Role of Plant Transcription Factors in Abiotic Stress Tolerance

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1. Introduction

Plants are constantly exposed to a wide range of environmental stresses such as drought, high salt, heat and extremes of temperature. Growth constraints due to these abiotic stresses result in reduced productivity and significant crop losses globally. Drought and salinity affect more than 10% of arable land, which results in more than 50% decline in the average yields of important crops worldwide (Bray et al., 2000). Tolerance or susceptibility to these stresses is also a very intricate event as stress may affect multiple stages of plant development and often several stresses concurrently affect the plants (Chinnusamy et al., 2004). Therefore, the basic mechanisms of abiotic stress tolerance and adaptation have been the area of comprehensive research.

Plants counter adverse environmental conditions in a complex, integrated way depending on the timing and length that allows them to respond and adapt to the existing constraints present at a given time. Plant stress tolerance involves changes at whole-plant, tissue, cellular, physiological and molecular levels. Exhibition of a distinct or a combination of intrinsic changes ascertains the capacity of a plant to sustain itself under unfavorable environmental conditions (Farooq et al., 2009). This comprises a range of physiological and biochemical adjustments in plants including leaf wilting, leaf area reduction, leaf abscission, root growth stimulation, alterations in relative water content (RWC), electrolytic leakage (EL), production of reactive oxygen species (ROS) and accumulation of free radicals which disturb cellular homeostasis ensuing lipid peroxidation, membrane damage, and inactivation of enzymes thus influencing cell viability (Bartels and Sunkar, 2005). Other than these, abscissa acid (ABA), a plant stress hormone, induces leaf stomata closure, thus reducing transpirational water loss and photosynthetic rate which improves the water-use efficiency (WUE) of the plant. Molecular responses to abiotic stress on the other hand include perception, signal transduction, gene expression and ultimately metabolic changes in the plant thus providing stress tolerance (Agarwal et al., 2006).

Several genes are activated in response to abiotic stresses at the transcriptional level, and their products are contemplated to provide stress tolerance by the production of vital metabolic proteins and also in regulating the downstream genes (Kavar et al., 2007). Transcript profiling can be a significant tool for the characterization of stress-responsive genes. Extensive transcriptome analyses have divulged that these gene products can largely be classified into two groups (Bohnert et al., 2001; Seki et al., 2002; Fowler and Thomashow, 2002). First group comprises of genes that encode for proteins that defend the cells from the
effects of water-deficit. These genes mainly include those that regulate the accumulation of compatible solutes (enzymes for osmolyte biosynthesis like proline, betaine, sugars, etc.); passive and active transport systems across membranes (water channel proteins and membrane transporters); and protection and stabilization of cell structures from damage by ROS (the detoxification enzymes such as glutathione S-transferase, catalase, superoxide dismutase, ascorbate peroxidase, etc.); fatty acid metabolism enzymes, proteinase inhibitors, ferritin and lipid-transfer proteins; and other proteins for the protection of macromolecules (LEA protein, osmotin, chaperons, etc.). Another group of genes stimulated by abiotic stresses includes regulatory proteins that further regulate the stress signal transduction and alter gene expression and hence possibly function in stress response. They comprise several transcription factors (TFs) emphasizing the role of various transcriptional regulatory mechanisms in the stress signal transduction pathways; protein kinases (MAP kinase, CDP kinase, receptor protein kinase, etc.); protein phosphatases and proteinases implicated in the regulation of stress signaling and gene expression (Seki et al., 2003; Shinozaki and Yamaguchi-Shinozaki, 2007).

2. Role of transcription factors in abiotic stress responses

Transcription factors (TFs) are proteins that act together with other transcriptional regulators, including chromatin remodeling/modifying proteins, to employ or obstruct RNA polymerases to the DNA template (Udvardi et al., 2007). Plant genomes assign approximately 7% of their coding sequence to TFs, which proves the complexity of transcriptional regulation (Udvardi et al., 2007). The TFs interact with cis-elements in the promoter regions of several stress-related genes and thus up-regulate the expression of many downstream genes resulting in imparting abiotic stress tolerance (Agarwal and Jha, 2010). In Arabidopsis thaliana genome about 1500 TFs are described which are considered to be involved in stress responsive gene expression (Riechmann et al., 2000). Transcriptome data in Arabidopsis and in numerous other plants suggest that there are several pathways that independently respond to environmental stresses (in both ABA dependent- and independent- manner), suggesting that stress tolerance or susceptibility is controlled at the transcriptional level by an extremely intricate gene regulatory network. (Fig.1) (Fowler and Thomashow, 2002; Umezawa et al., 2006).

