FUNCTIONS OF PLANT'S BZIP TRANSCRIPTION FACTORS

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Basic leucine zipper protein refers to a grand transcriptional factor family of all eukaryotes that is involved in various developmental and stress responses like flower development, plant height, maturation of seeds, biotic and abiotic stress signaling. About 127 bZIPs in Arabidopsis, 70 in cotton (*Gossypium hirsutum*), 266 in soybean (*Glycine max*), 47 in tobacco *(Nicotiana tabacum),* 70 in tomato (*Solanum lycopersicum*), 140 in rice, 102 in wheat and 218 in maize have been discovered. In this review, the classification of bZIP is according to the binding specificities of bZIPs as well as their role in transcription.
Keywords: Basic leucine zipper, abscisic acid, cold signalling, pathogen response, core sequence

INTRODUCTION

The basic leucine zipper termed as bZIP protein is a grand transcriptional regulator's family (Umezawa *et al.*, 2006) especially in eukaryotes. The proteins of bZIP normally consist of a bZIP domain having two fundamental characteristics: basic region and dimerization region. Basic region binds to DNA and dimerization region form homo as well as heterodimers. In the basic region, there is a nuclear localization signal which follows on an invariant N-x7-R/K motif which binds to DNA. Moreover, there is a repeat of a heptad of leucine located accurately nine amino acids along the C-terminus, giving rise to an amphipathic helix. Plant bZIP transcription factors favorably bind to ACGT core DNA sequences like G-box (CACGTG), C-box (GACGTC), A-box (TACGTA) (Jakoby *et al.*, 2002), PB-like (TGAAAA) ABRE (ABA responsive element i.e. CCACGTGG) (Liao *et al.*, .

2008) and GLM (GCN4-like motif i.e. GTGAGTCAT) (Holdsworth *et al.*, 1995) motif occur in promoters of many stress signaling genes. However, some non-palindromic sites are also found in bZIP (Zhang *et al.*, 2008).

***Mechanism of action of bZIP transcription factors*:** The transcription factors of bZIP family bind to promoter sequence of selected genes as they are characterized to homodimerize as well as heterodimerize. A transcription factor is termed as regulon when it is involved in the regulation of a great range of genes' expression by binding to the cis-acting regions of the promoters (Nakashima *et al.*, 2009). All bZIP family members are evolutionarily interrelated and conserved. Hence, they share a fundamental integrated construction encompassing a basic zipper (bZIP) domain (Fig. 1)
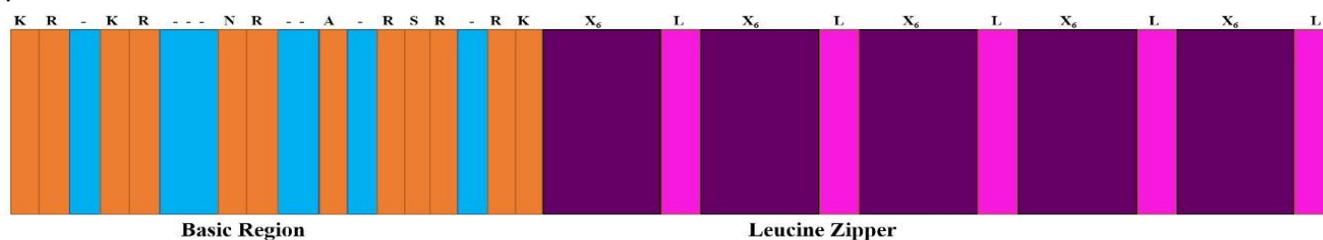
Figure 1. Basic leucine zipper motif showing basic region and leucine zipper region.

Leucine zipper is an extremely conserved protein as it contains a motif of five heptads of amino acids placed sequentially with a leucine at seventh spot. Leucine is highly stabilizing as compared to other amino acids (Vincentz *et al.*, 2001). The leucine zippers switch the homo- and hetero-connotation of bZIP members. They have incessant α-helices

in the framework of a dimer which show characteristic curling around the opposite homo or heterodimer, formulating a dimeric and parallel twisted coil with a trivial twist towards left. The basic regions of bZIP domain remain at the N-termini and hence it becomes able to attach at the promoter regions by making a parallel in the major groove of DNA (see

Fig. 2, Jakoby *et al.*, 2002). Recent researches through isothermal titration calorimetry (ITC) and analytical LASER scattering (ALS) technique have revealed that five heptads in leucine zippers are most important for the bZIP domain dimerization (Selvaraj *et al.*, 2010). It has also been elucidated that the sequential C-terminal truncation of residues reaching up to each leucine vividly liaises the binding of bZIP domains to DNA (Seldeen *et al.*, 2010).

***Regulatory functions of bZIP factors*:** Transcription factors regulate a lot of functions in plants in response to stressful conditions (Allen, 2012) by producing different types of proteins (Singh *et al.*, 2002) e.g. anti-oxidants, dehydrins and osmolytes synthesizing enzymes (Bartels and Sunkar, 2005). Like other transcription factor families, most of bZIP proteins play intersecting role due to which the study of mutant individual's phenotype might become obscure; making the recognition of all *bZIP* genes a compulsion for the identification of functions of bZIP proteins at individual level (Jakoby *et al.*, 2002). They are most common in plants to regulate a variety of phenomena like germination, photomorphogenesis, formation of flowers, floral development, maturation of seed, and are also important for plants in signaling of stress and hormones. Plant bZIP proteins have been extensively explored and their functions seem to be more complex and expanded than other transcriptional factors (Wei *et al.*, 2010). Abssisic acid (ABA) responsive element (ABRE) is one of the recognized gene expression regulatory systems dependent upon ABA production. All the genes of plants using ABRE system require bZIP for their expression (Liao *et al.*, 2008).

