 bZIPs in *Arabidopsis thaliana*were classified into 10 subfamilies of A, B, C, D, E, F, G, H, I and S. With similar method, the bZIP transcription factor family genes in other plants have also been categorized. The 131 bZIP transcription factors isolated from the soybean genome were also divided into abovementioned 10 subfamilies A-S (Liao et al., 2008). Though the 89 members of the bZIP transcription factor family in rice were also divided into 10 subfamilies, the subfamily S was replaced with J (Nijhawan et al., 2008). It seems that most of these subfamilies of bZIPs are conserved among different plants. Corrêa et al. (2008) identified the possible non-redundant complete sets of bZIPs in rice, comprising 92 proteins, and in black cottonwood, comprising 89 proteins. Based on both bZIP domain and other conserved motifs similarities, these collections of bZIPs together with the 77 bZIPs from Arabidopsis were categorized into 13 subfamilies, including A, B, C, D, E, F, G, H, I, J, K, L, and S, three subgroups J, K and L were added.

With the advancement of bioinformatics, more and more conversed motifs, except bZIP, were identified for categorizing bZIP subfamilies. Hence, the classification of bZIP transcription factors has become more and more sophisticated and scientific. Recent years, there are increasing reports on regulation mechanism of various bZIPs on different stress responses (Hwang et al., 2014; Ji et al., 2013; van Leene et al., 2016; Liu et al., 2012; Tsugama et al., 2016; Wang et al., 2019; Zhang et al., 2017a, b). Specific roles of bZIPs in different subgroups might also be categorized into corresponding biological pathways, considering plenty of functional annotated bZIPs been classified into the known subfamilies with those sophisticated and scientific bioinformatics.

ARCHITECTURE CHARACTERISTICS OF BZIP TRANSCRIPTION FACTORS

Transcription factor (TF), also known as *trans* -acting factor, is a category of proteins that can specifically bind to *cis* -acting elements in the promoter region of eukaryotic genes, thereby activating or silencing the expression of related genes in a specific time and space. The structure of plant transcription factors generally includes at least four functional domains, including the DNA binding domain, the transcriptional regulatory domain, the nuclear localization signal and the oligomerization site (Du et al., 2012). They work together to regulate various biological processes.

Although the classification of bZIP varies depending on the researcher's choice, there is currently a consensus on this type of transcription factor that the protein sequence contains a conserved bZIP domain with 60-80 amino acids length. This domain is consisted of at least two specific structures. Firstly, the N-terminus is a basic region composed of about 20 basic amino acids, containing a nuclear localization signal (NLS) and a N-x7-R/K structural unit that specifically binds to a DNA sequence. This region is involved in nuclear localization and DNA binding (Lee et al., 2006b). Secondly, the C-terminus, which is a leucine zipper region, a heptad repeat of leucine or other bulky hydrophobic amino acids (Ile, Val, Phe, or Met) positioned exactly nine amino acids towards the C-terminus, creating an amphipathic helix. This region is involved in the dimerization of the bZIP protein before it binds to DNA (Hurst, 1994; Jakoby et al., 2002; Landschulz et al., 1988). In addition to the bZIP conserved domain, the bZIPs also contain other domains with transcriptional activation functions, such as the R/KxxS/T and S/TxxD domains, which are phosphorylation sites of Ca^{2+} independent protein kinase and casein kinase II (Furihata et al., 2006). Besides, there are also some regions rich in acidic amino acids such as Pro and Gln, which can activate the transcriptional expression of downstream target genes (Liao et al., 2008).

MECHANISMS OF BZIP ON TRANSCRIPTIONAL REGULATION OF TARGET GENES

Through dimerization, phosphorylation, or interaction with other nuclear proteins, the specificity and affinity of bZIP binding to DNA will change, which will affect the activation of other genes, as well as its own stability and subcellular localization (Schütze et al., 2008). By forming homo- or heterodimers, binding specific gene promoters in its basic region and interacting with *cis* -acting elements of the promoter region, the bZIP transcription factor inhibits or activates the expression of multiple downstream related target genes, thereby participating in transcriptional regulation process.

The binding specificity of bZIP factors in plants is mainly determined by 3 bases flanking the 4 core nucleotides. Generally, bZIP factors preferentially select ACGT core palindromes or pseudo-palindromic *cis* -acting elements to bind, such as G-box (CACGTG), C-box (GACGTC), A-box (TACGTA), ABRE (ACGTGGC) (Izawa et al., 1993; Kim et al. 2004). Most of them are located in the ABA hormone-induced promoter region. When the bZIP protein interacts with these *cis* -acting elements, the N-terminus of its basic domain is inserted into the large groove of the DNA double-strand, and the C-terminus of the leucine zipper is dimerized to form a superimposed curl helix (Landschulz et al., 1988; Ellenberger et al., 1992).