The phytohormone ABA is the central regulator of abiotic stress particularly drought resistance in plants, and coordinates a complex gene regulatory network enabling plants to cope with decreased water availability (Cutler et al., 2010; Kim et al., 2010). ABA-dependent signaling systems have been illustrated as pathways that mediate stress adaptation by induction of at least two separate regulons (a group of genes controlled by a certain TF): (1) the AREB/ABF (ABA-responsive element-binding protein/ ABA-binding factor) regulon; and (2) the MYC (myelocytomatosis oncogene)/MYB (myeloblastosis oncogene) regulon (Abe et al., 1997; Busk and Pagés, 1998; Saibo et al., 2009). While ABA-independent regulons are: (1) the CBF/DREB regulon; and (2) the NAC (NAM, ATAF and CUC) and ZF-HD (zinc-finger homeodomain) regulon (Nakashima et al. 2009; Saibo et al., 2009). However in addition, several studies have identified the existence of both ABA-dependent and - independent pathways of stress response that function through AP2/EREBP (ERF) family members (Yamaguchi-Shinozaki and Shinozaki, 1994; Kizis and Pagés, 2002). In addition to these well-known regulons, a large number of other TFs are also involved in abiotic stress responses, thereby playing a crucial role in imparting stress endurance to plants. Although
Fig. 1. A schematic representation of transcriptional regulatory networks of cis-acting elements and transcription factors involved in abiotic-stress-responses. Transcription factors are shown in ellipses; cis-acting elements are shown in boxes; and target stress inducible genes are shown in long rectangular box at the bottom.

these different stress responsive TFs usually function independently, it is undoubtedly possible that some level of cross-talk exists between them.

This chapter focuses on these TFs and their role in regulating abiotic stress responses in plants (Table 1) as well as their utility in engineering stress tolerance for crop improvement programs (Table 2).
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### Table 1. Response of transcription factors to various stresses.

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3. The AREB/ABF regulon

A conserved cis-element named as ABA-responsive element (ABRE; PyACGTGG/TC) was identified from the promoters of ABA-inducible genes (Bray, 1994; Giraudat et al., 1994; Busk and Page’s, 1998). Subsequently it was revealed that ABA-responsive gene expression needs multiple ABREs or the combination of an ABRE with a coupling element (CE) as a functional promoter (Yoshida et al., 2010). For example, ABRE and coupling elements, including coupling element 1 (CE1) and coupling element 3 (CE3), constitute an ABA-responsive complex in the regulation of wheat HVA1 and HVA22 genes (Shen et al., 1996). For the expression of RD29B in seeds and vegetative tissues of Arabidopsis, two ABRE cis-acting elements are required (Uno et al., 2000; Nakashima and Yamaguchi-Shinozaki, 2006). The AREB or ABFs are bZIP (basic leucine zipper) TFs that bind to the ABRE motif and activate ABA-dependent gene expression were first isolated in a yeast one-hybrid screening (Choi et al., 2000; Uno et al., 2000). It was reported that in the ABA-deficient aba2 and ABA-

