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Modulating the Expression of Transcription Factors: An Attractive Strategy for Raising Abiotic Stress Tolerant Plants

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ABSTRACT

Plants, being sessile, are strongly influenced by abiotic stress such as high salt, drought, high temperature and freezing. These factors cause metabolic toxicity, membrane disorganization, closure of stomata, decreased photosynthetic activity, generation of reactive oxygen species (ROS) and altered nutrient acquisition. In order to meet the increasing demands for plant-based agricultural commodities, it would be imperative to enhance productivity of crop plants. It is well established that tolerance to abiotic stresses is mediated by a number of biochemical reactions and physiological processes, which essentially means that it is a 'multigenic' trait. A large number of stress related genes are expressed in an 'orchestrated manner' to bring about this stress response. For this 'stress-responsive' unique gene expression network to accrue, transcription factors play a very crucial role. Improvement in stress tolerance through engineering of transcription factors genes is emerging as an attractive strategy in recent years. The global expression analyses have also uncovered hundreds of genes encoding transcription factors that are differentially expressed under environmental stresses, thus implying that various transcriptional regulatory mechanisms are involved. Transcription factors often comprise families of related proteins that share a homologous DNA binding domain such as ERF, bZIP, MYC, MYB, NAC and WRKY binding transcription factors. There are several reports where increased tolerance has been achieved through the overexpression of selected transcription factor(s). The manipulation of a transcription factor can control a broad range of downstream events; therefore can combat abiotic stress efficiently. This review presents a brief description of important transgenic studies which have been attempted with a view to understand the role of various transcription factors towards abiotic stress tolerance in plants.

Keywords: abscisic acid responsive binding element, abiotic stress, salt stress, transcription factor

Abbreviations: ABRE, abscisic acid responsive binding element; **bZIP**, basic-domain leucine-zipper; **COR**, cold regulated; **DREB/CBF**, dehydration responsive element binding factors/C-repeat binding factor; **ERF**, ethylene responsive factor; **KIN**, cold induced; **MYB**, myeloblastosis oncogene; **MYC**, myelocytomatosis oncogene; **MYBR**, MYB recognition site; **MYCR**, MYC recognition site; **NAC**, NAM, ATAF and CUC; **PlnTFDB**, plant transcription factor database; **TF**, Transcription Factor

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INTRODUCTION

The challenge of maintaining a balance between mounting population and the capacity to produce food is increasing day by day. The world population is estimated to reach about 10 billion by 2050, which will witness serious food shortages. Plants experience various environmental stresses like drought, flooding, salinity, high and low temperatures,

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high light, oxidative stress and heavy metal toxicity along with pathogens like bacteria, fungi, viruses resulting in significant crop loss. Among the biotic and abiotic stresses, abiotic stress is the principle cause of crop loss worldwide, which accounts for more than 50% loss of average yield of major crops (Bray *et al.* 2000).

Abiotic stresses alter the cellular metabolic pathways such as inhibition of cell division, photosynthesis, cellular respiration, alteration of gene regulation, which leads to the altered morphology and physiology of plants. Particular environmental conditions may affect specific mechanisms e.g. low temperature harshly hampers reproductive development and exposure of rice plants to chilling temperature at anthesis (floral opening stage) leads to male sterility (Mamun *et al.* 2006). Extreme cold stress mainly results in disruption of membrane integrity and solute leakage, leading to severe cellular dehydration and osmotic imbalance (Thomashow 1999). Due to these alterations, various phenotypic symptoms appear in plants like reduced leaf expansion, wilting and chlorosis, which may eventually lead to necrosis. On the other hand, the fundamental physiology of high salt stress and drought stress overlap with each other. High salt depositions in soil generate a low water potential making it increasingly difficult for the plant to acquire both water as well as nutrients. Therefore, salt stress essentially results in a water deficit condition in the plant and takes the form of a physiological drought. Salinity is caused by the presence of elevated levels of different salts such as sodium chloride, magnesium and calcium sulphates and bicarbonates in soil and water (Ouda 2008). Salinity results in a reduction of K^+ and Ca^{2+} content and an increased level of Na^+, Cl^- and SO_4^{2-}, which forms its ionic effects (Mansour *et al.* 2005). Salinity stress induces cellular accumulation of hydroxyl radicals, which react with all components of the DNA molecule, including the purine and pyrimidine bases and the deoxyribose backbone (Khan and Panda 2008). High levels of Na^+ or high Na^+/K^+ ratio can disrupt various enzymatic processes in the cytoplasm by inducing changes in contents and activities of many enzymes (Khan and Panda 2008). Soluble protein contents of leaves have also been documented to decrease in response to salinity (Parida *et al.* 2002). Due to all the above mentioned reasons, there is eventually stunting of plants (Takemura *et al.* 2000) and considerable decrease in the fresh and dry weights of leaves, stems and roots (Chartzoulakis and Klapaki 2000). Reactive oxygen species (ROS) normally acts as a signaling molecule but its increased production is a common consequence of exposure to drought, salinity and low temperature. ROS causes photo-oxidative damage, peroxidation and de-esterification of membrane lipids as well as protein denaturation (Bowler *et al.* 1992).