G-box is one of the most common targets of bZIP transcription factors. de Vetten and Ferl (1995) firstly found that corn GBF1 is a basic region leucine zipper protein and could activate *Adhl* expression by binding to its G-box. After that, series of stress related genes were found to be bound at their G-box and regulated by various bZIPs. Kaminaka et al. (2006) found that*Arabidopsis thaliana AtbZIP10* can combine G-box to negatively regulate plant resistance to pathogenic bacteria and other stresses. Zou et al. (2008) demonstrated that the rice OsbZIP10/OsABI5 could bind the G-box element to *trans* -activate the expression of stress resistance genes, thereby inhibiting seed germination and seedling growth. Liu et al. (2012) also studied rice and found that under low temperature stress,*OsbZIP52 /RISBZ5* can recognize the G-box on the downstream target gene to enhance the low temperature sensitivity of rice. The *Arabidopsis thaliana*AtbZIP56/HY5 binds directly to the promoters of light responsible element containing the G-box and thus regulates their transcriptional activity (Yoon et al., 2006). Induced by salt, the *Tamarix hispida* bZIP1 bound to G-box of the stress response gene and regulated the expression of downstream genes (Ji et al., 2013). Using chromatin immunoprecipitation, Lee et al. (2006a) demonstrated that CabZIP1 binds to the G-box elements in native promoter of the hot pepper pathogenesis-related protein 1 (*CaPR-1*) gene in vivo. Shaikhali et al. (2012) identified the AtbZIP16 as a component binding to the G-box-containing promoter fragment of light-harvesting chlorophyll a/b-binding protein2.4 (LHCB2.4) from nuclear extracts of high light-treated Arabidopsis plants.

The ABRE element is also the most favorite target of bZIP transcription factors. Sun et al. (2011) found that AtbZIP1 binds to ABRE active elements and regulates the plant's response to low temperature stress through ABA-dependent signaling pathways. Yoshida et al. (2015) demonstrated that the *Arabidopsis thaliana* bZIP transcription factors ABF1, ABF2, ABF3, and ABF4 combined with ABRE and regulated the expression of downstream genes related to salt and drought tolerance. In maize, *ZmbZIP17* functions as an ER stress transducer, interacting with ABREs (Yang et al. 2013). Rice OsbZIP46/OsABF2 (Chang et al., 2017; Hossain et al., 2010; Tang et al. 2012a), *OsbZIP52/RISBZ5* (Liu et al., 2012),*OsbZIP10/OsABI5* (Zou et al., 2007; Zou et al., 2008), OsbZIP05/OSBZ8 (Mukherjee et al., 2006; Nakagawa et al., 1996) all regulate the expression of plant ABA-responsive genes by binding to the ABRE element of the target gene. Zhang et al. (2017b) proved that wheat TabZIP14-B showed transcriptional activation ability through the transactivation assay and was capable of binding the abscisic acid (ABA) responsive element (ABRE) in yeast. Wang et al. (2019) isolated and functionally characterized the sweet potato *IbABF4* gene, which encodes a bZIP transcription factor. The IbABF4 protein localized to the nucleus, exhibited transcriptional activation activity, and showed binding to the cis-acting ABA-responsive element (ABRE) in vitro.

In addition, bZIP transcription factors could target on genes by C-Box and A-box. Except for G-box, the C-box of pathogenic responsive genes could also bound and negatively regulated by *AtbZIP10* in*Arabidopsis thaliana* (Kaminaka et al., 2006). Induced by ABA and drought, the *Tamarix hispida* bZIP1 bound to C-box and A-box*cis* -elements of the stress response gene (Ji et al., 2013).

In summary, bZIP transcription factors regulate the transcriptional expression by interacting with specific *cis* -regulatory sequences in the promoter region of response genes to regulate plant stress tolerance (Sornaraj et al., 2016). To understand the actual relationship between bZIP subfamilies and their binding *cis* -regulator motifs (Table I and Figure I), all the functional annotated bZIPs were categorized into 13 known subgroups based on the method described by Corrêa et al. (2008). It seems that the G-Box and ABRE attracts most scientists' interests and are two most understood *cis* -elements of bZIP transcription factors (Table I). The bZIPs bind to G-Box are categorized into subfamilies A, C, G, H, K and S; while those recognize ABRE belong

to the subgroups A, B, C, G and S (Table I). Besides, there are also several reports on mechanisms about how bZIP transcription factors regulate other two *cis* -elements, C-box and A-box (Table I). Interestingly, the bZIPs bind to C-box are usually belong to subfamilies C and S; the functional annotated bZIP bind to A-box is classified into subfamily S. Though the number of functional annotated bZIP is limit, their binding activities of different subfamilies to specific *cis* -elements could also provide directional suggestions for further research on de novo bZIPs and potential targets. However, more evidences are still needed to fulfil the relevance between bZIP subfamilies and corresponding *cis* -elements.