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<th>Family</th>
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<th>Stress Tolerance</th>
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Table 2. Stress response of overexpressing transcription factors in transgenic plants.
insensitive abi1 mutants, the AREB/ABF proteins have less activity while they show an enhanced activity in the ABA hypersensitive era1 mutant of Arabidopsis suggesting that these TFs require an ABA-mediated signal for their activation (Uno et al., 2000). The reason possibly may be an ABA-dependent phosphorylation of the AREB/ABF proteins (Shinozaki and Yamaguchi-Shinozaki, 2007). The 75 AtbZIPs have been divided into 11 groups, and the ABFs/AREBs are classified to group A (Jakoby et al., 2002) which usually act in ABA signaling during seed maturation or stress conditions. Several studies have suggested that ABFs function in different stress response pathways; i.e. ABF1 in cold; ABF2 in salt, drought, heat and glucose; ABF3 in salt; ABF4 in cold, salt, and drought signaling pathways (Kim et al., 2004; Fujita et al., 2005). AREB/ABFs are phosphorylated by ABA-responsive 42-kDa kinases which suggest that ABA-dependent phosphorylation may be involved in activation of AREB subfamily proteins (Uno et al., 2000). These kinases (SnRK2-type) such as OST1/SRK2E in Arabidopsis phosphorylate Ser/Thr residues of R-X-X-S/T sites in the conserved regions of AREB1 (Mustilli et al., 2002; Yoshida et al., 2002; Furihata et al., 2006). AREB/ABF genes are mostly redundant in tissue-specific expression either in vegetative tissues or seeds (Choi et al., 2000; Uno et al., 2000). AREB1/ABF2, AREB2/ABF4, and ABF3 were mainly expressed in vegetative tissues, whereas ABI5 and EEL were expressed during seed maturation and/or germination (Choi et al., 2000; Uno et al., 2000; Bensmihen et al., 2002; Fujita et al., 2005; Nakashima and Yamaguchi-Shinozaki, 2006). Rice homolog TRAB1 and barley homolog HvABI5 activated ABA-responsive gene expression in seeds (Hobo et al., 1999; Casaretto and Ho, 2003). Expression of OsABI5 was stimulated by ABA and high salinity, but was down-regulated by drought and cold stress in seedlings, and its overexpression also improved salinity tolerance in rice (Zou et al., 2008; Nakashima et al., 2009). ZmbZIP17 was up-regulated by drought, heat, ABA and NaCl stress in maize seedlings (Jia et al., 2009).

Overexpression of ABF3 and ABF4 resulted in reduced transpiration and improved drought tolerance (Kang et al., 2002). AREB1/ABF2 was found to be a crucial component of glucose signaling, and its over-expression improved drought stress tolerance (Kim et al., 2004). Overexpressing OsbZIP23, a member of AREB/ABF subfamily can also significantly improve drought and high salinity resistance of transgenic rice at the reproductive stage (Xiang et al., 2008). Enhanced tolerance to drought and heat was also observed in 35S- OsAREB1 transgenic Arabidopsis plants (Jin et al. 2010). The over-expression of the constitutively active form of AREB1 in transgenic Arabidopsis plants showed ABA hypersensitivity and enhanced drought tolerance, and LEA-class genes and ABA- and dehydration-stress-inducible regulatory genes such as linker histone H1 and AAA ATPase were upregulated. Over-expressing SRK2C caused hypersensitivity to ABA, improved drought tolerance and lowered transpiration rate (Umezawa et al., 2004). Overexpression of AtbZIP60 led to improved salt tolerance (Fujita et al., 2007).

4. The MYC /MYB regulon

The MYC/MYB families of proteins are universally found in both plants and animals and known to have varied functions. Both MYC/MYB TFs participate in the ABA-dependent pathway of stress signaling for the upregulation of the abiotic stress responsive genes. The first MYB gene identified was the v-MYB gene of avian myeloblastosis virus (AMV) (Klempnauer et al., 1982). The first plant MYB gene, CI, was identified in Zea mays. It encodes a c-MYB-like TF that is involved in anthocyanin biosynthesis (Paz-Ares et al., 1987).
Wide existence of MYB genes indicates that these are very ancient evolutionarily. A MYB domain is usually composed of one to three imperfect repeats, each with about 52 amino acid residues that adopt a helix-turn-helix conformation intercalating in the major groove of the DNA (Yanhui et al. 2006). Plant MYB proteins are categorized into three major groups: (i) R2R3-MYB having two adjacent repeats; (ii) R1R2R3-MYB having three adjacent repeats; and (iii) MYB-related proteins, usually containing a single MYB repeat (Rosinski and Atchley, 1998; Jin and Martin, 1999; Stracke et al., 2001). The R2R3 family contains the largest number of MYB genes. Yanhui et al. (2006) have reported that there are 198 and 183 MYB genes in the Arabidopsis and rice genomes, respectively.