***Plant bZIP interactions with ABA*:** The ABA is an important plant hormone which shows a vital role in germination and maturation of seed, in addition to arbitrating adaptive responses to abiotic stresses (Wei *et al.*, 2010) as ABA is produced in plants when exposed to any type of abiotic stress (Allen, 2012). Many genes that are activated by ABA signal may be initiated by exogenous application of ABA (Kang *et al.*, 2002; Cheong *et al.*, 2003). ABA improves plant's capability to survive in adverse environments and productivity (Liao *et al.*, 2008). ABRE are *cis*-acting elements found in the upstream of ABA responding genes (ABFs) (Shen and Ho, 1995). Events of signal transduction during cold and drought stress are intersecting (Shinozaki *et al.*, 2003) and C-repeat/dehydration-responsive element (CRT/DRE) interacts with ABRE-binding bZIP proteins to control the cold and drought responsive genes expression (Narusaka *et al.*, 2003). ABA is also involved in enhancing the role of many genes like late-embryogenesis-abundant genes e.g., *HVA1*. The bZIP transcription factor TaABF1 is helpful in the signaling of ABA pathway which affects *HVA1* expression. Exploration of the interaction between ABA and

TaABF1 in the aleuronic cells of imbibing cereal grains showed that the TaABF1 and ABA are not additive in stimulation of the *HVA1* promoter (Keyser, 2010). However, abiotic stress response systems of genes may be dependent as well as independent of ABA signal like some genes are present that activate by water stress but they show no response to even exogenous application of ABA (Chinnusamy *et al.*, 2004).

***Binding specificities of bZIPs*:** The plant bZIPs are highly specific to their binding activity and their function totally depends upon their binding ability. Hence on the basis of specificity, all bZIPs can be divided into various groups.
***Group1*:** This can also be termed as G-box binding factor (GBF) which includes the bZIPs that recognize ACGT sequence in DNA. A GBF group includes EMBP-1 proteins in maize, CPRF-1 in Parsley, TAF1 in tobacco and GBF1 of Arabidopsis and many more. More than 40 bZIP transcription factors bind to the G-box.
***Group 2*:** This is not very versatile and grand as it includes RITA-1 in rice, CPRF-2 in parsley and opaque-2 proteins found in maize.
***Group 3*:** TGA factors are referred as the third group of bZIP transcription factors that binds to the TGACGT core sequence of DNA. The third group includes tobacco TGA1 (Quatrano, 1996).

***bZIP in different plants and their classification*:** Many bZIP proteins have been identified in various plants (Table 1) e.g. 127 bZIPs in Arabidopsis, 70 in cotton (*Gossypium hirsutum*), 266 in soybean (*Glycine max*), 47 in tobacco *(Nicotiana tabacum),* 70 in tomato (*Solanum lycopersicum*), 140 in rice, 102 in wheat and 218 in maize (*Zea mays*) have been discovered (For complete phylogeny please visit http://planttfdb.cbi.pku.edu.cn/). On the basis of sequences of amino acids found in basic and leucine zipper region, bZIPs are categorized into following groups (see Fig. 1, Fukazawa *et al*., 2000).

i. ***bZIPs in Arabidopsis*:** All bZIP transcription factors in Arabidopsis have been given a generic name *AtbZIP1 to AtbZIP75* (Table 1). This naming system is not according to a proper justification but gives a distinct identification to each *bZIP* gene. All identified bZIP genes and their structured nomenclature has been amalgamated into the MAtDB (MIPS *Arabidopsis thaliana* Database) where MIPS: Munich Information Center for Protein Sequences (Jakoby *et al.*, 2002). The classes of *Arabidopsis thaliana* genes (AtbZIP) are as follow:
***Group A*:** This consists of seven members: *ABI5, ABF2/AREB1, ABF4/AREB2, AREB3, GBF4, ABF1 and ABF3*. Abiotic stresses and ABA induces expression of abscisic acid binding factor (*ABF)* also termed as ABA-

responsive element-binding protein (AREB) (Liao *et al.*, 2008) and ABA also initiates phosphorylation of AREB1/2. ABA induced phosphorylation is essential for AREB1/2 for induction of downstream sequences in casein kinase II phosphorylation. Hence it is concluded that ABA and stress are most likely to perform both transcriptional and post-translational regulation as well as ABA signal transduction of group A-bZIP (Jakoby *et al.*, 2002; Schutze *et al.*, 2008). Plant bZIP transcription factors may lose their constancy due to phosphorylation. ABA- induced phosphorylation of AtABI5 enhances the steadiness of proteins and lessens its degradation. The same happens in HvABI5, AtABI5 homolog from barley. A unique ABI5-binding protein has been isolated, named ABI five binding protein (AFP) which is assumed to aim at ABI5 for its degradation mediated by ubiquitin. Still the relation of ABI5 phosphorylation and AFP has not been comprehended. One reason could be that ABI5 which is the phosphorylated form long hypocotyl 5 (Hy5) proteins is rather established in darkness. This is elucidated by the fragile interface of the ABI5 factor with the E3 ubiquitin ligase constitutive photo morphogenetic 1 (COP1), which degrades HY5 through proteasome. Proteasomes are the bodies degenerative to unnecessary proteins in the body. As we can see the unique role for HY5 and COP1 in Arabidopsis and identified unique in vivo characteristic HY5 genes, it has become interesting to examine whether the light regulated genes are highly specific in their function and the differential phosphorylation of HY5 might pave way for the classification of HY5 on the basis of different light qualities and responses to them (Schutze *et al.*, 2008). ABF1 is expressed in vegetative tissues after cold treatment whereas ABF2, ABF3 and ABF4 are induced by salinity, drought and ABA (Table 2). Over expression of ABF3 and ABF4 leads to improved drought tolerance (Liao *et al.*, 2008). A member of group-A of Arabidopsis assists in antagonistic stimulation of inflorescence, named as flowering locus D (FD). FD expresses in the tips of branches and interrelates with two genes terminal flower 1 (TFL1) and flowering locus T (FT) and it utilizes APETALA1 AP1 gene to promote flowering. FD is not an efficient flowering initiator, but when it associates with FT or TFL1, it is transmuted into a strong inflorescence activator and repressor, respectively (Schutze *et al.*, 2008). AREB1 is an essential component of various abiotic stresses like drought, heat and salt as its over expression plays important role in glucose signaling (Liao *et al.*, 2008).

