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A comprehensive overview of transcription factors (WRKY, NAC and BZIP) in plants

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Abstract

Transcription factors are involved in the regulation of transcriptional reprogramming associated with the plants stress responses. Large number of transcriptional factors has been identified so far, which are involved in defense responses in plants against certain biotic and abiotic stresses. These transcription factors are divided according to their DNA binding domains (DBDs) in plants that are believed to be distinct from prokaryotes and other lineages of eukaryotes. Recently, identification and characterization of large number of important transcription factors have been performed. In addition, structure of some important DBDs have also been elaborated in detail utilizing techniques such as NMR spectroscopy or X-ray crystallography. This review is about a comprehensive overview on the structure and role of some transcription factors in plants. This publication will provide information in plant transcription factors, including the important aspects and unifying themes to understand transcription factors and the important roles of particular families in specific processes.

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Introduction

Plants are sessile organisms, which are constantly exposed to different types of environmental variations. Stress is the customary response of plants to the rapid and extreme changes in their close vicinity. Exposure to various types of abiotic stresses like drought (water deficiency), salinity (excessive salt), flood, heavy metals accumulation in the soil, temperatures (freezing to scorching), nutrient starvation (reduced availability of essential mineral nutrients), fluctuations in light and biotic stresses such as pathogens, may affect the plants. Plants respond to biotic and abiotic stress stimulus by making alterations in their metabolism, growth and development. These have evolved several intricate mechanisms which help plants for adaption to hostile environmental conditions (Chen and Murata 2011).

Plants generally possess three different strategies to cope with environmental stresses. A strategy which comprises of physiological or biochemical adaptations is termed as “tolerance mechanism”. It involves the maintenance of protoplasmic viability in plants by utilizing energy for the exclusion of excess salts and other heavy metal ions (Sabovljevic and Sabovljevic 2007). In this way, plants protect themselves from toxic effects of increased salt content in the rhizosphere e.g., protein aggregation (Ashraf and Foolad 2007).

Some plants utilize “avoidance mechanisms” in order to cope with environmental stresses. Escaping is a phenomenon in which plant tries to keep the excess salts and other heavy metals away from the part of the plants where these kinds of toxic ions can be lethal. The plant utilizes different strategies such as shedding, exclusion (Flowers and Yeo 1995), secretion (Weber *et al.* 2008), succulence (Weber *et al.* 2008) and stomatal responses (Robinson *et al.* 1997) as a part of avoidance mechanisms. For example, plants close stomata under drought conditions and reticence of vegetative plant growth occur (Chaves *et al.* 2009). However, the most important strategy which is being exploited by the plants against different types of stresses, consists of the mechanisms which operates at cellular levels in response to stress. The cellular level responses include the activation of certain stress responsive and stress tolerance genes, whose products provide assistance to adapt unfavorable environmental conditions (Matsui *et al.*, 2008).

There are two broad groups of gene products. Functional proteins group constitutes the first group of proteins which is likely to perform function in stress tolerance, for instance, key enzymes for ABA (abscisic acid) biosynthesis , kinases (Nambara and Marion-Poll 2005), osmotic adaptation and dehydration tolerance proteins in the cell (Yao *et al.*, 2011), cellular protective enzymes (Puckett and Barton 2007), numerous signaling proteins such as protein phosphatases (Zhu 2002), water channel proteins (Mochida *et al.*, 2009), detoxification enzymes such as catalase, chaperons, LEA proteins (late embryogenesis abundant proteins), antifreeze proteins, osmotin, vital enzymes for osmolyte biosynthesis, mRNA binding proteins, several proteases, proline and sugar transporters etc. (Shinozaki *et al.* 2003).

A second group known as regulatory proteins, contains protein factors that are part and parcel in stress responsive gene expression and regulation of signal transduction e.g., transcription factors (WRKY, NAC, MYB etc.) and other molecules like calmodulin-binding protein etc. (Shinozaki *et al.* 2003). Transcription factors (TFs) comprise of various gene networks which are accountable for the expression of stress-inducible genes, independently or collectively. They perform vital roles in the regulation of genome expression in response to several physiological and environmental signals and some of them have the role of switching on plant adaptive and physiological pathway. In fact, a single transcription factor (encoded by one gene) can activate a complex adaptive mechanism against stress. Transcription factors are modular proteins that possess DNA-binding domain, which interacts with Cis-regulatory elements of its target genes and a protein-protein interaction domain. It eventually facilitates in oligomerization between TFs or other regulators (Wray *et al.* 2003). It is very important to note that genes participating in transcription and signal transduction have been specially retained after the most recent whole genome duplication in Arabidopsis (Seoighe and Gehring 2004; Blanc and Wolfe 2004). These studies advocate vital role of TFs duplicates in the plant evolution.