MYB TFs play important roles in many physiological processes under normal or unfavorable growth conditions (Jin and Martin, 1999; Chen et al., 2006; Yanhui et al., 2006) and also in secondary metabolism (Paz-Ares et al., 1987), cell morphogenesis (H Higginson et al., 2003), meristem formation and floral and seed development (Kirik et al., 1998), cell cycle control (Araki et al., 2004), defense and stress responses (Abe et al., 2003), and hormone signaling (Newman et al., 2004). MYC and MYB TFs accumulate only after ABA accumulation. AtMYB4 (At1g22640), AtMYB6 (At4g09460), AtMYB7 (At2g16720), AtMYB44 (At5g67300), AtMYB73 (At4g37260), AtMYB77 (At3g50060), and AtMYBDC5 (At1g09770) were found to be constitutively expressed in all organs and during all stress treatments (Yanhui et al., 2006). AtMYB2 and AtMYC2 function cooperatively as transcriptional activators in the dehydration- and ABA-inducible rd22 expression (Urao et al., 1993; Abe et al., 2003). According to Denekamp and Smeekens (2003), AtMYB102 integrates dehydration, osmotic, or salinity stress, ABA application, and wound-signaling pathways. AtMYB60 and AtMYB61 are involved in light-induced opening of stomata (Cominelli et al., 2005) and dark-induced closure of stomata, respectively (Liang et al., 2005). AtMYB44, AtMYB73, and AtMYB77 are activated by wounding (Cheong et al., 2002), white-light (Ma et al., 2005), cold stress (Fowler and Thomashow, 2002), and salt stress (Kamei et al., 2005). AtMYB44 and AtMYB77 expression is reduced in fus3 (fusca3), lec1 (leafy cotyledon1), and abi3 (ABA-insensitive3) mutants that are defective in development of dormancy and drought tolerance during late embryogenesis and seed maturation (Kirik et al., 1998). AtMYB44 TF confers abiotic stress tolerance through enhancing stomatal closure in an ABA-independent manner (Jung et al., 2008). Recent studies have shown that AtMYB15 expression is detectable in both vegetative and reproductive organs and is up-regulated by cold and salt stresses (Agarwal et al., 2006). AtMYB15 has been found to negatively regulate freezing tolerance in Arabidopsis with its ability to repress the expression levels of CBF genes (Agarwal et al., 2006). AtMyb41 from Arabidopsis is transcriptionally regulated in response to salinity, drought, cold, and ABA (Lippold et al., 2009). Liao et al. (2008c) identified 156 GmMYB genes of which the expression of 43 genes changed on treatment with ABA, salt, drought and/or cold stress.

Overexpression of MYB15 results in improved drought and salt tolerance in Arabidopsis (Ding et al., 2009). Increased expression levels of AtMYB2, AtMYC2 or both enhance ABA sensitivity and improve osmotic tolerance (Abe et al., 2003). Overexpression of 35S:AtMYC2 and 35S:AtMYB2 and 35S:AtMYC2+AtMYB2 in Arabidopsis induced ABA responsive stress genes and showed an ABA-hypersensitive phenotype with increased osmotic stress tolerance (Abe et al., 2003). Transgenic plants overexpressing AtMyb41 showed dwarf phenotype due to alterations of cell expansion and cuticle integrity and enhanced drought sensitivity (Cominelli et al., 2008). Overexpression of AtMyb75 and AtMyb90 led to increased...
anthocyanin levels (Borevitz et al., 2000; Xie et al., 2006), while Met-derived glucosinolate content of Arabidopsis increased with overexpression of AtMyb28 (Gigolashvili et al., 2007). In contrast, OsMYB3R-2 transgenic plants showed enhanced tolerance to freezing, drought and salt stress and decreased sensitivity to ABA (Dai et al., 2007). Different level of tolerance was imparted by overexpression of OsMYB4 depending on the nature of the host plants. Arabidopsis transgenic plants overexpressing OsMYB4 showed increased chilling and freezing tolerance with a dwarf phenotype (Vannini et al., 2004), the tomato transgenic showed higher tolerance to drought stress (Vannini et al., 2007), whereas increased drought and cold tolerance was observed in the apple transgenic (Pasquali et al., 2008). Overexpression of a SuMYBIR-1 transgene in potato plants improved plant tolerance to drought stress while having no significant effects on other agricultural traits (Shin et al. 2011).

5. The CBF/DREB regulon

The dehydration responsive element binding proteins (DREBs) are important AP2/ERF plant TFs that induce a set of abiotic stress-related genes, thus imparting stress tolerance to plants. These play an important role in the ABA-independent pathways that activates stress responsive genes. The first isolated cDNAs encoding DRE binding proteins, CBF1 (CRT binding factor1), DREB1A and DREB2A were identified through yeast one-hybrid screening from Arabidopsis (Stockinger et al., 1997; Liu et al., 1998). Since then, many DREBs have been isolated from various plants. These proteins specifically bind to and activate the expression of genes regulated by the DRE sequence (5'-TACCGACAT-3') and were first identified in the promoter of the drought-responsive gene rd29A (Yamaguchi-Shinozaki and Shinozaki 1993). DREB1 and DREB2 are two main subgroups of DREB subfamily, involved in two different signal transduction pathways under cold and dehydration respectively. DREB1B/CBF1, DREB1A/CBF3 and DREB1C/CBF2 genes are positioned in consonance on chromosome 4 of Arabidopsis (Gilmour et al., 1998; Liu et al., 1998). Arabidopsis also contains major DREB2 proteins namely, DREB2A and DREB2B (Liu et al., 1998). DREB1/DREB2-homologous genes have also been identified in various cereals and millet crops (Nakashima et al., 2009; Lata et al., 2011).