Group B: This includes three bZIP members AtbZIP17, AtbZIP28 and AtbZIP49 which contain a putative trans-membrane domain (TMD) and putative protease site-1 (S1P) which is a cleavage site in their luminal parts. AtbZIP17 has been reported to be involved in the unfolded protein response (UPR), and AtbZIP17 and AtbZIP28 are involved in various types of endoplasmic reticulum stress responses (Table 1,2)

(Schutze *et al.*, 2008).

Group C: This group contains common plant regulatory factor 2 (CPRF2) and G-box binding factor1 also known as Histone binding factor1 (G/HBF-1) and has same structural features as Opaque 2 (O2) transcription factors in many monocots. O2 interacts with prolamin-box binding factor (PBF) protein and controls seed storage protein production. CPFR2 and G/HBF-1 show responses to environmental stresses and pathogens. It is yet to be verified whether the contiguous *Opaque2* homologues *AtbZIP10* and *AtbZIP25* also control the seed storage protein production in *Arabidopsis* (Jakoby *et al.*, 2002).

AtbZIP10 is disseminated equally to the cytoplasm as well as the nucleus. Nuclear export activity of AtXPO1 (nuclear export receptor exportin 1) interacts with AtbZIP10 and a gene for lesion simulating disease 1 (LSD1). LSD1 is a zinc finger protein regarded as a negative controller of cell death induced by reactive oxygen species (ROS). N-terminal nuclear export sequence (NES) facilitates the collaborative activity of AtbZIP10 with AtXPO1, and its interaction with LSD1 is reconciled by a region in the C terminus. LSD1 covers the AtbZIP10 to eliminate its nuclear uptake. Being a repressor, LSD1 can inhibit the bZIP factors from binding to the DNA e.g. by attaching to AtbZIP10 in the nucleus (see Fig. 3, Schutze *et al.*, 2008).

AtbZIP10 gets successful in formulating heterodimers with AtbZIP53, an S-group bZIP, when it has been accommodated in the nucleus. AtbZIP10 also starts interaction with non-bZIP proteins like ABI3. ABI3 is a vital co-regulator of a developing seeds bZIP-dependent gene expression (Schutze *et al.*, 2008). AtbZIP10 is unrestricted under oxidative stress conditions like pathogen attack, ROS conditions or salicylic acid (SA) treatment (Table 2). The exact mechanism of release of AtbZIP10 is yet to be known. AtbZIP10 is then moved to the nucleus where it can initiate the transcription of objective genes (see Fig. 2, Jakoby *et al.*, 2002). AtbZIP10 functions as a basal defense and initiator of pathogen reaction. Hence it is repressor of oxidative cell death along with LSD1(Kaminaka *et al.*, 2006).

Group D: Members of this gene group are involved to confer resistance against diseases and in the development of plant. These genes are also involved in transduction of different systemic signals e.g., SA and ethylene at the pathogenesis related (PR) promoter in response to pathogen infection (Jakoby *et al.*, 2002). Members of the D group of Arabidopsis bZIP factors are also termed as TGAs, symbolizing the transcription factors binding to the core region of TGACGT in DNA. Orthologs of TGAs from other plant species play role in transcriptional activity during their plant's protection against diseases particularly in systemic acquired resistance (SAR). SAR is a broad spectrum, long-term safeguard against microbes and is initiated when plants are exposed to pathogens. When the pathogen has been identified, PR genes

become transcriptionally stimulated by a mechanism of SA initiated at the sites of prime infection, and in related portions of plants. TGAs recognize the AS-1 (activation sequence-1)-type cis-element in the promoter of PR genes. TGAs activate at the PR promoters upon the SA signaling and hence initiate the PR expression. The non-expressor-of-pathogenesis-related-genes-1 protein (NPR1), synonym non-inducible immunity 1 (NIM1) suppresses the DNA binding and transcriptional capabilities of TGAs. When the SA signals are lacking, NPR1 gathers as a heavy molecular weight molecule in the cytoplasm, maintained by intermolecular cysteine bridges. SA treatment reconciles any modification in the redox condition of the plant cell. Hence it resolves cysteine bridges and performs the nuclear import of NPR1. On the other hand TGA interfaces with NPR1 in the nucleus, trailed by PR gene activation. Thorough analysis of SAR initiation has revealed that DNA–TGA2–NPR1 formulate a ternary complex, which acts as an enhanceosome. Function of DNA-TGA2-NPR1 complex is dependent on SA. Analysis of SA treated cell's nucleus, disclosed that NPR1 and TGA2 can initiate gene expression after treatment with SA in transitorily altered Arabidopsis leaves, whereas TGA2 alone could not perform so (Schutze *et al.*, 2008). It was also clear that BTB–POZ (BTB: bric-a-brac tramtrack broad and POZ: Pox virus and zinc finger) interaction domain was compulsory for the co-activator function of NPR and the oxidation of Cys 521 and Cys 529. In actual, TGA2 is a repressor of PR gene expression in the existence of other TGAs. Hence it is postulated that TGA2 works as transcriptional activator as well as a repressor. The control of SAR through TGA-dependent signaling mechanisms has been assumed alike in the whole plant kingdom after the discovery of NPR. In rice, about four TGA-like factors operate including rTGA2.1 and rTGA2.2. They act together with rice NPR1 ortholog NH1 and Arabidopsis NPR1. It has been observed that overexpression of both rice NH1 and Arabidopsis NPR1 augments the resistance of the transgenic plants to bacterial disease *Xanthomonas oryzae* PV. Oryzae (Xoo). At the same time there arises a negative function by rTGA2.1 in rice against bacterial pathogens. Removal of rTGA2.1 function reduces the disease symptoms in the infected rice plants with Xoo pathogen (see Fig 2, Schutze *et al.*, 2008).