REGULATION MECHANISM OF PLANT BZIPS TO VARIOUS STRESSES

Previous studies have found that bZIPs play important roles in response to a variety of plant stresses, such as salinity, drought and cold damage (Table II). Their regulation mechanism varies depending on species of plant and types of stress.

bZIP TFs involved in salt stress response

Under salt stress, plant cell should successively face challenges of osmotic stress, ion toxicity and oxidative stress (Rozema et al., 2008; Munns et al., 2005). In these responses, bZIP transcription factors play key roles in various physiological processes in *Arabidopsis thaliana* , tomato, tobacco, rice, and soybeans, etc.

In *Arabidopsis thaliana* , AtbZIP17 was proven as a positive regulator in the processes salt stress responses, it activates both the expression of salt stress response gene *ATHB-7* and *SES1*(Liu et al., 2007, 2008); while the AtbZIP24 was revealed as a negative regulator in plant tolerance to salinity by RNAi interference technology (Yang et al., 2009). Tang et al. (2012b) found that heterologously expressing *Arabidopsis thaliana AtbZIP60* could increase salt resistance and superoxide dismutase (SOD) activity of tobacco, rice, and *Pinus elliottii* . In *Glycine max* , overexpression of the *GmbZIP1* enhances salt tolerance in transgenic plants (Gao et al., 2011). Besides, heterologously expressing *GmbZIP44* ,*GmbZIP62* , and *GmbZIP78* could significantly increase salt resistance of transgenic *Arabidopsis thaliana* plants (Wang et al., 2015). In maize, the *ABP9* was found as a salinity responsible bZIP gene by Zhang et al. (2011a). Then, Wang et al. (2017a) heterologously expressed it to improve the salt tolerance of transgenic cotton. In *Oryza sativa* , the *OsbZIP05/OSBZ8* firstly found with a higher transcriptional level in salt tolerant cultivar than in salt sensitive cultivar, indicate that *OsbZIP05/OSBZ8* might play as a positive role in this stress responses (Mukherjee et al., 2006). After that, OsbZIP12/OsABF1, OsbZIP23, OsbZIP46/OsABF2, OsBZIP71 and OsbZIP72 were successively proven to act as positive regulators in the process of salt tolerance (Amir Hossain et al., 2010; Chang et al., 2017; Hossain et al., 2010; Liu et al., 2014a; Lu et al., 2009; Tang et al. 2012a; Xiang et al., 2008; Zhang et al., 2017a). OsbZIP71 can form both homodimers and heterodimers with Group C members of the bZIP gene family, and overexpression of *OsbZIP71* can significantly enhance the salt tolerance of transgenic rice (Liu et al., 2014a). On the contrary, the plants overexpressing *OsbZIP10/OsABI5* showed more obvious chlorosis than wild type under high salt concentration, indicating that *OsbZIP10/OsABI5* participates in the salt stress tolerance response of rice as a negative regulator, and gene silencing can reduce the sensitivity of transgenic rice to salt (Zou et al., 2008).

Recent years, bZIPs in other plants have also been revealed to participate salinity responsive processes. Cheng et al. (2013) isolated a salt responsive transcriptional factor LrbZIP in lotus root and found that transgenic lotus with *LrbZIP* overexpression could grow with normal root biomass, chlorophyll content, and electrolyte exudation rate under NaCl treatment. Zhao et al. (2016) revealed that *Brassica napus* bZIP transcription factor BnaABF2 enhanced salt tolerance of plants through the ABA pathway.