The DREB TFs contain an extremely conserved AP2/ERF DNA-binding domain throughout plant kingdom. The domain consists of a three-stranded β-sheet and one α-helix running almost parallel to it that contacts DNA via Arg and Trp residues located in the β-sheet (Magnani et al., 2004). Two conserved functional amino acids (valine and glutamic acid) at 14th and 19th residues respectively, exist in the DNA binding domain, which are crucial sites for the binding of DREBs and DRE core sequences (Liu et al., 1998). An alkaline N-terminal amino acid region that serve as a nuclear localization signal (NLS) and a conserved Ser/Thr-rich region responsible for phosphorylation near the AP2/ERF DNA binding domain are also mostly present (Liu et al., 1998; Agarwal et al., 2006). The proteins contain an acidic C-terminal region which might be functional in trans-activation activity (Stockinger et al., 1997).

The activation of these transcripts is organ-specific and comparative to the extent of the stress given. When exposed to salt stress, AhDREB1 was highly expressed in roots but less significantly in stems and leaves (Shen et al., 2003b). It was observed that OsDREB1F was constitutively expressed throughout the plant with highest expression in panicles and callus than in the other tissues (Wang et al., 2008). AtDREB2A accumulated in roots, stems and
leaves under control conditions (Liu et al., 1998). DREB2C expressed in mature embryo and the cotyledons of germinating seedlings (Lee et al., 2010). Almoguera et al. (2009) reported that sunflower HaDREB2 expresses in all vegetative tissues. Chrysanthemum DvDREB2A was expressed in all organs under normal conditions (Liu et al., 2008). SiDREB2, a DREB2 gene accumulated in leaves, roots, young and mature spikelets of foxtail millet indicating its function in developmental pathways also (Lata et al., 2011).

AtDREB1 was induced within 10 min at 4°C (Liu et al., 1998). The transcript of CBF genes was detectable after 30 min at 4°C with highest accumulation at 1 h (Medina et al., 1999). HvDREB1 gene in barley leaves significantly accumulated on salt, drought, and low-temperature treatments (Xu et al., 2009). OsDREB1A and Os-DREB1B were induced early (within 40 min) after cold exposure but not on ABA treatment. OsDREB1A was induced within 5 h of salinity stress whereas OsDREB1C showed constitutive expression (Dubouzet et al., 2003). PNDREB1 strongly responded to low temperature and dehydration (Mei et al., 2009). However, hot pepper Ca-DREBLP1 was quickly activated by dehydration, high salinity and mechanical wounding but not at all by cold stress (Hong and Kim, 2005). The expression of Arabidopsis DREB2A and its homolog DREB2B were stimulated by dehydration and high salinity, but not by cold and ABA (Liu et al., 1998; Nakashima et al., 2000). Similarly, ABA, mannitol and cold treatments had minimal effect on DREB2C expression (Lee et al., 2010). A detailed study of all five rice OsDREB2s showed that OsDREB2A expressed to the highest levels under the control condition, and its expression was increased to some extent by high temperature, drought and high salinity, but not by low temperature treatments. Expression of OsDREB2B was markedly increased after 20 min of high and 24 h of low temperature stress. While the transcript levels of OsDREB2C, OsDREB2E and OsABI4 were low under the control condition and were transiently induced by the abiotic stresses (Matsukura et al., 2010). Wheat TaDREB1 and WDREB2, maize ZmDREB2A, and pearl millet PgDREB2 are responsive to cold stress while foxtail millet SiDREB2 was not (Shen et al., 2003a; Egawa et al., 2006; Agarwal et al., 2007; Qin et al., 2007; Lata et al., 2011). Expression of chickpea CAP2 was induced by dehydration, NaCl, ABA and auxin treatments but not by low temperature, salicylic acid and jasmonic acid (Shukla et al., 2006). The transcript expression of Salicornia brachiata SbDREB2A was stimulated by NaCl, drought and heat stress (Gupta et al., 2010).