There are two more genes which perform developmental progressions; *AtbZIP46/Perianthia (PAN)* controls inflorescence in *Arabidopsis and liguleless2* controls the formation of blade sheath edges in maize. Arabidopsis NPR1-gene is a homolog of BLADE-ON-PETIOLE1 (BOP1) and BOP2. BOP1 and BOP2 function is redundant to check disproportionate growth and prefiguring of leaves and flowers. In the developmental processes only BOP1 and BOP2 act together with a TGA factor (PAN); NPR1 is not involved. Detailed exploration of genetic mechanisms has revealed that interaction of BOP proteins with PAN monitors

the asymmetric leaf growth and as the NPR1- related signaling is similar to that for controlling the SAR is also used for the organ formulation (Schutze *et al.*, 2008).
Group G: The group consists of *GBF* genes from *Arabidopsis and* their homologues *CPRF1*, *CPRF3*, *CPRF4a* and*CPRF5* are found in parsley. Their function has not been explored properly yet.
Group E: The group E shares a highly similar zipper motif with the members of *group I* but there is no lysine at position −10, that's why it has been allotted a different group.
Group H: This group has only two members, *AtbZIP56/HY5* and *AtbZIP64*. HY5 plays role in promoting photomorphogenesis (Table 2) i.e., proper hypocotyl and cotyledon development and expression of light sensitive genes (Jakoby *et al.*, 2002). HY5 responds to a broad range of wavelengths as well as hormones to express downstream genes (Chang *et al.*, 2008). In Arabidopsis light-harvesting-chlorophyll A/B (Lhcb) proteins are produced by the genes regulated by circadian clock. Circadian clock associated 1 (CCA-1) is the protein that binds to the CCA-1 binding site (CBS). There is an important interaction between transcription factors binding to the CBS and G-box binding Hy5 proteins in order to conduct a properly rhythmic circadian cycle. G-box core element is found in the Lhcb promoter and physical interface of Hy5 and CCA1 brings about normal circadian expression of Lhcb (Andronis *et al.*, 2008).
Group I: Group I of Arabidopsis bZIP include 13 members that are AtbZIP18, AtbZIP29, AtbZIP30, AtbZIP31, AtbZIP32, AtbZIP33, AtbZIP51, AtbZIP52, AtbZIP59, AtbZIP69, AtbZIP71, AtbZIP73 and AtbZIP74 (Table 1). This group of bZIP transcription factors specifically expresses in stem and controls the activity of gibberellin and hence ultimately controls the height of the plant (Table 2). Disturbance in the function of bZIP group I may result in dwarfism and aberrant stem formation (Jakoby *et al.*, 2002).
Group S: Group S includes four members *AtbZIP1*, *AtbZIP2*, *AtbZIP44* and *AtbZIP53* and are transcriptionally active after stress like drought, cold, wound and/or anaerobiosis (Table 1,2). Group S members of bZIP transcription factors are mainly expressed in basic flower organs. Group S members are most probably involved in sucrose signaling and control demand and supply of carbohydrates in organisms (Jakoby *et al.,* 2002).

ii. bZIP in cotton:
Cotton is a major cash crop throughout the world. Intense observations of cotton genome and its expression patterns have revealed that a major part of the genome expresses during the fibre development and ultimately cell wall thickening. There is a tremendous change in the transcripts abundance during genes regulation for fibre development and subsequent metabolism (Al-Ghazi *et al.*, 2009). About 70

bZIP proteins have been identified in cotton (*Gossypium hirsutum* spp). Among them GhbZIP was first that was identified by Jiang with his collaborators (2004). GhbZIP has multiple domains and functions as a transcriptional activator in the ovule and fibre cells of cotton, ultimately helping in the fibre elongation of cotton. It has been observed that GhbZIP expresses after three days of anthesis. Sequence analysis of GhbZIP has revealed that it has 24% sequence similarity with a rice bZIP protein accession number AF268596 and 29% sequence similarity with *Arabidopsis* bZIP accession number NM_100091. GhbZIP is a transmembrane protein, according to hydropathy examination, which has its carboxyl end inside the membrane and amino terminal at the outside (Table 1) (Jiang *et al.*, 2004). Four bZIP-like transcription factors have also been detected that are down regulated upon salinity stress (Rodriguez-Uribe *et al.*, 2011).

iii. bZIP in Soybean:
About 131 bZIP genes have been discovered in Soybean (*Glycine max*) and termed as GmbZIPs. GmbZIPs are involved in negative signaling of ABA, cold, salt, drought (Liao *et al.*, 2008) and pathogen responsive (Alves *et al.*, 2013). Whole genome shot gun approach was employed by Schmutz and co-workers (2010) to sequence 1.1-gigabase genome of soybean. They generated a chromosome scale draft sequence assembly by using high density genetic maps. They claimed 4630 genes that code various proteins in soybean and this is 70% bigger than Arabidopsis (Schmutz *et al.*, 2010).