As we know, abiotic stress tolerance is a complex and multigenic phenomena involving orchestrated functioning of different category of genes starting from signaling to regulation of expression of genes to different functional component for alleviating environmental stresses in plant. Interestingly, it has been observed that most of the crop species are relatively more sensitive to stress than their wild relatives. In light of these observations, it is quite pertinent to mention that to develop abiotic stress tolerant plants; the prime exercise is to understand the molecular interactions between various components of abiotic stress response machinery. Inhibition of vegetative growth and reproductive development is the first general response of plants to stress, which invests all their resources to survive under these adverse environmental conditions (Zhu 2001). Depending on the extent of stress, plants try to adapt to the changing environmental conditions. Although, most of the biochemical factors necessary for stress tolerance are present in all species, the difference is how fast this machinery is activated, and how the stress is perceived and how the signals are further transduced into a series of responses (Mizoguchi *et al.* 2000). In addition to external abiotic signals, a variety of internal signals such as hormones and solutes also modify plant cell growth and development. A cascade of complex events involving several interacting components for signal recognition and subsequent transduction of these signals to the physiological response is triggered. The complex stress-induced changes in physiology and growth of the plants are often the result of altered patterns of gene expression.

Among various components of stress responsive cascades, transcription factors (TFs) are the master regulators that control gene clusters. Plants devote a large portion of their genome capacity in transcription e.g. around 2000 transcription factors coding genes are present in the *Arabidopsis* genome. Identifying stress responsive TF is a crucial step towards generating abiotic stress tolerant plant, because a single TF can control expression of many target genes through specific binding of the TF to the *cis*-acting element in the promoters of downstream target genes. TFs induce (activators) or repress (repressors) the activity of the RNA polymerase, thus regulating gene expression. TFs can be grouped into families according to their DNA-binding domain (Riechmann *et al.* 2000). A group of genes controlled by a certain type of TF is known as a regulon. In the plant response to abiotic stresses, at least four different regulons can be identified and grouped on the basis of ABA sensitivity. First group includes two regulons, which are ABA independent, namely the C-repeat binding factor/dehydration responsive element binding protein (CBF/DREB) regulon and the NAM, ATAF and CUC (NAC) regulon. The second group includes two ABA-dependent regulons such as the ABA-responsive element-binding protein/ABA-binding factor (AREB/ABF) regulon and the myelocytomatosis oncogene (MYC)/myeloblastosis oncogene (MYB) regulon.

In the present review, we focus on effect of abiotic stress like dehydration, cold and especially high salinity on plant growth and development and role of ABA and transcription factors in the regulation of gene expression under these stresses. Finally, we discuss about DREB1/CBF, MYC/MYB, AREB/ABF (bZIP) and NAC regulon under abiotic stress and stress tolerance due to its over expression in model as well as crop plants.