Transgenic Arabidopsis plants over-expressing DREB1B/CFB1 or DREB1A/CFB3 show strong tolerance to freezing, drought, and high salinity stresses implying that DREBs/CFBs affect multiple genes (Jaglo-Ottosen et al., 1998; Liu et al., 1998; Kasuga et al., 1999). DREB1A/CFB3 overexpressing transgenics accumulated proline and various sugars under non-stress conditions (Gilmour et al., 2000). Transgenic Arabidopsis and rice plants overexpressing OsDREB1A too displayed tolerance to low temperatures, high salinity and drought (Dubouzet et al., 2003; Ito et al., 2006). The rd29A:DREB1A/CFB3 wheat transgenic showed improved drought stress tolerance (Pellegrineschi et al., 2004). Likewise, the constitutively overexpressing CFB3/DREB1A and AFB3 transgenic rice showed better drought and salinity tolerance without any growth inhibition or phenotypic anomalies (Oh et al., 2005). The overexpression of AhDREB1 accumulated putative downstream target genes and also conferred improved survival rate to transgenic tobacco plants under salt stress as compared to the wild-type plants (Shen et al., 2003b). The over-expression of OsDREB1F greatly enhanced tolerance of plants to high salinity, drought, and low-temperature both in rice and Arabidopsis, thus playing a significant role in plant stress signal transduction (Wang et al., 2008). Microarray analysis of transgenic Arabidopsis plants...
suggested that over-expression of DREB2A-CA induced drought-, salt-responsive and heat-shock (HS)-related genes. These transgenic plants also exhibited enhanced thermotolerance which was significantly decreased in DREB2A knockout plants (Sakuma et al., 2006). Overexpression of DREB2C was also found to activate the expression of many HS responsive genes (Lim et al., 2007). Transgenic Arabidopsis plants overexpressing maize ZmDREB2A were dwarf and also displayed improved drought and heat stress tolerance. Transgenic Arabidopsis plants overexpressing OsDREB2B showed enhanced expression of DREB2A target genes and improved drought and heat-shock stress tolerance (Matsukura et al., 2010). Transgenic tobacco plants overexpressing PgDREB2A showed better tolerance to both hyperionic and hyperosmotic stresses (Agarwal et al. 2010). Transgenic tobacco plants overexpressing CAP2 showed improved growth and development, and tolerance to dehydration and salt stress (Shukla et al., 2006). While its expression in yeast (Saccharomyces cerevisiae) enhanced heat tolerance, with increased expression of heat shock factor 1 (Hsf1) and its target yeast heat shock protein 104 (Hsp 104) suggesting strong evolutionary conservation of the stress response mechanisms (Shukla et al., 2009). In another remarkable study it was described that the recombinant E. coli cells expressing SbDREB2A exhibited better growth in basal LB medium as well as if supplemented with NaCl, PEG and mannitol (Gupta et al., 2010).

These studies indicate that the DREB proteins are important TFs in regulating abiotic stress-related genes and play a critical role in imparting stress endurance to plants.

6. The NAC (NAM, ATAF and CUC) and ZF-HD (zinc-finger homeodomain) regulon

The NAC family of plant-specific TFs is one of the largest in the plant genome, with 106 and 149 members in Arabidopsis and rice, respectively (Gong et al., 2004, Xiong et al., 2005). NAC family TFs contains a highly conserved N-terminal DNA-binding domain and a diversified C-terminal domain (Hu et al., 2008). NAC was derived from the names of the first three described TFs containing NAC domain, namely NAM (no apical meristem), ATAF1-2 and CUC2 (cup-shaped cotyledon) (Souer et al., 1996; Aida et al., 1997). The cis-element of NAC TF [NAC recognized sequence (NACRS)] was also identified in Arabidopsis (Tran et al., 2004).