G/HBF-1: G/HBF-1 protein is among the very first bZIP proteins characterized in soybean. G/HBF-1 binds to the cis-elements in the H-box and G-box motif, also called pathogen elicitors. *Chs15* is a gene in soybean responsible of producing flavonoids and diterpenoids in response of pathogen attack. *Chs15* promoter contains these G-box and H-box motif. G/HBF-1 gets phosphorylated in the diseased cells unlike G/HBF-1 proteins and transcript levels that remain constant during the stimulation of *chs15* (Alves *et al.*, 2013).

iv. bZIP in tobacco:
RSG: RSG (Repression of Shoot Growth) gene of tobacco shows high resemblance to the Group I of Arabidopsis as it play a role in vascular bundles development. The *RSG in tobacco* precisely expresses in the phloem and stimulates gibberellin biosynthesis pathway by *GA3* gene (Table 1). Experiments on tobacco showed that the production of dominant negative RSG restricted *GA3* promoter stimulation, consequently gibberellin production was reduced and dwarf transgenic plants were produced (Jakoby *et al.*, 2002). In tobacco BZI-1 transcription factor forms a protein complex with tobacco ankyrin repeat protein ANK1 which is assumed to be involved in both the auxin-facilitated growth and response to pathogen attack (Schutze *et al.*, 2008).

v. bZIP in tomato:
VSF-1: This is a member of bZIP transcription factors which is expressed in vascular tissues and it also stimulates a gene that encodes a structural protein found in the cell wall. VSF-1 is the same transcription factor as RF2a in rice and group I in Arabidopsis but there is convergence of its function that provides evidence that some group I bZIPs perform the function of vascular development but there is no proof of such performance by VSF-1 (Jakoby *et al.*, 2002).

vi. bZIPs in rice:
In rice 89 OsbZIP genes have been identified (Nijhawan *et al.*, 2008). To have a deep discernment into the gene configuration of these 89 OsbZIP genes, their exon/intron arrangement was dissected. Out of 89, 17 (19.1%) OsbZIP genes have no introns. In the remaining 72 OsbZIP genes in which introns have been detected in ORF have 1-12 numbers of introns. The arrangement of intron locations within the basic and pivot regions of the bZIP domain and intron phases regarding codons are shown in the Figure 2 (Nijhawan *et al.*, 2008). Detailed exploration of OsbZIP has proved that bZIP proteins perform miscellaneous physiological and developmental functions during panicle development, flower development and seed also controls various abiotic pressures and light signaling in rice (Table 2). Detailed knowledge of all functions of OsbZIP has not been unwrapped yet (Nijhawan *et al.*, 2008).

TRAB1: TRAB1 (transcription factor responsible for ABA regulation1) (Schutze *et al.*, 2008) is the group resembles the group A of Arabidopsis in which ABA induces the expression of ABI5 protein and its phosphorylation. TRAB1 ABI5 performs the function of recruiting the OsVP1. OsVP1 is an ABI3 transcriptional factor in rice to the LEA promoter. TRAB1 also plays the role of ABA signal transduction like group-A in Arabidopsis (Jakoby *et al.*, 2002). ABA stress promptly phosphorylates TRAB1 at the point Ser102 into aspartic acid (Umezawa *et al.*, 2006). TRAB1 is phosphorylated due to hyper-osmolarity too; demonstrating that all of the modifications recruited ABA signal pathway during stress conditions (Kagaya *et al.*, 2002). TRAB1 efficiently enhances the transcriptional activity in the rice protoplast transient assay even in the unavailability of inducer ABA (Umezawa *et al.*, 2006). The rice SnRK2 protein kinase family members cause this alteration. In an automated response to ABA, SnRK2 kinase phosphorylates TRAB1 and brings ABRE-controlled reporter gene expression (Schutze *et al.*, 2008). OsbZIP have been divided into a-g groups and Intron distribution arrangements are depicted. In the figure above, basic and axis regions have been mentioned. The dissecting arrows figure out introns. The number of OsbZIP proteins and introns are also given. Splicing stages of bZIP domains are also mentioned as P0 and P2

Table 1. Taxonomy of bZIP gene family of plants and their functions.