To sum up, many bZIP genes have been excavated in different plants and confirmed that they can significantly enhance the salt tolerance of plants, making the bZIP gene family a gene treasure house for improving the salt tolerance of crops. Therefore, the use of bZIP transcription factors to improve the salt tolerance of crops and breed new salt-tolerant varieties is of great significance for improving agricultural productivity and improving saline soils.

bZIP TFs involved in drought stress response

Drought is an adverse environmental factor that threatens plant growth and development. Many plant bZIP family members are involved in response to drought stress. Series of studies have shown that many rice bZIP transcription factors are involved in drought resistance. Liu et al. (2014b) found that rice *OsbZIP71* directly binds to the promoters of *OsNHX1* and *COR413-TM1* and activates their transcription so as to enhance drought resistance of transgenic rice. Except rice, some drought-related bZIP transcription factor genes cloned in other plants also significantly enhanced the drought resistance of transgenic crops. Overexpression of maize *ABP9* confers excellent drought tolerance to transgenic *Arabidopsis thaliana* plant (Wang et al., 2017a). During seed germination and plant development, transgenic ramie plants overexpressing ramie *BnbZIP2* were more tolerant to salt stress than wild-type and more sensitive to drought stress (Huang et al., 2016). In addition, overexpression of transcription factors such as *Arabidopsis thaliana* ABF3 (Wang et al., 2016b) and wheat TabZIP60 (Zhang et al., 2015b) in plants can significantly improve the drought resistance of transgenic plants. On the contrary, Lim et al. (2018) found that the pepper bZIP transcription factor CaDILZ1 plays a negative regulatory role in response to drought stress.

bZIP TFs involved in cold stress response

Low temperature stimulation will disturb the normal physiological and metabolic activities and further affect the plant growth and development. The plant mainly responds to low temperature stress through the ICE-CBF-COR pathway. When the plant is exposed to low temperature, it induces CBFs (C-repeat-binding Factors) expression by ICE (inducer of CBF expression), which recognizes CRT/DRE (C-repeat/dehydration responsive element) located on the target gene promoter and combines with *COR* (cold regulated genes) genes to regulate transcriptional expression, thereby enhancing plant cold stress resistance (Shi et al., 2018). bZIP transcription factors also play an indispensable role in regulating plant cold stress responses.

According to incomplete statistics, the first rice bZIP-like transcription factor identified and reported was OsbZIP38/LIP19 of the H subfamily. Induced by low temperature, as a Fos-like molecular switch, it is involved in the plant's response to cold signal pathways (Aguan et al., 1991; Aguan et al., 1993; Shimizu et al., 2005). OsbZIP38/LIP19 and subfamily member OsbZIP87/OsOBF1 are able to bind DNA and form homodimers, and they are more likely to interact with OsbZIP38/LIP19 and form heterodimers to participate in the plant's response to cold signaling (Shimizu et al., 2005). In addition, OsbZIP52/RISBZ5, OsbZIP68/ROS-bZIP1 and OsbZIP73/OsTFX1 in the rice bZIP transcription factor family were also involved in cold resistance. OsbZIP52/RISBZ5 is a member of the G subfamily. It is not induced by drought, salt, PEG, and ABA, but by low temperature. It can form homodimers and specifically bind G-box. However, the test of the cold tolerance of rice showed that the survival rate of over-expressed *OsbZIP52/RISBZ5* rice plants was significantly lower than that of wild type. It can be seen that the expression of *OsbZIP52/RISBZ5* is inversely related to low temperature tolerance (Liu et al., 2012). Cheng et al. (2007) found that OsbZIP68/ROS-bZIP1 could be induced and responded quickly within 24 hours when rice was treated at 10 °C. Liu et al. (2018) identified a total of 8 bZIP genes in rice, *OsbZIP08* , *OsbZIP35* ,*OsbZIP38* , *OsbZIP46* , *OsbZIP63* , *OsbZIP72* ,*OsbZIP73* and *OsbZIP76* , which are associated with low temperature resistance at seedling stage. In addition, Liu et al. (2018, 2019a) also found and revealed the molecular mechanism of *OsbZIP73/OsTFX1* adapting to the cold climate in northern China by comparing the whole genome sequences of Japonica and Indica rice.

Except for rice, carrot, soybean, wheat, tomato and other crops have been successively excavated bZIP transcription factors in response to low temperature stress. For example, Ito et al. (1999) found that the expression of bZIP-like protein Lip (Low temperature-Induced protein) in the roots of radish was up-regulated under low temperature treatment, thereby enhancing the cold resistance of radish. Soybeans GmbZIP44, GmbZIP62 and GmbZIP78 can regulate and promote the synthesis of proline (plant cold tolerance osmotic regulator) to enhance the tolerance of plants to cold stress. At the same time, GmbZIP44, GmbZIP62, and GmbZIP78 can enhance their ability to respond to cold damage and high salt stress by activating the expression of their downstream genes *ERF5* , *KIN1* ,*CORl5A* , and *COR78* (Liao et al., 2008). Hwang et al. (2014) treated *Brassica rapa* with low temperature stress and found that the expression of 27 BrbZIPs were significantly up-regulated, among which *Bra000256* , *Bra003320* , *Bra004689* ,*Bra011648* , *Bra020735* and