Transcription factors can be grouped into numerous protein families based on their structure resemblances in the DNA binding domains (Riechmann *et al.*, 2000). Interestingly, genomic comparisons have highlighted the fact that TF families in plants experience more intense gene growth as compared to fungi and animals. It is believed that subterranean evolutionary analysis of transcription factors families with the identy proof of the ancestral gene sets in mixture with functional assignments will greatly assist in addressing this issue (Floyd and Bowman 2007). One possibility is that it reflects the capability of flowering plants to efficiently adapt to different and unstable environmental conditions (Shiu and Shiu 2005). Therefore, the basic goal of this review is to develop a comprehensive overview of the role of some important transcription factors in plants.

Few transcriptional factors (TFs) gene families

TFs have been differentiated into diverse families founded on the preserved structural domains, which participatein the DNA binding to functional modular structures or to CREs (cis regulatory elements) in the target genes. Several transcription factors, like WRKY, NAC, CBF, DREB, bZIP, zinc-finger and MYB are directly or indirectly present in the regulation of defense and responses to different of stress in plants (Mukhopadhyay *et al.*, 2004; Chen *et al.* 2006). Studies into the functional and mutational analysis to understand the putative functional domains of TFs have revealed that a typical plant transcription factor consists of an oligomerization site, DNA-binding region, a transcription regulation domain (some may lack) and NLS (nuclear localization signal) (Goff *et al.*, 1992, Vetten *et al.*, 1995). A brief description of few transcription factors is given below:-

WRKY Transcription Factor (TF)

Large family of TFs which plays an essential role in different processes of physiology in plants are WRKY transcription factors. They are DNA-binding proteins and have been firstly identified from sweet potato and wild oats (Ishiguro and Nakamura 1994; Rushton *et al.*, 1995). They can recognize the W-box elements in the promoter region and hence, can help in the process of gene expression. Although most WRKYs are plant specific yet several reports have shown the presence of genes coding WRKY proteins in other organisms like the protist *Giardia lamblia* and slime mold *Dictyostelium discoideum*. These evidences support that WRKY proteins have developed earlier through the evolution of plant phyla (Zhang *et al.*, 2005; Zheng *et al.*, 2007; Pan *et al.*, 2009). It is considered that the function of some WRKY is conserved between phylo-genetically distant species (Mangelsen *et al.*, 2008). Yamasaki *et al.*, (2008) is of the view that they have some links with transposons, for instance mutator-like elements and from BED finger intermediate. BED finger intermediate is a typical zinc finger DNA-binding domain found in animal transposases and in both BEAF (chromatin-boundary-element-binding proteins) and DREF (Yamasaki *et al.*, 2008). But still this debate is controversial. In the course of selection and polyploidization, the replicated WRKY genes have been conserved in cultivated and wild plant species (Petitot *et al.* 2008). About 70 WRKY TFs are identified from the genome of Arabidopsis (Riechman *et al.* 2000; Euglem *et al.* 2000). In plants, WRKY perform representative functions such as growth and development, metabolic regulation, abiotic stress responses like drought and salinity, development of seed, leaf senescence pathogen responses morphogenesis and cold tolerance (Huang *et al.*, 2002; Seki *et al.*, 2002; Luo *et al.* 2005; Miao *et al.* 2004; Rushton *et al.* 1996; Juhnson *et al.*, 2002) are increasingly acknowledged.

Structure, Characterization and Classification of WRKY TF

WRKY-GCM1 super family of zinc finger TFs constitute a big family of WRKY proteins which are evolved from MULE (mutator or mutator-like transposes) (Babu *et al.*, 2006). There are three groups of these proteins, established on the design of the zinc finger motif and the number of WRKY domains. Normally, there are two WRKY domains in group 1 proteins which includes a C_2H_2 motif. On the other hand, there is only single WRKY domain in group 2 proteins and additionally established on phylogeny of the WRKY domains, C_2H_2 zinc-finger motif (ZFM) can further be alienated into five subgroups. Moreover, a single WRKY domain is also present in group 3 proteins, their zinc finger like motif is C_2-H-C. In the group 1 proteins, the DNA binding activity is being carried out by C-terminal WRKY domain instead of N-terminal (Euglem *et al.*, 1996). A W-box sequence of WRKY domains, which is often referred to as the target recognition sequence constitutes of (T) TTGACY, where Y could be T or C (Rushto *et al.*, 1996; de Peter *et al.* 1996).