bZIP name	Function
Arabidopsis thaliana	
AtbZIP36, AtbZIP38, AtbZIP39, AtbZIP66	Involved in phosphorylation (Schutze *et al.*, 2008) and activation of stress responsive genes (Choi *et al.*, 2000).
AtbZIP 10	Basal defense and positive regulator of pathogen response. Repressor of oxidative cell death LSD1 (Kaminaka *et al.*, 2006).
AtbZIP25	Controls the seed storage protein production (Onate *et al*., 1999).
AtbZIP46	Controls inflorescence (Jakoby *et al.*, 2002), involved in cellular pathogen defense and abiotic stresses (Xiang *et al.*, 1997) and gives auxin- mediated response (Miao *et al.*, 1994).
AtZip56, AtbZIP64	Promotes photomorphogenesis (Ang *et al.*, 1998).
AtbZIP18, AtbZIP29, AtbZIP30, AtbZIP31, AtbZIP32, AtbZIP33, AtbZIP51, AtbZIP52, AtbZIP59, AtbZIP69, AtbZIP71, AtbZIP73, AtbZIP74	Expresses in stem and controls the activity of gibberellin; ultimately controls the height of the plant (Igarashi *et al.*, 2001).
AtbZIP1, AtbZIP2, AtbZIP44,AtbZIP53	Transcriptionally active after stress like drought, cold, wound and/or anaerobiosis, involved in sucrose signaling and control demand and supply of carbohydrates Interacts with GA₃ gene and repress GA production (Fukazawa *et al.*, 2000).
Soybean (*Glycine max*)	
GmbZIP44, GmbZIP62, GmbZIP78	Negative regulation of ABA, cold and salinity resistance (Liao *et al.*, 2008).
Cotton (*Gossypium hirsutum*)	
GhbZIP	Transcriptional activation of genes for fibre elongation (Jiang *et al.*, 2004).
Wheat (*Triticum aestivum*)	
EMBP1-a	Concerned to the ABA facilitated expression through binding to the ABA response element of Em gene in wheat (Guiltinan *et al.*, 1990).
HBP-1a(1)	Induction of histone genes (Mikami *et al.*, 1994).
HBP1-a(17)	Involved in the expression of histone H3 gene's cell cycle-dependent transcription in wheat (Mikami *et al.*, 1994).
HBP1-a(c14)	Induction of histone genes (Mikami *et al.*, 1994).
HBP1-b(c1)	Induction of histone gene (Mikami *et al.*, 1994).
HBP1-b(c38)	Involved in the core histone gene's cell cycle-dependent expression (Tabata *et al.*, 1991).
HALF1	Induction of histone gene (Nijhawan *et al.*, 2008).
SPA	Controls the seed specific genes expression (Albani *et al.*, 1997) and seed storage protein production (Oñate *et al.*, 1999).
Wlip19, TaOBF1	Cold and drought stress tolerance (Rahaie *et al.*, 2013)
Rice (*Oryza sativa*)	
TRAB1	Induces the ABA- mediated expression of genes (Nijhawan *et al.*, 2008).
RF2a, RF2b	Expresses in stem and controls the activity of gibberellin; ultimately controls the height of the plant (Jakoby *et al.*, 2002); Vascular and leaf tissues differentiation (Yanhai *et al.*, 1997).
OsBZ8	Regulate transcription by dint of ABA signaling (Nijhawan *et al.*, 2008).
OsZIP-1a	Stimulation of *Em* gene promoter by dint of ABA (Quatrano, 1996).
LIP19, OsBF1	Cold and drought signaling (Aguan *et al.*, 1993; Rahaie *et al.*, 2013).
RISBZ1	Vital in endosperm-specific storage protein genes expression, regulate metabolic enzymes in new seeds (Onodera *et al.*, 2001).
RITA-1	Regulate genes during development of seed (Foster *et al.*, 1994).
REB	Binds DNA to an α-globulin gene promoter found in rice Endosperm (Nijhawan *et al.*, 2008).
OsZIP-2a, OsZIP-2b	Inactivates several G-box binding factors (Quatrano, 1996).
Maize (*Zea mays*)	
CK-2	Ck-2 induces phosphorylation (Schutze *et al.*, 2008).
ZmGBF1	Regulates gene expression through hypoxic stress (De Vetten and Ferl, 1995).
AREB2/ABF4	Performs the function of phosphorylation (Schutze *et al.*, 2008).
EMBP-1a	Induces the zein gene expression (Nijhawan *et al.*, 2008).
OsbZIP58	Controls the expression of starch synthesizing genes (Wang *et al.*, 2013).
Tobacco (*Nicotiana tabaccum*)	
RSG	Expresses in the phloem and actuates gibberellin biosynthesis pathway by *GA3* gene (Jakoby *et al.*, 2002), involved in both the auxin-facilitated growth and response to pathogen attack (Schutze *et al.*, 2008) Reduces height of plant by reduced internodal length and repression of GA production (Fukazawa *et al.*, 2000).
Tomato (*Solanum lycopersicum*)	
VSF-1	Perhaps performs the function of vascular development (Jakoby *et al.*, 2002).

Table 2. Morphological traits associated with different functions regulated by different bZIPs.