Bra023540 may be the key genes involved in the response to low temperature stress. Compared with wild-type *Arabidopsis thaliana* , heterologous expression of*TabZIP6* in wheat under cold treatment significantly reduced the expression of *CBFs* , key *CORs* and other genes in transgenic plants, making the transgenic plants sensitive to low temperature (Cai et al., 2018). However, the over-expressed wheat *TabZIP14-B* ,*TaAREB3* and *TabZIP60* in *Arabidopsis thaliana* can significantly enhance the ability of plants to resist cold stress, and the expression of corresponding stress-responsive genes in transgenic plants was significantly up-regulated. In addition, transgenic plants are more sensitive to ABA than wild type, indicating that T*abZIP14-B* , *TaAREB3* , and *TabZIP60* all enhance the cold resistance of plants through the ABA pathway (Wang et al., 2016a; Zhang et al., 2015b; Zhang et al., 2017b). Xu et al. (2014) found that over-expression of wheat bZIP transcription factor TaABL 1 (ABI-like) elevated cold tolerance in wheat. Apple bZIP transcription factor MdHY5 can respond to low temperature stress at both the transcriptional and protein levels. Overexpression of *MdHY5* can significantly enhance cold stress resistance in apple callus and transgenic *Arabidopsis thaliana* . EMSA results indicate that MdHY5 can bind to G-Box on the*MdCBF1* promoter, thereby increasing its transcription level and regulating the expression of *COR* genes independent of CBF (An et al., 2017b). Wang et al. (2017b) found that transgenic *Arabidopsis thaliana* plants showed reduced survival, increased electrical conductivity, increased malondialdehyde content, and reduced soluble sugar content when overexpressed *Camellia sinensis CsbZIP6*in it. Transcriptome analysis found that the expression of low-temperature and drought-responsive genes in over-expressed plants was significantly lower than that of wild type, indicating that*CsbZIP6* plays a negative regulatory role in low-temperature stress response.

bZIP TFs involved in osmotic stress response

Salinity and drought usually induce secondary stress, osmotic stress. Hence, it's not difficult to understand that plant bZIPs also act as significant roles in response to osmotic stress.

The rice OsbZIP71 transcription factor recognizes and combines with the promoter of the osmo-regulatory gene *OsNHX1* , transports excess Na^+ and K^+ in the cytoplasm to the vacuole, reducing salt concentration in the cytoplasm to improve rice salt tolerance (Liu et al., 2014a). In *Arabidopsis thaliana* , the AtbZIP63 can regulate protein-protein interactions to regulate the activity of proline dehydrogenase I, thereby enhancing the ability of the plant to tolerate hypotonic stress (Veerabagu et al., 2014); the VIP1 (AtbZIP51) rapidly accumulates in the nucleus in response to hypotonic stress (Hwang et al., 2014; Tsugama et al., 2016). Actually, VIP1/AtbZIP51 and bZIP29 can form a heterodimer to enhance their binding to the hypotonic response element (AGCTGK) in the promoters of osmotic response genes *CYP707A1* and *CYP707A3* (Van Leene et al., 2016).

bZIP TFs involved in regulating ABA signaling pathway

As a 'emergency hormone' in plants, ABA is an important signaling molecule in plants. When plants encounter abiotic stress such as salt, drought, or low temperature, they will activate both ABA-dependent and ABA-independent signaling pathways (Bray et al., 1997; Shinozaki et al., 1996; Thomashow et al., 1998; Verslues et al., 2005). Genes involved in the ABA-dependent pathway not only induce ABA biosynthesis, but also regulate the expression of genes containing ABRE elements (Shinozaki et al., 2007; Zhu et al., 2002). The bZIP transcription factor family can bind to ABRE elements and is called ABA response element binding factors (AREBs) or ABRE binding factors (ABF) (Choi et al., 2000; Uno et al., 2000). So far, bZIP transcription factors are proven to participate in ABA-dependent stress signaling in various plants, including *Arabidopsis thaliana* , rice, soybean, wheat. (Casaretto et al., 2003; Fujita et al., 2005; Kobayashi et al., 2008; Lu et al., 2009).