In 2007, one WRKY domain of crystal structure has been determined (Duan 2007). It highlights the binding of well-preserved remains of WRKY domain to relate DNA-element, W-box. WRKY proteins consist of either one or two WRKY domains. Total 60 amino acids have been were present in WRKY protein. WRKYGQK is an extremely preserved amino acid motif (responsible for its name derivation), and it exists at its N-terminus. However, a metal chelating zinc finger signature is present at the C-terminus (Euglem *et al.*, 2000). These zinc fingers can bind to W-box DNA motif (Eulgem *et al.*, 1999; Dpater *et al.*, 1996; Wang *et al.* 1999; Rushton *et al.* 1999; Yang *et al.*, 1998). In 2005, the NMR structure of the C-terminal domain of WRKY4 has evolved in Arabidopsis (Fig. 1A) (Yamasaki *et al.*, 2005).

It has been revealed that WRKYGQK (conserved sequence) is present in N-terminal b-strand whereas, C-terminal domain consists of four b-strands which forms an antiparallel b-sheet. Various plant lineages have been known to contain the variants of the WRKYGQK motif including, WRKYSEK, WRKYGKK, WRKYGEK WSKYEQK (Mohanta *et al.*, 2016). A difference can exists only in WRKY patterns, such as, WIKY, WKKY, WSKY, WRMC, WRRY, WKRY, WKRY, WVKY and WRIC (Jiang *et al.*, 2017). DNA binding affinity can be altered due to changes in the WRKYGQK pattern, while some of these variants might lack DNA binding affinity and even ability. One end of sheet-b formed a zinc-binding pocket with conserved Cys/ His remains. It is worthy to note that the terminal-N strand is majorly involved in the center by an "addition of the Gly residue" of the motif. Hydrogen bonding occurs in b-strand with adjacent strand in antiparallel fashion in the absence of this residue (Yamasaki *et al.*, 2005). Quite recently in 2007, structure of WRKY domain of Arabidospis WERKY1 has been analyzed and found that it contains five b-strands, adding N-terminal strand to four-stranded structure (Fig. 1B) (Duan *et al.*, 2007). The major cause of this pattern is due to peptide length difference as it may happen during NMR analysis that additional strand starts to add in the middle. The 4-stranded structure is interestingly stable because this section is not preserved among the WRKY domains. Hence, 4-stranded core is considered as the common structure of WRKY, though it may have an additional N-terminal strand. A computational cropping model of WRKY domain complex and DNA showed residues responsible for DNA binding (Fig. 1C).

The WRKYGQK sequence (found in N terminal b-strand) arrives the major trench of the DNA in such a way that sheet-b plane is approximately vertical to the DNA axis. The vital residues responsible for sequence-specific recognition are the two Lys, Gln, Arg and Tyr residues in the motif. The DNA-binding activity is not likely to be engaged during this presumable evolutionary pathway.

Role of WRKY protein

WRKY proteins play critical and vital role in various physiological processes, for instance, seed coat development, hormonal signaling, senescence, embryogenesis and regulation of biosynthetic pathways (Johnson *et al.*, 2002). Signaling pathways involving nutrient deficiency response have also been accomplished by WRKY proteins. Moreover, numerous studies have shown an evidence about the role of WRKY proteins in both cold and heat stresses in plants. In tobacco (*Nicotiana tobacum* L.), WRKY transcription factor responds to a combination of heat and drought stress (Rizhsky *et al.*, 2002). Environmental stresses (biotic and abiotic) are found to induce WRKY gene expression in plants (Ryu *et al.*, 2006).

In addition, they are believed to be involved in defense against phyto-pathogens such as fungi (Marchieve *et al.*, 2007), bacteria (Dong *et al.*, 2003) and viruses (Yoda *et al.*, 2002).

Functions of WRKY transcription factors (TFs) in defense signaling

A variety of herbivores and microbial pathogens attack on the plants. In response to these stimuli, multiple defense signaling pathways are activated in the plants. There are two interconnected branches in plant innate immunity (PTI) or pathogen-associated molecular pattern (PAMP)-triggered immunity and effectors-triggered immunity (ETI) (Chisholm *et al.* 2006). PTI is initiated, when plants detect and recognize molecular signatures of various pathogens and frequently triggers downstream MAP kinase (mitogen-activated protein) cascades and defense genes. ETI is driven by major R gene products (plant disease resistance proteins), which can distinguish specific pathogen either directly or indirectly. Phytohormones such as Jasmonic acid (JA) and Salicyclic acid (SA) modulate ETI and PTI local as well as systemic acquired resistance (Bostock 2005; Durrant and Dong 2004).