Numerous studies have examined the involvement of several types of NAC TFs in plant developmental programs (Sablowski and Meyerowitz 1998; Xie et al. 2000; Weir et al. 2004), and disease resistance (Collinge and Boller, 2001; Oh et al., 2005; Nakashima et al., 2007). A few NAC genes were found to be involved in response to various environmental stresses also such as ANAC019, ANAC055, and ANAC072 from Arabidopsis (Tran et al., 2004), and BnNAC from Brassica (Hegedus et al., 2003). SNAC1 is activated mainly in guard cells under dehydration (Hu et al., 2006). AtNAP and its homologs play an important role in leaf senescence in Arabidopsis (Guo and Gan et al., 2006). ERD1 promoter analysis showed that TFs belonging to the NAC family and ZF-HD are important for the activation of the ERD1 (early responsive to dehydration stress 1) gene (Tran et al., 2007). XND1 is expressed in xylem and associated with stress, ABA response and leaf senescence in Arabidopsis (Zhao et al., 2008). In soybean 101 NAC domain containing proteins, identified as functionally non-redundant were involved in response to abiotic stresses and in cell death events whereas GmNAC2, GmNAC3 and GmNAC4 were strongly induced by osmotic stress (Pinheiro et al., 2009). Soybean NACs GmNAC3 and GmNAC4 were also induced by ABA, JA and salinity.
but differed in their response to cold. *GmNAC1*, *GmNAC5* and *GmNAC6* transiently expressed in tobacco leaves, resulting in cell death and enhanced expression of senescence markers. Flavonoid biosynthesis is regulated by *ANAC078* under high-light (Morishita et al., 2009). A rice NAC gene, *ONAC045* was induced by drought, high salt, low temperature, and ABA treatment in leaves and roots (Zheng et al., 2009). The transcription level of *CaNAC1* could be elevated by exogenous SA, ET, and MeJA treatment (Oh et al., 2005). A novel wheat NAC TF, *TaNAC4* was found to be induced in response to cold, salt, wounding, ABA, ethylene and MeJA, suggesting a significant cross-talk between abiotic and biotic stress conditions (Xia et al., 2010). Kim et al. (2008) reported that a salt-inducible *NTL8* (membrane associated NAC) regulates gibberellic acid-mediated salt signaling in seed germination. Very recently a membrane associated NAC TF from foxtail millet was found to be up-regulated in drought, salinity, ethephone and MeJA treatments (Puranik et al., 2011). Several target genes of the *ANAC019*, *ANAC055*, and *ANAC072* transcriptional activators were identified in the Arabidopsis transgenic plants using cDNA microarray. These transgenic plants also exhibited improved drought tolerance (Tran et al., 2004). The *SNAC1*-overexpressing transgenic rice seedlings showed significantly higher survival rate than wild type under drought treatment and significantly enhanced salinity tolerance as well (Hu et al., 2006). A rice *R2R3-MYB* gene (*UG55*) containing putative NACRS in the promoter region was also induced in the *SNAC1*-overexpressing plants (Hu et al., 2006). Many abiotic and biotic stress responsive genes were upregulated in the *OsNAC6* transgenic plants, and the transgenics were tolerant to dehydration, high salt stresses (Nakashima et al., 2007). *ONAC045* overexpressing rice plants showed enhanced tolerance to drought and salt treatments (Zheng et al., 2009). *XND1*overexpressing showed severe stunting, premature death, and repression of TE differentiation (Zhao et al., 2008). Hence NAC TFs play an indispensable role in physiological adaptation for successful plant propagation under abiotic stress conditions.

### 7. Other TFs in abiotic stress response and tolerance

There are a number of TFs which are involved in abiotic stress responses other than the TFs belonging to the well known regulons described above. A new class of homeodomain TF known as **HIGHER EXPRESSION OF OSMOTICALLY RESPONSIVE GENE 9** (*HOS 9*) and a R2R3-type MYB protein *HOS 10* have been identified recently which are found to be associated with cold stress (Zhu et al., 2004, 2005). *hos9* and *hos 10* mutants show freezing hypersensitivity but at the same time enhance expression of *RD29A* and other cold responsive genes without changes in the CBF/DREB1 regulon implicating their role as negative regulators of cold stress-responsive genes. Another homeodomain TF, *HDG11* which codes for HD-START TF plays a significant role in drought tolerance by enhancing the water homeostasis of the plants (Yu et al., 2008). *HARDY* (*HRD*), an AP2-EREBP IIIc TF gene is expressed in inflorescence tissue to protect it from desiccation (Nakano et al., 2006). Rice plants overexpressing *HRD* exhibited drought and salinity tolerance as well as improved WUE (Karaba et al., 2007). ERFs (ethylene responsive factors) also belong to the AP2-EREBP TF and have been found to be involved in growth, development, metabolic regulation and biotic and abiotic stress responses (Hussain et al., 2011). Transgenic tobacco plants expressing *SodERF3* exhibited extremely improved drought and salt tolerance (Trujillo et al., 2008). Zhang et al., (2009) reported that transgenic tobacco plants overexpressing soybean *GmERF3* exhibited tolerance not only to high salinity
and drought stresses but also to various pathogens, suggesting its crucial role in both abiotic and biotic stresses.