PLANT RESPONSE TOWARDS ENVIRONMENTAL STRESSES

Plants being sessile, respond remarkably to mitigate environmental stresses. The crop response to abiotic stresses involves a simultaneous synthesis and/or activation of various proteins, enzymes, nucleotides and redistribution of simple solutes, etc. Shinozaki *et al.* (2003) have identified stress inducible gene products in *Arabidopsis* through microarray analysis that can be broadly classified into two groups: one is the group of functional proteins and other is the group of regulatory proteins. Functional proteins are directly involved in different stress responses and the related corrective measures to protect the cell from stress, such as membrane protein (sensor), channels and transporters for osmotic balance, proteins involved in stability of macromolecules e.g. heat shock proteins (HSPs), late embryogenesis abundant proteins (LEA proteins), enzymes involved in detoxification, osmotin and antifreeze proteins, etc. The second group of proteins i.e. regulatory proteins includes various protein kinases, protein phosphatases, enzymes involved in phospholipid metabolism, signaling molecules (calmodulin-binding protein) and transcription factors (regulation of stress dependent gene expression), etc. Regulatory proteins like transcription factors (DREB, NAC, MYB/MYC, ABRE) are very important for expression of stress inducible genes (RD29A, LEA, COR, KIN) under drought, cold or high salinity stress (**Fig. 1**). The transcription factors interact with *cis*-elements present in the promoter region of various abiotic stress-related genes and thus up-regulate the expression of many genes resulting in imparting tolerance towards abiotic stresses. Thus, transcription factors are powerful tools for genetic engineering as their over expression can lead to the up-regulation of a

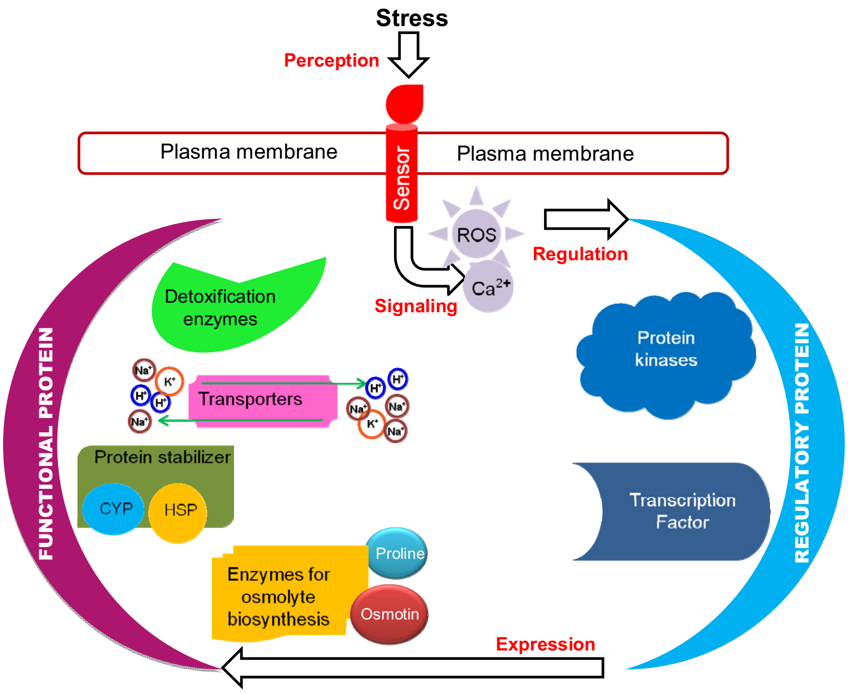

Fig. 1 Plant response towards environmental stresses. Plant cells perceive stress signals through various sensors (not yet known completely), and the signals are transduced by various signaling pathways involving many secondary messengers, molecules, hormones etc. Different regulatory proteins like kinases, phosphatases and transcription factors control stress-inducible gene expression. Various functional proteins protect the cell from damage by stresses.