The WRKY genes play role in these responses by transcriptional reprogramming (Ryu *et al.*, 2006). It has been reported recently that a majority of WRKY genes are receptive pathogenic and several of them comprise of W-box elements within their promoters (Eulgem and Somssich 2007). These observations suggest the presence of a positive or a negative control over WRKY genes by WRKY features via specific response mechanisms. A promoter PcWRKY1 contains specific arrangement of W-boxes that regulates its temporal expression upon treatment with PAMP (Eulgem *et al.*, 1999). This observation has been confirmed by ChIP (chromatin immuno-precipitation) analysis, which exhibited PAMP-dependent in vivo binding of PcWRKY1 to the PcPR10 (defense-response gene) as well as to its own promoter (Turck *et al.*, 2004). Work shown by Marchive *et al.*, (2007) is of the view that plants become susceptible to a variety of fungi, when the VvWRKY1 gene of grapevine (*Vitis vinifera*) is overexpressed in tobacco (*N. tabacum*). Though, ectopic expression of VvWRKY2 grapevine gene resulted in an improved resistance to the necrotrophic fungi *Alternaria tenuis*, *Botrytis cinerea*, and *B. pythium* (Mzid *et al.*, 2007). In 2008, a WRKY factor from chili pepper (*Capsicum annuum*) has been observed to perform as a defense negative regulator. Virus persuaded gene silencing and overexpression studies showed that *Xanthomonas* growth is decreased in former, whereas the latter resulted in an enhanced hypersensitive cell death of *tobacco mosaic virus* and *Pythium syringae* (Oh *et al.*, 2008). These all findings suggest the importance of WRKY TFs in plant defense responses against various pathogens. Numerous WRKY TFs have been known to found in other plant species such as 104 in poplar (*Populus* spp.), 66 in papaya (*Carica papaya*), 38 in moss (*Physcomitrella patens*) and 68 in sorghum (*Sorghum bicolor*). The role of these factors in mediating plant immunity is still unclear (Shree *et al.*, 2009). Hence, a lot of research can be done in this direction.

WRKY transcription factors (TFs) role against different abiotic stresses

Although WRKY TFs have been discovered recently, these factors are considered as one of the best characterized classes of plant TFs. In the past, it remained a big challenge to uncover the role of WRKY TFs against abiotic stresses. The functional analysis of these factors in the plants in response to abiotic stresses (i.e., cold, drought and nutrient deficiency) have been currently studied by some researchers. Growth and development of the plants is affected mainly because of severe environmental factors like flooding, drought, salinity, and high and low temperatures. Scientists have also estimated that increasing CO_2 concentrations would cause the increase in more adverse and unpredicted abiotic stresses for the plant growth (Feng *et al.*, 2014). Hence, it is imperative to study in detail about the molecular mechanisms of abiotic stresses in plants (Chen *et al.* 2013a). WRKY TFs have been found to be very important for many trades during plant signaling (Bakshi and Oelmuller 2014). Transcriptional profiling has been found to be useful in finding out the WRKY proteins against biotic stress responses. The regulation and fine-tuning of WRKY proteins are important for the establishment of complex signaling webs, which are involved in imparting stress tolerance. Different studies have shown that WRKY genes respond successfully to drought, wounding, cold or heat pre-treated chilling (Hara 2000; Song *et al.*, 2010; Bakshi and Olemuller 2014). WRKY genes expression promise the successful signal transduction in order to activate and regulate the stress-related genes, which ultimately result in plant stress tolerance. A single WRKY gene can respond to several stress factors, which indicate its diversity to regulate various function in plant stress response as for example, AtWRKY 25 and AtWRKY53 are induced by heat as well as salt treatments (Ohama *et al.*, 2016). Numerous WRKY proteins are found to be taking part in salinity and drought tolerance responses (Golldack *et al.*, 2011; Lu *et al.*, 2016). Recently, a study has been conducted that reveals the overexpression of OsWRKY11 under the control of HSP101 promoter. It concludes that overexpression of OsWRKY11 caused in an enhanced drought tolerance as indicated by the reduced leaf wilting and increased survival rate of green plant parts (Wu *et al.*, 2009). OsWRKY genes from rice respond to NaCl, cold and heat treatment (Qiu *et al.* 2004). Similarly, eight WRKY genes in wheat are found to be responsive at low temperature, and PEG and NaCl treatments (Wu *et al.*, 2008).