WRKYs are another important class of plant TFs which have shown to possess multiple functions in plants including abiotic stress responses. OsWRKY45 in rice was up-regulated by dehydration, cold, heat and salt (Qiu and Yu, 2009). Arabidopsis overexpressing OsWRKY45 also showed improved drought tolerance. They have suggested that OsWRKY45 may be involved in ABA synthesis that induces a signaling cascade resulting in lowered transpiration and enhanced tolerance to drought. Overexpression of the OsWRKY89 in rice led to growth inhibition at early stages of plant development, but showed increased tolerance to UV irradiation and fungal infection (Wang et al., 2007). GmWRKY13, GmWRKY21 and GmWRKY54 were found to be differentially expressed under abiotic stresses (Zhou et al., 2008). Transgenic Arabidopsis plants overexpressing GmWRKY21 were tolerant to cold stress, whereas GmWRKY54 conferred salt and drought tolerance, possibly through the regulation of DREB2A and STZ/Zat10. However, transgenic plants overexpressing GmWRKY13 showed increased sensitivity to salt and mannitol stress, decreased sensitivity to ABA, and an increase in lateral roots. Archana et al., (2009) reported that down-regulation of NbWRKY; an abiotic stress related WRKY TF, by virus-induced gene silencing produced chlorosis and senescing phenotype in tobacco plants.

Zinc finger proteins (ZFPs) are one of the important TFs found abundantly in plants and animals. They contain sequence motifs in which cysteines and/or histidines coordinate zinc atom(s) forming local peptide structures required for their specific functions (Singh et al., 2010). Cys2/His2 (C2H2)-type ZFPs containing the EAR transcriptional repressor domain, play a key role in regulating the defense responses of plants to biotic and abiotic stress conditions (Singh et al., 2010). Over-expression of Alfin1, a novel member of the ZFP family confers salt tolerance to the transgenic Alfalfa plants (Winicov and Bastola, 1999). The constitutive over-expression of soybean SCOF-1 induced cold-regulated (COR) gene expression and transgenic Arabidopsis and tobacco plants (Kim et al., 2001). ZPT2-3, a C2H2-type Petunia ZFP, when constitutively over-expressed in petunia, resulted in dehydration tolerance of transgenic plants (Sugano et al. 2003). OSISAPI from rice was inducible by cold, desiccation, salt, submergence, heavy metals and wounding, and its overexpression in tobacco exhibited cold, dehydration and salt tolerance at the seed germination/seedling stages (Mukhopadhyay et al., 2004). Constitutive expression of Zat12 in Arabidopsis resulted in the increased expression of oxidative- and light stress responsive genes (Davletova et al., 2005). Transgenic Arabidopsis plants constitutively expressing the Zat7 exhibited suppressed growth and were more tolerant to salinity stress (Ciftci-Yilmaz et al., 2007). CaZF, a C2H2 ZFP provided salinity-tolerance in transgenic tobacco (Jain et al., 2009). Interestingly, heterologous expression of CaZF provided osmotolerance in S. cerevisiae through Hog1p and calcineurin dependent as well as independent pathways (Jain et al., 2009).

8. Conclusion and future perspectives

In response to abiotic stresses such as, drought, salinity, heat, cold and mechanical wounding many genes are regulated, and their gene products function in providing stress tolerance to plants. Understanding the molecular mechanisms of plant responses to abiotic stresses is very important as it facilitates in exploiting them to improve stress tolerance and productivity. This review summarizes the role of important plant TFs namely; ABRE,
MYC/MYB, CBF/DREBs and NAC that regulate various stress responsive gene expression. They play a crucial role in providing tolerance to multiple stresses generally in both ABA-dependent and -independent manner and through respective cis-elements and DNA binding domains. These TFs can be genetically engineered to produce transgenics with higher tolerance to drought, salinity, heat and cold using different promoters. Functional analysis of these TFs will thus provide more information on the intricate regulatory networks involved in abiotic stress responses and the cross-talk between different signaling pathways during stress adaptation. Further, considering TFs as candidate genes in breeding and other crop improvement programs will give us a clear understanding of abiotic stress related signal transduction events and eventually will lead us to develop crop varieties superior in stress tolerance by genetic manipulation.

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10. References


Role of Plant Transcription Factors in Abiotic Stress Tolerance


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