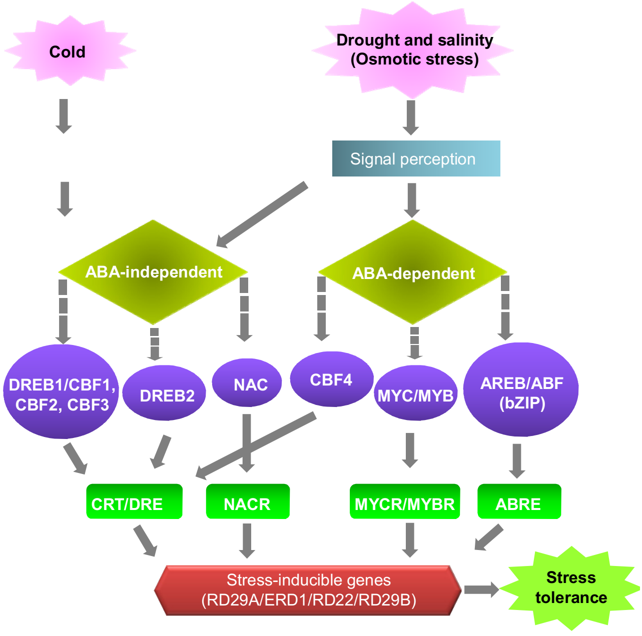

Fig. 2 A schematic representation of cellular signal transduction pathways and transcription factors involved in abiotic-stress-responses. Transcription factors are shown in oval box; *cis*-acting elements are shown in rectangular boxes; and target stress inducible genes are shown in pointed end box at the bottom of diagram. ABA-independent pathway includes two regulons i.e. DREB/CBF and NAC regulon. In DREB/CBF regulon, DREB1, CBF-1, 2 and 3 are induced by cold stress, whereas DREB2 are induced by osmotic stress. ABA-dependent pathway includes mainly two regulons i.e. MYC/MYB and bZIP regulon induced by dehydration/salt stress. CBF4 (a DREB/CBF member) exceptionally falls in ABA-dependent pathway. DREB1/CBF and DREB2 bind to DRE/CRT, MYC/MYB to MYCR/MYBR, NAC to NACR and bZIP to ABRE *cis*-acting elements. DRE: drought responsive element, ABRE: abscisic acid responsive binding element, MYBR: MYB recognition site, MYCR: MYC recognition site, bZIP: basic-domain leucine-zipper.

whole array of genes under their control. Recent research has identified several transcription factors, details for which are presented in the later part of text.

In plants, the acclimation/adaptation process towards abiotic stress is, in large part, mediated by the plant hormone abscisic acid (ABA). The hormone level increases under common stress conditions to trigger metabolic and physiological changes. Most of the stress-inducible genes are controlled by abscisic acid (ABA), but some are not, indicating the involvement of both ABA-dependent and ABA-independent regulatory systems in stress-responsive gene expression (Zhu 2002; Yamaguchi-Shinozaki and Shinozaki 2005). Several stress inducible genes, such as RD29A and COR15A, are induced through the ABA-independent pathway. This situation necessitates the involvement of TFs in stress response both in presence and absence of ABA as shown in **Fig. 2**. Details pertaining to this aspect are also presented in the later part of the text.

TRANSCRIPTION FACTORS AS KEY REGULATORY MOLECULES OF PLANT RESPONSE TOWARDS STRESSES

Transcription, the first step in the expression of any gene, plays a central role in the regulation of the expression of genes, which is controlled by numerous transcription factors that mediate the effects of various signals. Therefore, the analysis of transcription factors is essential for understanding of mechanisms of gene expression and the adaptation process of plants to their environment and is preferred target for engineering of complex agronomical traits of interest. Transcription factors are the proteins interacting with the specialized DNA sequence of eukaryotic promoters or the protein having structural characteristics of known DNA-binding regions, whose main function is to activate or suppress transcriptional effect of corresponding genes (Shao *et al.* 2005). Plant transcription factor contains the following essential structural features:

1. A DNA-binding region
2. An oligomerization site
3. A transcription-regulation domain
4. A nuclear localization signal

Most transcription factors exhibit only one type of DNA-

Table 1 Plant-specific transcription factor databases.

Database	Species	References
RARTF	*Arabidopsis*	Lida *et al.* 2005
DATF	*Arabidopsis*	Guo *et al.* 2005
RARTF	*Arabidopsis*	Lida *et al.* 2005
AtTFDB	*Arabidopsis*	Palaniswamy *et al.* 2006
GRASSIUS, GrassTFDB	*Brachipodium*, *Oryza sativa*, *Sorghum bicolor*	Yilmaz *et al.* 2009
SoybeanTFDB	*Glycine max*	Mochida *et al.* 2009
SoyTFKB	*Glycine max*	Chen 2009; Wang *et al.* 2010
LegumeTFDB	*Glycine max*, *Lotus japonica*	Mochida *et al.* 2010
TOBFAC	*Nicotiana tabacum*	Rushton *et al.* 2008
DRTF	*Oryza sativa*	Gao *et al.* 2006
DPTF	*Populus*	Zhu *et al.* 2007
wDBTF	*Triticum* spp.	Romeuf *et al.* 2010
PlnTFDB	20 plant species	Riano-Pachon *et al.* 2007
PlantTFDB 2.0	50 plant species	Zhang *et al.* 2011
DBD	>700 species	Wilson *et al.* 2008
PLACE	Vascular plants	Higo *et al.* 1999