Plants have an optimal temperature range and if temperature exceeds or decreases from that range, plants perceive it as a stress. The major limiting factor for the crop production is either low or high temperature. Since the past two decades a lot of work has been done to uncover the complex molecular mechanism in plants response to various temperature ranges. Literature has showed the significant importance of WRKY proteins in retorts to both cold and heat stress. For example, studies conducted on tobacco have shown that a WRKY transcription factor responds to cold and drought stress (Rizhsky 2002; Kim 2016). Transgenic Arabidopsis plants have been produced in one experiment which over expressed Gm WRKY21. These plants have shown to have an improved tolerance to cold stress when related with the wild type plants (Wu *et al.*, 2009). In Arabidopsis, three genes AtWRKY 25, AtWRKY26 and AtWRKY 33 have been found to be important in regulation of resistance to heat stress (Li *et al.*, 2011). Plants require various important elements for their normal growth and development, and if any one of the essential nutrients is missing, it will adversely affect plant's architecture formation as well as its ability to withstand adverse environmental conditions. Several studies have revealed that WRKY TFs played important roles in various signaling pathways in response to nutrient deficiency. AtWRKY 75 is a member of WRKY protein family, which played a significant role in phosphate starvation.

It is strappingly encouraged in plant during deficiency of Pi and conquest of the AtWRKY 75 expression convened the plant's susceptible to Pi stress and reduced Pi uptake during Pi famishment. Appearance of many Pi-starvation associated genes, such as phosphatases, Mt4/TPS1-like genes and high kinship Pi transporters has been reduced in AtWRKY 75 RNAi plants (Devaish *et al.*, 2007). Similarly, WRKY 45 and WRKY 65 from Arabidopsis is important in carbon starvation (Conntento *et al.*, 2004).

Similarly, the expression of 3 So WRKY genes showed noteworthy change in sucrose famished stage in rice suspension cells (Wang *et al.*, 2007). In addition to this, WRKY TFs are also involved in responses such as UV radiations and wounding. The expression of Os WRKY 23 and AtWRKY22, hastened leaf senescence in darkness in Arabidopsis plant. Hence, the fundamental participatory role of WRKY TFs in variety of abiotic stresses is significant in the eukaryotic lineage.

WRKY transcription factors (TFs) role in development process

WRKY proteins play a remarkable role in the biosynthesis of sesquiterpene and starch (Xu *et al.*, 2004) seed size (Luo *et al.* 2005), and embryogenesis (Lagace and Matton 2004), senescence (Ishida *et al.*, 2007), trichome and seed coat development (Jing *et al.*, 2009) (Table 1). Giberellic acid (GA) and absicic acid (ABA) antagonistically regulate the production of a-amylase in aleurone layers, which is important in seed germination (Sun and Gubler, 2004). Studies have revealed that in the aleurone layers, GArepressible pathway and ABA-inducible pathway has been regulated by OsWRKY 51 and OsWRKY 71, respectively (Zhang *et al.*, 2004).

In rice, overexpression of the OsWRKY 31 gene induces constitutive expression of early auxin-response genes (OsCrl1 and OsIAA4 genes), which resulted in the reduction of lateral root formation and root elongation. Hence, the findings concludes that transport and response of auxin signaling in rice have been regulated by OsWRKY 31 (Zhang *et al.*, 2008). In Arabidopsis, AtWRKY 70 and ATWRKY 53 are found to play a dual role as the regulation of senescence and plant pathogen defense. Accelerated leaf senescence has been recorded in overexpressed AtWRKY 53 plants while knock-out plants delayed leaf senescence. Alternatively, AtWRKY 70 knock-out plants hastened leaf senescence. Therefore, AtWRKY 53 and AtWRKY 70 act as positive and negative regulators during leaf senescence, respectively.

NAC

The second major family of plant specific TFs are NAC TFs, named as no apical meristem (NAM), cup-shaped cotyledon (CUC2) and ATAF1 and 2 (Riechmann *et al.*, 2000). They have NAC domain which share DNA binding domain of about 150 amino acids in length. At present, hundreds of NAC genes have been recognized in rice and Arabidopsis (Nakashima *et al.*, 2012). NAC transcription factors have been derived from petunia NAM initially and Arabidopsis CUC2 (Aida *et al.* 1997; Souer *et al.* 1996) and many more have been identified from all the classes of plant families.

The functional analysis of NAC TFs have been available in species such as Arabidopsis due to the availability of plant genome sequence (Hisako *et al.* 2003), soybean (Le *et al.*, 2011), potato (Singh *et al.*, 2013), apple (Su *et al.* 2013), rice (Mohammed *et al.* 2010), foxtail miler (Puranik *et al.*, 2013), wheat (Borrill *et al.*, 2017), maize (Shirigaa *et al.*, 2014), cassava (Hu *et al.* 2015), Chinese cabbage (Ma *et al.* 2014) and melon (Wei *et al.*, 2016). In other eukaryotes, no examples have been recognized to date (The Arabidopsis Genome Initiative, 2000; Riechmann *et al.*, 2000). They serve a variety of important functions in plants, such as development of plant specific organs (Aida *et al.*, 1997), responses to plant hormones (Xie *et al.* 2000), and responses to abiotic stresses such as salinity and drought. NAC proteins are thus evolving as central proteins in plant biology as well as development.