Gene name	Functions	Morphological traits
AREB1/ABF2, AREB2/ABF4, ABF3	Involved in phosphorylation (Schutze *et al.*, 2008) and activation of stress responsive genes (Choi *et al.*, 2000).	Show rigorous growth (Bartels and Sunkar, 2005) and high survivability in stress conditions (Fujita *et al.*, 2005).
AtbZIP1, AtbZIP2, AtbZIP44, AtbZIP53	Transcriptionally active after stress like drought, cold, wound and/or anaerobiosis, involved in sucrose signaling and control demand and supply of carbohydrates (Fukazawa *et al.*, 2000).	Stomatal closure at daytime (Yordanov *et al.*, 2003), adopt thick leaves with hairs and waxiness. Many drought-tolerant species have thick, waxy, or hairy leaves that minimize water loss (Shinozaki *et al.*, 2007).
LIP19, OsBF1	Cold signaling(Aguan *et al.*, 1993).	More spikelets, awn less plants, reduced height and biomass, longer panicle but lower seed set. (James, 2012)
AtbZIP18, AtbZIP29, AtbZIP30, AtbZIP31, AtbZIP32, AtbZIP33, AtbZIP51, AtbZIP52, AtbZIP59, AtbZIP69, AtbZIP71, AtbZIP73, AtbZIP74	Expresses in stem and controls the activity of gibberellin; ultimately controls the height of the plant (Igarashi *et al.*, 2001).	Over expression increase the vegetative growth and plant height whereas some mutants show reduced response to gibberellins (Radi *et al.*, 2006).
AtbZIP46	Controls inflorescence (Jakoby *et al.*, 2002).	Results in pentamerous flowers (Chuang *et al.*, 1999).
AtZip56, AtbZIP64	Promotes photomorphogenesis (Ang *et al.*, 1998).	Below par development of cotyledons and enlarged hypocotyl (Jakoby *et al.*, 2002). Reduced lateral roots development (Ang *et al.*, 1998).
GhbZIP	Transcriptional activation of genes for fibre elongation (Jiang *et al.*, 2004).	Fibre elongation (Jiang *et al.*, 2004).
RF2a, RF2b	Expresses in stem and controls the activity of gibberellin; ultimately controls the height of the plant (Jakoby *et al.*, 2002) Vascular and leaf tissues differentiation(Yanhai *et al.*, 1997).	Produce dwarf plants and anomalous vascularization (Jakoby *et al.*, 2002).
OsbZIP58	Controls the expression of starch synthesizing genes (Wang *et al.*, 2013).	Excellent quality grain and mutants show abnormal seed formation with low starch (Wang *et al.*, 2013)
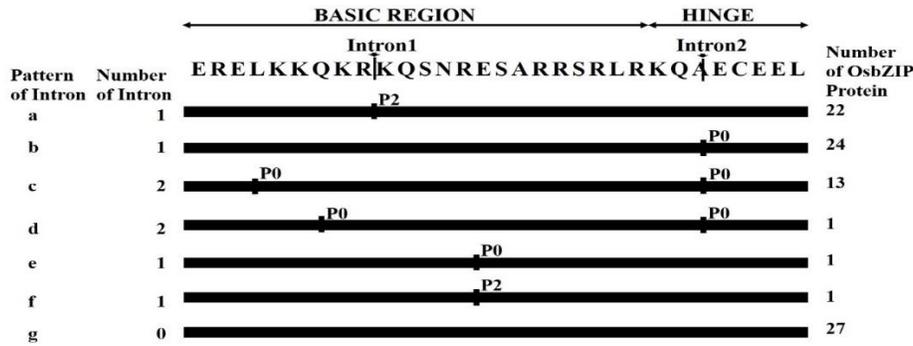
Figure 2. BZIP domains of OsbZIP showing Intron distribution.

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RF2: RF2A has been identified in rice which is similar to the bZIP I group in Arabidopsis. Suppression lines of *RF2a* antisense gene have been developed in rice which exhibit short stature phenotype. This phenomenon might be due to suppression in biosynthesis pathway of gibberellin (Figure 3). Moreover, these plants show peculiar development of vascular tissue (Jakoby *et al.*, 2002).
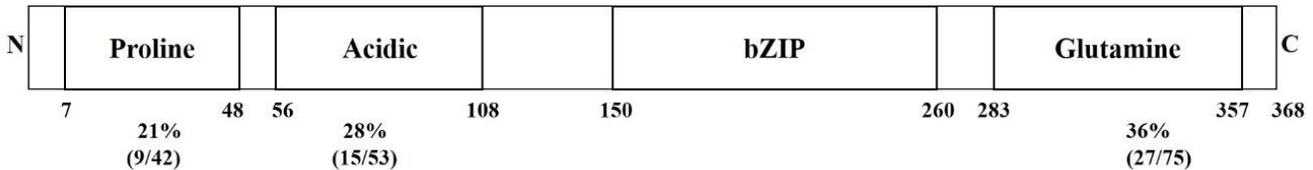
Figure 3. Domain structure of RF2a with percentages of proline, acidic amino acids and glutamine residues in each presumed domain.

There is an important viral disease of rice caused by rice tungro bacilliform virus (RTBV) which replicates in infected phloem cells of rice plants. In rice plants, promoter of RTBV induces a reporter gene expression. RF2a encodes for a basic leucine zipper protein and binds to Box II *cis* element. Box II *cis* element is a compulsory requirement for the promoter expression of RTBV. RF2a is mostly found in phloem cells, shoots and very small amount in roots and rouses Box II hooked transcription in homologous *in vitro* system of transcription. In transgenic antisense plants in which RF2a amassing was bottled-up had normal roots but underdeveloped and curled leaves with small, disordered vascular tissues, bloated sclerenchyma and outsized air spaces. Hence it was concluded that a host transcription factor has been exploited by the RTBV promoter that is vital for differentiation of leaves and vascular tissues development (Yanhai *et al.*, 1997).

***OsbZIP-1a*:** OsbZIP-1a is a homolog of EMBP-1 and binds to the G-box in the DNA sequence. OsbZIP-1a is found in the rice protoplast and induces Em promoter through ABA induction. There is a P-ring at its amino terminal which is referred as ATP/GTP binding domain (Quatrano, 1996).

***OsbZIP58*:** OsbZIP monitors the expression of starch synthesis genes in rice i.e. ISA2, OsSSIIa, Wx, OsBEIIb, OsAGPL3, SBE1; by directly attaching to their promoters and help in production of high quality starch in seeds. In the absence of OsbZIP58 the rice grain becomes deformed with lower quantity of amylose and starch and aggregation of a different type of starch in the belly portion (Table 2). OsbZIP58 is a good indicator of high quality rice plant (Wang *et al.*, 2013).

***VSF-1*:** VSF-1 is a bZIP transcription factor that binds to the promoters of *grp1.8* genes. VSF-1 rouses *grp1.8* transcription in protoplast (Yanhai *et al.,* 1997).