binding and oligomerization domain, occasionally in multiple copies. DNA-binding regions are normally adjacent to or overlap with oligomerization sites, and their combined tertiary structure determines critical aspects of transcription factor activity. Pairs of nuclear localization signals exist in several transcription factors, and basic amino acid residues play essential roles in their function, this is also true for DNA-binding domains.

Post-translational modifications also affect binding of transcription factors to DNA. Regulation of transcription factor binding to DNA via protein phosphorylation and dephosphorylation may determine the expression of many target genes, including those that encode transcription factors. Both external and internal stimuli affect the regulatory mechanisms. For example, serine residues in the DNA-binding domain of the bZIP transcription factor HBP-1a (Foster *et al.* 1994) are phosphorylated in a Ca^{2+}-dependent manner (Meshi *et al.* 1998) while phosphorylation of another bZIP TF, Opaque2, is controlled by a circadian-clock-related mechanism (Ciceri *et al.* 1997). Till now, hundreds of transcriptional elements of environmental stress-responsive genes in higher plants have been isolated, which regulate and control the stress reaction related to drought, salinity, cold and heat (Glombitza *et al.* 2004).

EVOLUTION OF TRANSCRIPTION FACTORS AND THEIR GENE FAMILIES

The evolution of many morphological traits during the domestication of plants has been associated with changes in TFs. Any minor change in TF regulation, their sequences or their target DNA sequences can greatly alter gene regulatory networks, and plant physiology or morphology and structural changes to these genes may represent a significant evolutionary force (Clark *et al.* 2006). Hence, TFs are given adequate emphasis while creating varieties with a better tolerance to diverse stresses. Transcription factor genes of the same family but from diverse eukaryotic organisms show structural and functional similarity, suggesting that they evolved from a common ancestor. Gene duplication played an important role during this evolution (Kerstetter *et al.* 1994). After duplication, transcription factor gene distribution may be altered through translocation and related family members are either dispersed throughout the genome or clustered on one chromosome (Janssen *et al.* 1998). Sequence alignment of transcription factor genes indicates that nucleotide substitution played a central role in the evolution of conserved regions, whereas substitutions and small insertions/deletions contributed to variable region diversification (Purugganа and Wessler 1994). In addition, exon capture through recombination of different genes or parts thereof formed new transcription factor genes (Chen *et al.* 1997). Sequence comparisons suggest that homeodomain leucine zipper genes, homeodomain ring-finger genes (Schindler *et al.* 1993), bHLH (basic helix-loop-helix) leucine zipper genes (Kawagoe and Murai 1996) and HMG-finger genes (Christiansen *et al.* 1996) originated through exon capture.

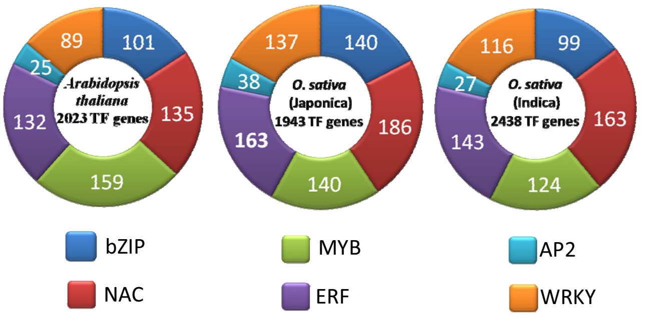

Fig. 3 Total number of genes coding for transcription factors in *Arabidopsis* and *Oryza sativa*. Total number of genes encoding TFs is shown in the centre of the pie chart while number of genes encoding various types of transcription factors (bZIP, NAC, MYB, ERF, AP2 and WRKY) are depicted in the periphery of the circle.