Structure of NAC proteins

The presence of extremely conserved terminal-N domain of NAC is the characteristic property of NAC protein family, which is escorted by diverse C-terminal domains. Recently, it has been revealed that NAC domain of Arabidopsis contains a crystal structure known as abscisic acid-responsive NAC protein (ANAC) (Fig. 2A) (Ernst *et al.*, 2004). It has been found that NAC structure is symmetric homodimer. Antiparallel sheet-b (6-stranded) and 3 a-helices have been present in each monomer. A short anti parallel sheet-b and hydrogen bonds/ salt bonds between Arg and Glu side-chains result in the formation of a dimerization interface. Interestingly, striking resemblance has been found in terms of the alignment of fundamental four strands of the NAC monomer to the four-stranded b-sheet of WRKY domain. The b-strand of NAC sequence and WKATGXD sequence is found to be preserved, that seems to be moderately alike as WRKYGQK motif of the WRKY domain. Charge distribution experiments have shown that this strand is probable to be the interface of DNA-binding. Hence, it can be predicted that NAC is closely related to WRKY (Fig. 2B) (Yamasaki *et al.* 2005). This structure is significant to understand the molecular function of NAC and several interactions, which also includes DNA binding by NAC proteins.

NAC transcription factors role in plants

Development of shoot apical meristem (SAM), floral organs and lateral root development are the important and significant functions performed by these proteins (Souer *et al.* 1996; Xie *et al.* 2000; Aida *et al.* 1997). In low oxygen conditions, AtNAC102 regulates seed germination (Christianson *et al.*, 2009). In *Brassica napus* L., characterization of 9 NACs has been done under numerous biotic and abiotic circumstances to understand the diverse expression patterns (Hegedus *et al.*, 2003). These NACs have been observed to play an active part in both biotic and abiotic stress conditions including dealing with drought, pathogens, cold, salt, and low-oxygen stress. Several proteins have been linked with NAC domains such as viral proteins and RING finger proteins (Xie *et al.*, 2002; Xie *et al.*, 1999; Greve *et al.*, 2003). For example, a NAC *Arabidopsis* protein (ANAC) has been recognized as a contact partner of extra RING protein (Greve *et al.*, 2003). It is also observed that interactions occur between different RING domains and ANAC, which are important in regulating the pathways controlled by the plant stress hormone ABA (abscisic acid). One of the most recent studies conducted in 2012 on rice NAC TFs i.e., ONAC131 and ONAC122 have proved that these two transcription factors are involved in defense response against a fungus namely *Magnaporthe grisea* (Sun *et al.*, 2012).

An improved drought tolerance has been found in overexpressed transgenic rice and Arabidopsis plants with stress-responsive NAC (SNAC) genes. In Arabidopsis, 3 members of NAC, i.e., ANAC072, ANAC055 and ANAC019 bind to the ERD1 promoter in order to produce enhanced drought tolerance (Tran *et al.*, 2004). Similarly, in case of rice, several NACs have been characterized. Studies showed the involvement of SNAC1 in guard cells under drought stress and its over-expression causes improved drought tolerance during anthesis (Hu *et al.*, 2006). Overexpression of OsNAC10 (root specific NAC TF) improves grain yield and drought tolerance in rice (Jeong *et al.*, 2010). Multiple abiotic stress tolerance has been observed due to the overexpression of SNAC2/ OsNAC6, OsNAC045 and OsNAC063 (Nakashima *et al.* 2007; Hu *et al.*, 2008; Zheng *et al.*, 2009). ANAC2 is involved in response to plant hormones, such as 1 aminocyclopropane-1- carboxylic acid, ABA and a-naphthaleneacetic acid (aNAA), salt stress as well as lateral root development (He *et al.*, 2005). Negative role has been observed under drought stress by ATAF1 and ATAF2 along with a barley counterpart HvNAC6 and known to enhance pathogen resistance (Delessert *et al.*, 2005; Lu *et al.*, 2007, Jensen *et al.*, 2007). In tomato, SINAC1 and SINAM1 are involved in salt response (Yang *et al.*, 2010). Overexpression of TaNC2 (originated from wheat and expressed in *A. thaliana*) has been studied to characterize its function. Results revealed that overexpression results in an improved tolerance to salt, drought and freezing stresses in *Arabidopsis* (Mao *et al.*, 2011).