The A subfamily bZIP transcription factor in *Arabidopsis thaliana* is a major regulator of ABA-dependent responses (Satoh et al., 2004). AtbZIP1 regulates ABA signal transduction by binding to the ABREs and alters the expressions of the ABA responsive genes to tolerate the cold stress (Sun et al., 2011). In rice, OsbZIP23 and OsbZIP46 can directly target the expression of multiple stress genes through the ABA pathway, thereby significantly improving drought- and salt-resistance of rice (Dey et al., 2016; Tang et al., 2012a; Xiang et al., 2008; Zong et al., 2016). In the transgenic plants over-expressing *OsbZIP42* , it showed

a rapid rise of transcriptional expression of ABA responsive *LEA3* and*Rab16* and increased tolerance to drought stress (Joo et al., 2019). In soybeans, GmbZIP44, GmbZIP62, and GmbZIP78 can positively regulate the expression of *ABI1* and *ABI2* genes and further induce the expression of downstream genes such as *ERF5* ,*KIN1* , *COR15A* , and *COR78* in response to ABA treatment (Liao et al., 2008).

Recent years, bZIPs are also found with increasing contributions in regulating ABA responses in other plants. Overexpression of the ABA-depended grapevine *VvABF2* gene could enhance osmotic stress tolerance in *Arabidopsis thaliana*and thereby reduce the cell membrane damage (Liu et al., 2019b). Wang et al. (2019) found that sweet potato *IbABF4* gene, encodes a bZIP transcription factor, overexpression in *Arabidopsis thaliana* and sweet potato could enhance their tolerance to multiple abiotic stresses through the ABA signaling pathway.

In short, bZIP family members play an important role in the abscisic acid signaling pathway under various stresses. A large number of studies have shown that bZIP transcription factors affect ABA biosynthesis through the ABA-mediated signal transduction pathways and thus improve plant stress resistances.

To reveal the relevance between bZIP subfamilies and stress types, the functional annotated bZIPs were also classified into 13 verified clades followed the approach used by Corrêa et al. (2008) (Table II and Figure I). There is yet not any functional report on bZIPs in subfamilies H, J and L on abiotic stresses. Among the rest 10 subfamilies, there are 8, 7, 6 and 3 of which involved in salinity, drought, cold and osmotic stress, respectively. The bZIPs for regulating salinity tolerance are most frequently found in subgroups A, D, G and S; while for modulating resistances to both drought and osmotic stress are most members in subgroup A; and for controlling cold responses are most those from subgroups A, C and S (Table II).

REGULATION OF BZIPS ON METABOLISM OF FLAVONOIDS

Recently, a plenty of flavonoids show significant contributions to plant tolerances to abiotic stresses (Agati et al., 2012; Pi et al., 2016, 2018, 2019; Yamasaki et al., 1997; Yan, et al., 2014). Interestingly, many bZIP transcription factors usually play a key regulatory roles in the process of flavonoid biosynthesis. They regulate the expression of key enzyme genes in the synthetic pathway, thereby regulating the metabolism and synthesis of flavonoids.

Matousek et al. (2010) found that both hop HlbZIP1 and HlbZIP2 could activate the expression of chalcone synthase *chs_H1* and the *O-methyl transferase 1* genes to regulate the accumulation of flavonoid glycosides and anthocyanins. Akagi et al. (2012) found that ectopic *DkbZIP5* overexpression in persimmon calluses could induced the up-regulation of *DkMyb4* and then affect the seasonal biosynthesis of proanthocyanidins in persimmon fruit. Malacarne et al. (2016) showed that VvibZIPC22, a member of clade C of the grapevine bZIP family, was able to activate the transcriptional expression of specific genes of the flavonoid pathway including*VviCHS3* , *VviCHI* , *VviFLS1* and *VviANR* , alone or together with other factors to participate in the biosynthesis of flavonols during flowering and UV light-mediated induction. Dash et al. (2017) found that the poplar PatbZIP1 transcription factor regulated the expression of two flavonol synthase genes *PtaFLS2* and*PtaFLS4* in the flavonoid synthesis pathway to promote the synthesis of related flavonoids and thus promotes the lateral root formation. bZIP transcription factor HY5 plays a multifaceted role in plant growth and development. Apple *MdHY5* gene, induced by light and abscisic acid treatments, promoted anthocyanin accumulation by regulating expression of the *MdMYB10* gene and downstream anthocyanin biosynthesis genes (An et al., 2017a). Zhang et al. (2011b) found that the protein levels of two bZIP transcription factors AtbZIP56/HY5 and AtbZIP64/HYH in *Arabidopsis thaliana* induced the accumulation of anthocyanins under low temperature induction. In addition, ABA can induce the expression of *Artemisia annuaAabZIP1* to activate the expression of downstream gene *ADS*and *CYP71AV1* , thereby regulating the biosynthesis of artemisinin (Zhang et al., 2015a). Fan et al. (2019) showed that the expression of*RsbZIP011* and *RsbZIP102* was significantly up-regulated in radish tissue with higher anthocyanin content under heat and salt stress.