TFs gene families vary considerably in size among different organisms (Riechmann *et al.* 2000; Wray *et al.* 2003). AP2-ERF (Apetlla2-ERF), NAC, Dof (DNA binding with one finger), YABBY, WRKY, GARP, TCP, SBP, ABI3-VP1 (B3), EIL and LFY are plant-specific TFs. MYB, MADS box, bHLH, bZIP and HB, which are not plant specific families, also form large families. NAC, which is one of the largest family of transcription factors (Olsen *et al.* 2005) specifically found in plants. Dozens of transcription factors are involved in the plant response to abiotic stress (Bartels and Sunkar 2005; Vincour and Altman 2005). Most of these TFs fall into several large transcription factor families, such as AP2/ERF, bZIP, NAC, MYB, MYC, Cys2His2 zinc-finger and WRKY (Umezawa *et al.* 2006). These TFs can be classified into several families based on the structure of their binding domains. Various TFs databases are now available for many plant species including crop plants (**Table 1**). PlnTFDB (2.0) is a public database where various TF gene families have been identified and catalogued in different plant species (**Fig. 3**). Among a number of TFs listed (Gosal *et al.* 2009), members of the MYB, MYC, ERF, bZIP and WRKY transcription factor families have already been implicated in the regulation of stress responses (Schwechheimer *et al.* 1998; Singh *et al.* 2002). Therefore, these are attractive targets for the purpose of gene regulation and manipulation of the regulatory elements, which may be beneficial for improving tolerance of plants toward abiotic stresses.

Table 2 Predicted number of genes coding for transcription factor in various plant species.

Plant species	Genome size (Mb)	Total number of chromosomes	Total number of predicted genes	Total number of predicted genes coding for TFs	Predicted % of genes coding for TFs
Arabidopsis	145	n=5	32825	2304	7.0
Glycine max	1115	n=20	66153	5557	8.4
Medicago truncatula	500-550	n=8	38835	473	1.2
Oryza sativa japonica	430	n=12	67393	1913	2.8
Populus	550	n=19	45555	2758	6.0
Sorghum bicolor	730	n=10	36338	2464	6.7
Zea mays	2400	n=10	125435	5383	4.2

GENOME-WIDE DISTRIBUTION OF TRANSCRIPTION FACTORS: *IN SILICO* STUDY

Recent progress in plant genomics has allowed us to discover and identify important genes that regulate yield and tolerance to environmental stress. The whole genome sequencing of *Arabidopsis thaliana* was completed in 2000 (The *Arabidopsis* Genome Initiative 2000). The genome sequencing project of japonica rice was completed in 2005 (International Rice Genome Sequencing Project 2005; Itoh *et al.* 2007). In the past decade, with the availability of complete genome sequences, we have been able to compile catalogs describing the function and organization of TF regulatory systems in a number of organisms. There are many databases that provide data sets of genes putatively encoding TFs in many plant species; these are usually predictions based on computational methods such as sequence similarity search and/or Hidden Markov Model search of conserved DNA-binding domains. Plant genomes contain a large number of transcription factors; for example, *Arabidopsis* and rice dedicates 7.4% and 6.58% of their genome coding for 2304 and 4432 TFs, respectively (**Table 2**) (Riano-Pachon *et al.* 2007; Libault *et al.* 2009).

High-throughput expression profiling, such as microarray technology, has been used widely to study abiotic stress responsive machinery in plants. Genome-wide transcript profiling with *Arabidopsis* has identified many genes that are regulated by cold, salt and drought stress. Similar studies have also been conducted with crop plants such as rice, barley, maize and soybean. Transcriptional profiling of chickpea using a cDNA microarray revealed that 109, 210 and 386 genes were differentially regulated after drought, cold and high-salinity treatment, respectively (Mantri *et al.* 2007). It has been suggested that as many as 30% of the genes in *Arabidopsis* genome may be affected by abiotic stress at the transcript level (Feng *et al.* 2005). About 45% of *Arabidopsis* TFs are plant-specific, whereas the rest of them share DNA-binding domains common to other eukaryotes (Riechmann *et al.* 2000). There are >4000 transcription factor gene loci occupying 8.4% of non redundant gene loci in soybean genome, more than a double of that in *A. thaliana* (Mochida *et al.* 2009). Categorizing the annotated loci according to Gene Ontology (GO) terms suggests that more than 500 transcription factors in soybean would probably respond to osmotic stresses (Mochida *et al.* 2009). These studies suggest that TFs are critical regulators of the changes in gene expression and environmental stress responses.