bZIP transcription factors

Transcription factors of basic leucine zipper (bZIP) family are present exclusively in eukaryotes and are considered as one of the largest TFs families in plants. bZIP domain consists of 2 structural features; leucine zipper dimerization region and DNA binding basic region (Hust 1994). It also consists of 60 to 80 amino acids. Alonso *et al.* (2009) are of the view that bZIP genes have been encoded by the genome of most recent ancestors of all plants. The expression of the members of the bZIP TFs family occurs constitutively or in an organ-specific manner (Rodriguez-Uribe and O'Connell 2006), development-dependent (Chern *et al.* 1996), stimulus responsive (de Vetten and Ferl 1995), and cell cycle- specific (Minami *et al.* 1993) manner. In humans, bZIP plays critical roles in reproductive functions, cancer development in epithelial tissues, steroid hormone synthesis in endocrine tissues and ultimately affects human health.

In plants, bZIPs regulate energy homeostasis, photo-morphogenesis, light and stress signaling, leaf and seed formation, biotic and abiotic stress responses, pathogen defense, flower development and seed maturation. In *A. thaliana*, 75 bZIP TFs genes have been designated (AtbZIP1–AtbZIP75) and classified into ten groups according to the sequence similarity of their basic region (Jakoby *et al.*, 2002). Till now, the number of functionally analyzed bZIP TFs are few in *Arabiodpsis*. Initially, the classification of 50 plant bZIP proteins have been done into five families by considering similarities of their bZIP domain (Vottore 1998).

Classification and structure

Members of the bZIP super family bind target DNA-duplex sites as homo-dimers or hetero-dimers that recognize linked but different palindromic sequences. The DNA-binding domain of bZIP is the simplest known protein-DNA recognition motif and entails of a segment that is positively charged (basic region) linked to a sequence of repeats of leucine residues (leucine zipper). The bZIP family dimers form a chopsticks-like structure via dimerization of their leucine-zipper parts and each basic region segment contacts one-half of a palindromic site in the DNA main channel. The bZIP TFs are considered by a 40 to 80-amino-acid-long preserved domain (bZIP domain) that is poised of two motifs: a basic region accountable for specific binding of the TF to its target DNA and a leucine zipper compulsory for TF dimerization (Wingender 2001).

One of the classes of bZIP proteins is connected to stress response and contains of TGA/ octopine synthase (ocs)-element-binding factor (OBF) proteins. These bind to the beginning sequence-1 (as-1)/ ocs element, that control the expression of some stress-responsive genes such as the PR-1 and Glutathione S-Transferase 6 (GST6) genes (Lebel *et al.* 1998; Chen and Singh 1999). TGA/ OBF proteins are originate to vary in their DNA-binding specificity, protein-protein interaction properties and expression patterns (Niggeweg *et al.*, 2000).

bZIP transcription factors role in plants

bZIP proteins have been originated to have a role in stress signaling like salt, drought and UV radiation (Jakoby *et al.*, 2002). Uptill now, bZIP TFs have been extensively used in numerous plants like Arabidopsis, rice, sorghum, maize, tomato, carrot and so on (Riechmann *et al.*, 2000; Jakoby *et al.*, 2002; Zou *et al.*, 2008; Yanez *et al.*, 2009; Ying *et al.*, 2012; Wang *et al.*, 2011; Que *et al.*, 2015). They have been found to be the an essential part in many biological processes, for example organ and tissue differentiation (Abe *et al.*, 2005; Shen *et al.*, 2007; Silveira *et al.*, 2007), cell elongation (Fukazawa *et al.*, 2000), embryogenesis and seed maturation (Lara *et al.*, 2003), energy metabolism (Baena-González *et al.*, 2007) and so on. These TFs are also involved in plant responses to abiotic and biotic stresses, including hormone and sugar signaling, pathogen defense, light response, salt and drought tolerance (Thruow *et al.*, 2005; Kaminaka *et al.*, 2006; Nieva *et al.* 2005; Uno *et al.* 2000; Wellmer *et al*,. 1999; Ulm *et al.*, 2004; Liu *et al.*, 2014; Ying *et al.*, 2012). This fact has been observed with the help of a study which showed the ABRE binding factor (ABF)/ ABA-responsive-element-binding (AREB) proteins respond at the transcriptional and post-transcriptional level to salt and drought stress. These proteins work through ABA-dependent signal transduction pathway (Uno *et al.* 2000; Choi *et al.*, 2000).