So far, the bZIPs that involve in flavonoid synthesis varies from plant species and their target genes (coding for different enzymes in flavonoid metabolism). To uncover the relationship between bZIP subfamilies and flavonoid synthesis, all the functional annotated bZIPs were also categorized into the 13 known subgroups

according to Corrêa et al. (2008) (Table III and Figure I). It seems that only bZIPs in subfamilies A, H and S could regulate flavonoid metabolism.

EFFECTS OF FLAVONOID METABOLISM ON PLANT RESPONSE TO STRESS TOLERANCE

Flavonoids are a class of secondary metabolites of polyphenols with C6-C3-C6 as the basic structure or phenyl-benzopyran structure. Flavonoids also are a large class of secondary metabolites formed by plants in the long-term ecological adaptation process to withstand the stress of harsh ecological conditions, animals, and microorganisms. They are widely distributed in the plant kingdom and are abundant in flowers, fruits and leaves of many plants (Du et al., 2010). Based on the different oxygen rings and conformations of the basic molecular structure of flavonoids, flavonoids are generally divided into six categories: flavone, flavonol, isoflavone, flavanone, flavanol and anthocyanidin (Rice-Evans et al., 2010). The starting substrate for plant flavonoid biosynthesis is derived from coumaroyl-CoA of the phenylpropane metabolic pathway and malonyl-CoA from acetyl-coenzymes. Under the action of chalcone synthase (CHS), they first form chalcone (Aoki et al., 2000), and then the naringenin is formed by the catalytic action of chalcone isomerase (CHI) (McKhann and Hirsch, 1994). Under the catalysis of cytochrome P450 monooxygenase (CPM) and other enzymes, naringen can be used as a major intermediate metabolite to synthesize other flavonoids (Akashi et al., 1999; Falcone Ferreyra et al., 2012; Lam et al., 2014; Liu et al., 2003; Uchida et al., 2015).

More than 10,000 plant flavonoids have been discovered (Aoki et al., 2000; Jiang et al., 2010). They play very important roles in plant resistance to various stress tolerances (Agati et al., 2012; Yamasaki et al., 1997; Yan, et al., 2014). They could remove free radicals under ultraviolet radiation (Li et al., 1993; Treutter et al., 2005), improve seed storage capacity and prolong life (Debeaujon et al., 2000), change petal color (Mola et al., 1998), interfere with the polar distribution of auxin (Buer et al., 2004), affect the accumulation and composition of fatty acids (Lian et al., 2017), etc.

Early studies on the mechanism of flavonoids involved in stress resistance mainly focused on their regulations on response to ultraviolet radiation (Mellway et al., 2009; Tattini et al., 2006). Later, flavonoids were found with strong antioxidant activity (Agati et al., 2007; Hernández et al., 2009; Pourcel et al., 2007; Treutter et al., 2006). Since various stresses can cause excessive peroxide to accumulate in plants, the significant role of flavonoids in plants' stress resistance attracts increasing interests (Fasano et al., 2014; Qiu et al., 2008; Rai et al, 2016; Watkins et al., 2014). Tattini et al. (2004) reported that European privet flavonoids as antioxidants respond to strong light and drought stress. Li et al. (2011) found a conserved trans-acting element (G-box, CACGTG) in the promoter region of the chalcone synthase family gene (*AtCHS*) in *Arabidopsis thaliana* , which regulates the accumulation of H_2O_2 by responding to cGMP signals (Abu Zahra et al., 2014). Yan et al. (2014) found that the cytochrome P450 monooxygenase GmFNSII/GmCPM in soybean was beneficial to the accumulation of flavonoid aglycones in plants and the reduction of H_2O_2 content. In previous studies, we found that the content of flavonoids such as quercimeritrin in salt-tolerant soybeans is relatively higher than that of salt-sensitive soybeans, which is beneficial for soybeans to adapt to salt stress (Lu et al., 2013). With the deepening of research, we further discovered that enzymes related to the flavonoid metabolism pathway are important salt stress response factors, and they can significantly regulate the salt tolerance of plants such as *Arabidopsis thaliana* and soybean (Pi et al., 2016). We recently found that the salt-triggered phosphorylation of GmMYB173, subsequent elevates the transcription of *GmCHS5* for enhancing the accumulation of dihydroxy B-ring flavonoids (such as cyaniding-3-arabinoside chloride) (Pi et al., 2018); while salt-inhibited phosphorylation of GmMYB183 subsequently decreases the transcription of *GmCYP81E11* for reducing monohydroxy B-ring flavonoids (such as ononin) (Pi et al., 2019). Actually, both GmMYB173 phosphorylation and GmMYB183 dephosphorylation contribute to soybean salt tolerance.