TRANSCRIPTION FACTORS: USEFUL TARGETS FOR IMPROVING STRESS TOLERANCE

Transcription activators and repressors both have been shown to participate in conferring abiotic stress tolerance (Abe *et al.* 2003; Sakuma *et al.* 2006). Over expression of the genes that regulate the transcription of a number of down-stream stress responsive genes seems to be a promising approach in the development of stress-tolerant transgenic plants when compared to engineering individual functional genes (Bartels and Hussain 2008). The novelty as well as importance of this approach stem from the fact that the *cis*-acting promoter sequences of different stress-responsive genes induced in response to the same stress are similar to an extent and thus can possibly be governed at the same time by modulating the transcriptional factor gene (Wasilewska *et al.* 2008). The best characterized transcription factor genes, which have been shown to have a definite role in stress tolerance are the AREB1 (ABA responsive element binding protein1), ABF2 (ABA responsive binding factor 2), DREB (dehydration responsive binding protein) genes, MYB genes and bZIP encoding genes (Umezawa *et al.* 2004). **Table 3** and **4** describes the list of TFs, which are induced under abiotic stresses and for improving stress tolerance in various plants, respectevely.

On the basis of involvement of ABA, these genes can be grouped in four regulons:

I. ABA-independent regulons are:
(1) CBF/DREB regulon
(2) NAC regulon
II. ABA-dependent regulons are:
(1) AREB/ABF regulon
(2) MYC /MYB regulon.

TRANSCRIPTION FACTORS INVOLVED IN ABA-INDEPENDENT PATHWAY

CBF/DREB Regulon

An important class of transcription factors is the DREB/ CBF that binds to the dehydration responsive element (DRE/CRT) in the promoter of cold and dehydration responsive LEA genes including *rd29A*, *rd17*, *cor6.6*, *cor15a*, *erd10* and *kin1* (Kasuga *et al.* 1999; Yamaguchi-Shinozaki and Shinozaki 1994). Yamaguchi-Shinozaki and Shinozaki (1994) identified DRE/CRT elements, which is a nine base pair conserved sequence (5′-TACCGACAT-3′) from the promoter of a stress inducible *rd29A* gene that is essential for *rd29A* induction under dehydration and cold stress in transgenic *Arabidopsis*. DREB/CBF belongs to the ERF (ethylene responsive element binding factors) family of transcription factors. ERF proteins are a subfamily of the APETLA2 (AP2)/ethylene responsive element binding proteins (EREBP), which are a distinctive feature of plants. On the basis of stress response, DREBs/CBFs are further divided into two subclasses, i.e. DREB1/CBFs and DREB2, which is induced by cold and dehydration stress respectively. Both DREB1/CBFs and DREB2 induces stress responsive genes in ABA-independent manner except CBF4, which is the part of ABA-dependent pathway of stress response (**Fig. 2**). DREB1B/CBF1, DREB1A/CBF3 and DREB1C/CBF2 genes are reported to be present in *Arabidopsis* genome (Gilmour *et al.* 1998; Liu *et al.* 1998). *Arabidopsis* also contain DREB2-like genes, DREB2A and DREB2B (Liu *et al.* 1998). Homologous DREB1/DREB2 genes have also been known in various cereals and millet crops (Lata *et al.* 2011).

In *Arabidopsis*, expression of *DREB1A* was induced by cold, while *DREB2A* was induced by dehydration and salt stress (Liu *et al.* 1998). Expression of CBF1/DREB1B, CBF2/DREB1C and CBF3/DREB1A was induced only by cold stress in *Arabidopsis* (Gilmour *et al.* 1998). Similarly, in *Brassica* the BnCBFs 5, 7 and 16 were induced by cold stress (Gao *et al.* 2002). More recently, the isolation of *BjDREB1B* was reported to be induced by low temperature

Table 3 Induction of transcription factors in various plant species in response to various abiotic stresses.