ABA hypersensitivity is found in *Arabidopsis* plants and some other ABA-associated phenotypes that overexpress ABF3 or ABF4, which showed a reduced transpiration and an improved drought tolerance due to altered expression of ABA/ stress regulated genes (Kang *et al.*, 2002). In 2002, it has been noticed that the promoter of acyl-CoA oxidase gives positive response to UV radiations, whereas negative response is observed to a pathogen-derived elicitor through an inversely controlled promoter unit containing two almost similar ACGT comprising elements. It is thus predicted that single promoter element is responsible for crosstalk among stress responses in plants. Hence, the complexity of bZIP regulation has been confirmed by screening that pathogen responses over-ride UV protection through an contrariwise associated ACGT-containing element (ACE)/ ACE promoter motif. Fascinatingly, two similar ACE motifs establish both UV-responsive element and a negative elicitor responsive element, permitting plants to eagerly shut off a less significant UV-protection program under pathogen attack (Logemann and Hahlbrock 2002).

Indirectly, several bZIP DNA-binding proteins perform vital roles in the plant defense response. One such study conducted on *Arabidopsis* showed that *Arabidopsis NPR1-interacting protein* (NIP) fits to the TGA/ *ocs* element-binding factor (OBF) family of bZIP factors and have role in the initiation of salicyclic acid (SA)-responsive genes such as PR-1 (Zhou *et al.*, 2001). In 2000, a study on tobacco exposed that tobacco bZIP TFs, TGA2.2, is a major component of the activating sequence-1 (*as-1*)-binding factor (ASF-1) protein. This protein binds to As-1, which is a functionally important element of SA-inducible defense genes such as *PR-1a* (Niggeweg *et al.*, 2000). However, very few literatures are available on the direct induction of bZIP factors by plant pathogens.

In 2002, PPI1's role in plant defense response against pathogen attack has been determined (Sang *et al*., 2002). It is a novel and unique bZIP TF from pepper. Most of the family members of bZIP are directly induced by abiotics such as methyl Jasmontae (MeJA), SA, H_2O_2, ethephon, or ABA but PPI1 is induced by pathogen. Generally, the activation is not caused by abiotic stress factors. Hence, PPI1 acts as a nuclear factor in a signaling pathway that activates plant defense responses at the time of pathogen attack.

Highly coordinated and tightly regulated metabolic changes occur during seed germination and maturation in plants (Gutierrez *et al*., 2007). The role of gene expression in these processes has been tackled from early studies in plant molecular biology with maize (*Zea mays*) Opaque2 (O2) and considered as the first plant TF genes to be characterized and cloned (Hartings *et al*., 1989; Schmidt *et al*. 1990). The important genes involved in seed maturation are well characterized and identified. These are known as MAT (maturation genes) and typically include protein (SSP) genes, such as cruciferin and albumin genes (induced at early or mid-maturation phase). The promoter of MAT genes has shown to consist of cis-regulatory elements which are recognized by corresponding TFs that are linked to the bZIP, MYB, B3, and DOF TF families etc. In 2009, the role of bZIP 53 as a transcriptional regulator of MAT genes has been recognized. It has been suggested that heterodimers containing bZIP 53 participate to produce a dramatic increase in MAT gene transcription. bZIP factors are also involved in regulation of diverse plant-specific phenomena including photo morphogenesis, floral induction and development, and are also involved in stress and hormone signaling. These factors are also involved in organ and tissue differentiation (Waish 1998), nitrogen/ carbon balance control (Ciceri 1999), cell elongation (Yin 1997), unfolded protein response (Lin 2007), energy metabolism (Baena-Gonzalez 2007), light response (Welner 1999), hormone and sugar signaling (Finkelstein 2000), seed storage protein gene regulation (Lara 2003) and osmotic control (Satoh 2004).

Conclusion

Plants are continuously open to different types of abiotic stresses such as drought, flood, high temperature, cold stress, salinity, heavy metal stress, nutrient deficiency and biotic stresses such as attack by different pathogens. To survive with these stresses, plants have changed different mechanisms such as avoidance, tolerance and cellular responses which involve the induction of different stress responsive genes. These genes product can either function in stress tolerance such as chaperons, late embryogenesis abundant proteins (LEA) and catalases, or may be involved in regulation of stress responsive genes, which are widely known as transcription factors.

Transcription factors are involved in the control of plant specific reactions and very fascinatingly, most of them exhibited no noticeable sequence similarity to those of other bacteria or eukaryotes. These transcription factors were have been recognized and categorized according to their DNA binding domains.

They are involved in the regulation of variety of processes in plant's life such as growth, development and stress tolerance etc. In this review, the role of some transcription factors in plant's life has been summarized. Further studies conducted on transcription factors in future will be very helpful in the production of transgenic crop plants, which will help us to give, the world those agricultural products with high yields, better nutritional qualities and stress resistance traits, which can be more helpful to cope with the increasing world's population and decreasing resources.

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