The abovementioned studies showed that flavonoids played a very important role in the response of plants to stress. However, there is no direct evidence been found to show us whether bZIP could regulate flavonoid accumulation for plant adaption to these stresses.

CONCLUDING REMARKS Due to their significant roles in plant tolerances to various stress, the

bZIP transcription factors have been comprehensively studied, including their categorization and regulatory mechanisms of target genes. However, there is at least one interesting issue worthy of further investigation: Whether bZIP transcription factor regulates plant stress tolerance by modulating the synthesis of flavonoids.

To date, plenty of literatures show that bZIPs regulate plant tolerances to various abiotic stresses, such as low temperature, drought, and high salt. Besides, there are many reports reveal that flavonoids participate in various stress responses. Moreover, a lot of researches have now confirmed that bZIP transcription factors play an important role in the synthesis of flavonoids. Specially, bZIPs in subfamily H could bind to G-box in promoter of cold responsive genes (Table I and II); members of this subfamily also could modulate the synthesis of some flavonoids (Table III). Since members in this group shares similar conversed protein motifs (supplemental Figure S1 and S2), it is reasonable to hypothesize that plant bZIPs in subfamily H could bind to G-box of cold-responsive genes to further regulate the synthesis of flavonoids. Similarly, it also makes sense that bZIPs in subfamily A could regulate the synthesis of flavonoids by binding to G-box or ABRE of genes involved in cold, salinity, drought and osmotic stresses; subfamily S could regulate the synthesis of flavonoids by bind to G-box or C-box or A-box or ABRE of genes involved in cold, salinity and drought stresses (Table I, II and III). However, these hypotheses are still needed to be further verified.

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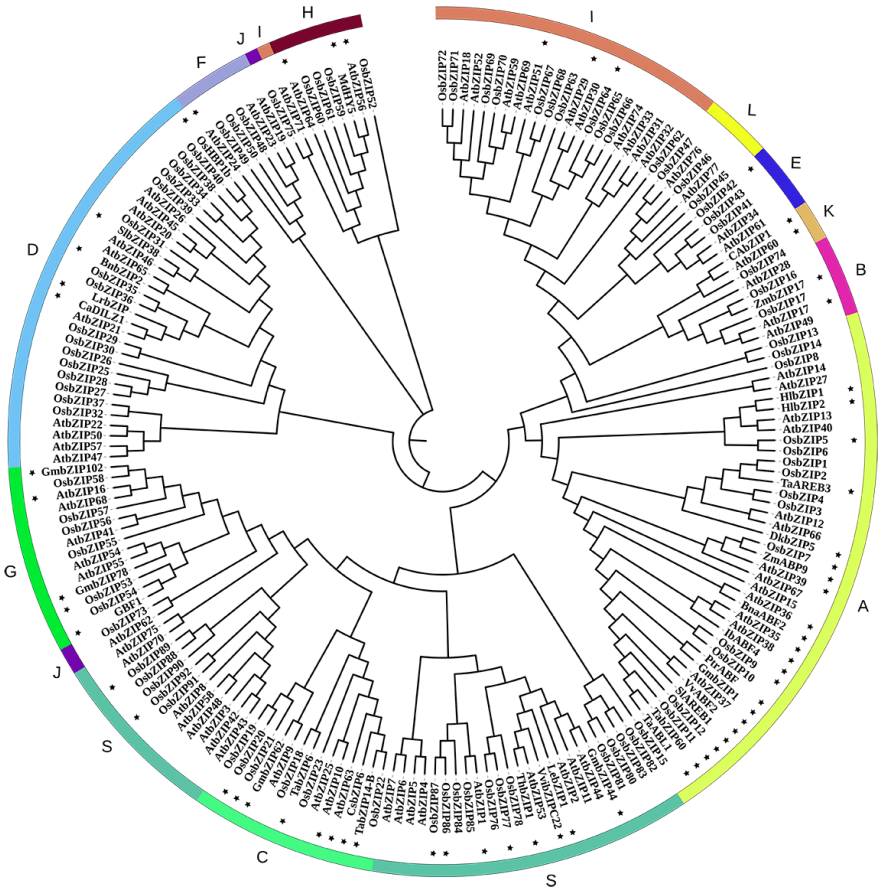

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