***vii. bZIP in wheat*:**

***HBP1a*:** Histone binding protein 1a (HBP1a) is bZIP which particularly bind to the ACGT core sequence of promoter. HBP-1 has a characteristic bZIP domain at C-terminal and a proline rich domain at N-terminal and bZIP domain binds to the CCACGT motif. HBP1 is further divided into sub groups e.g., HBP1a-1, HBP1a-17 and HBP1a-c14. All members of HBP1 binds to the same CCACGT motif but their binding tendencies are diverse. HBP1a is specific to bind to the H3 promoter that is a hexamer motif. HBP1a-17 aggregates at meristematic tissues, in which the S-phase is plentiful. Thus it is assumed that the cell cycle dependent transcription of H3 gene is controlled by HBP1a-17. HBP1a-17 makes a homodimers with the hexamer motif and it is also involved in the activation of the CTF domain in humans and GBF1

domain in *Arabidopsis thaliana*.

Keeping in view a great variety of functions of the members, HBP1a has been categorized into various sub groups i.e., common plant regulatory factors as CPRF-1, CPRF-3, G-Box binding factors as GBFs and TGACGT core binding as TGAlb. Hence it can be assumed that a separate superfamily of HBP-1a could be found in various plant species (Mikami *et al.*, 1994).

HBP1b: HBP1b is the second subclass of histone binding protein. This is an isoform of HBP1a but binds to a different hexamer motif i.e. ACGTCA, also termed as Hex-b motif. Both HBP1a and HBP1b have the same bZIP domain but in contrast to HBP1a, there are glutamine residues at C-terminal in HBP1b. The binding specificities of HBP1a and HBP1b are defined by the flanking core sequence of the hexamer as the ACGT core is common for both. In some plants and animals, some other transcription factors also act as trans-activation domain. HBP1b-c38 also gathers at meristematic tissues of plant in which S-phase is abundant, hence controlling the cell cycle dependent transcription of H3 gene in wheat.

HBP1-b has also some recognized proteins like vitellogenin gene binding protein (VBP1), TGA1 and TGAla. Hence HBP1b can also contribute towards the new expected superfamily of gene termed as Histone binding proteins (Mikami *et al.*, 1994).

Wlip19: Wheat *lip19* is a cold, drought and ABA responsive bZIP-type transcription factor with an exclusively higher expression in cold tolerant cultivars of wheat than cold-sensitive genotypes. *Wlip19* mends the expression of four Cor/Lea genes of wheat named *Wrab17, Wrab18, Wrab19 and Wdhn13* of wheat callus to impose stress tolerance. Its heterolog in tobacco shows major tolerance to abiotic stresses specifically cold. Even *Wlip19* shows its expression upon exogenous application of ABA (Kobayashi *et al.*, 2008). Further investigation has showed that *Wlip19* and another bZIP type Transcription factor TaOBF1 has same protein-protein interface in all cereals (Rahaie *et al.*, 2013).

TaABF1: Autonomously replicating sequence i.e. ARS-binding factor (ABF1) in wheat is a seed specific gene (Johnson *et al.*, 2002), involved in ABA stimulated regulation of *HVA1* gene in wheat in a non-additive manner and expresses in the seeds during imbibition (Keyser, 2010). TaABF1 is not expressed vegetative tissues of plant neither upon ABA application nor in response to abiotic stress (Johnson *et al.*, 2002; Rahaie *et al.,* 2011). Detailed exploration of mechanism of action of TaABF1 revealed that during maturation and dormancy development of wheat grain mRNA of TaABF1 along with an ABA-induced protein kinase (PKABA1) mount up in seeds. Transcripts of TaABF1 tremendously add up in seed during imbibition (Rahaie *et al.,* 2011). TaABF1 is not responsive to abiotic stresses but its homologous bZIP1 shows response to salinity by down regulation (Rahaie *et al.*, 2013).

SPA: Storage protein activator (SPA) is a unique transcription factor of wheat, particular to seed storage proteins. SPA is analogous to the O_2 transcription factor in maize. Endosperm motif (EM) is an essential requirement for the transcriptional activity of SPA. SPA activates the reporter gene by binding to the long endosperm box (LEB) and GCN_4 like motif (GLM) (Albani *et al.*, 1997).

viii. bZIP in maize:

CK2: The group A-bZIP undergoes phosphorylation induced by ABA. CK2 protein kinase in maize phosphorylates two maize bZIP factors. CK2-induced phosphorylation enhances the DNA binding process of EmBP-2 and lowers that of ZmBZ-1 (Schutze *et al.*, 2008).

AREB2/ABF4: There is a protein kinase dependent on calcium, AtCPK32 that phosphorylates AREB2 at Ser 110 position *in vitro*. This residue is necessary for ABF4 transcriptional activity too which depicts the straightforward contribution of AtCPK32 in ABA-responsive gene manifestation (Schutze *et al.*, 2008).

SPA: SPA is involved in 22-kD zein gene transcription. SPA and O2 have similar sequence to some extent but their transcriptional activity potential is same (Albani *et al.*, 1997).

Conclusions: Plant bZIPs show a grand diversity in nature like DNA binding and transcriptional activities, ability to form homodimers and heterodimers and interaction with proteins other than leucine zipper proteins. Its diversity of activities makes it adaptive to a variety of stresses and responds accordingly in both forward and reverse manner. Most of the higher plants bZIP proteins depend upon the hexamer motif in DNA region for binding to the particular transcription factor. All bZIP proteins show binding specificity to the hexamer motif in DNA which gives a clear cut view of the importance of the bZIP transcription factors for higher plants. These traits make the bZIP transcription factors more complex and finely tuned and still there is a huge potential yet to be disclosed. Here we have given a classification of bZIP transcription factors according to their binding specificities as well as their functions but still there is a great range of unknown bZIP transcription factors which need to be allotted their special place in any of these groups or new.

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