Gene	Sources	ABA responsive	Stress responsive	Reference
DREB/CBF				
AvDREB1	*Aloe vera*	No	Cold	Wang and He 2007
AtDREB1A	*Arabidopsis thaliana*	No	Cold	Liu *et al.* 1998
AtDREB2A	*Arabidopsis thaliana*	No	Drought, salt	Liu *et al.* 1998
AtDREB2A	*Arabidopsis thaliana*	No	Drought, salt	Liu *et al.* 1998
AtDREB2C	*Arabidopsis thaliana*	No	Salt, osmotic, cold	Lee *et al.* 2010
AtCBF1	*Arabidopsis thaliana*	No	Cold	Gilmour *et al.* 1998
AtCBF2	*Arabidopsis thaliana*	NA	Cold	Gilmour *et al.* 1998
AtCBF3	*Arabidopsis thaliana*	NA	Cold	Gilmour *et al.* 1998
AtCBF4	*Arabidopsis thaliana*	Yes	Drought	Haake *et al.* 2002
PNDREB1	*Arachis hypogea*	No	Drought, cold	Zhang *et al.* 2009
AhDREB1	*Artiplex hortensis*	NA	Salt	Shen *et al.* 2003b
BjDREB1B	*Brassica juncea*	No	Drought, salt, low temperature	Cong *et al.* 2008
BnCBFs 5, 7 and *16*	*Brassica napus*	No	Cold	Gao *et al.* 2002
CaDREBLP1	*Capsicum annum*	No	Drought, salt	Hong and Kim 2005
CAP2	*Cicer arietinum*	Yes	Drought, salt	Shukla *et al.* 2006
DmDREBa	Chrysenthemum (*Dendranthema*×*morifolium*)	Yes	Cold	Yang *et al.* 2009
DmDREBb	Chrysenthemum (*Dendranthema*×*morifolium*)	Yes	Cold	Yang *et al.* 2009
FaDREB1	*Festuca arundinacea*	No	Cold	Tang *et al.* 2005
GmDREBa	*Glycine max*	No	Cold, drought, salt	Li *et al.* 2005
GmDREBb	*Glycine max*	Yes	Cold, drought, salt	Li *et al.* 2005
GmDREBc	*Glycine max*	No	Drought, salt	Li *et al.* 2005
DREB2-type *HvDRF1*	*Hordeum vulgare*	Yes	Drought, salt	Xue and Loveridge 2004
HvDREB1	*Hordeum vulgare*	No	Drought, salt, cold	Xu *et al.* 2009
OsDREB1A	*Oryza sativa*	No	Cold, salt	Dubouzet *et al.* 2003
OsDREB1B	*Oryza sativa*	No	Cold	Dubouzet *et al.* 2003
OsDREB1C	*Oryza sativa*	Yes	Drought, salt, cold	Dubouzet *et al.* 2003
OsDREB1F	*Oryza sativa*	No	Drought, salt, cold	Wang *et al.* 2008
OsDREB2A	*Oryza sativa*	No	Drought, salt, cold	Dubouzet *et al.* 2003
OsDREB2B	*Oryza sativa*	No	Heat, cold	Matsukura *et al.* 2010
OsDREB2C	*Oryza sativa*	No	None	Matsukura *et al.* 2010
OsDREB2E	*Oryza sativa*	No	None	Matsukura *et al.* 2010
PgDREB2A	*Pennisetum glaucum*	No	Drought, salt, cold	Agarwal *et al.* 2007
SbDREB2A	*Salicornia brachiata*	NA	Drought, salt, heat	Gupta *et al.* 2010
SiDREB2	*Setaria italica*	No	Drought, salt	Lata *et al.* 2011
SbDREB2	*Sorghum bicolor*	NA	Drought	Bihani *et al.* 2011
TaDREB1	*Triticum aestivum*	No	Cold, drought	Shen *et al.* 2003a
TaDREB2	*Triticum aestivum*	Yes	Drought, salt, cold	Egawa *et al.* 2006
ZmDREB2A	*Zea mays*	No	Drought, salt, cold, heat	Qin *et al.* 2007
NAC				
ATAF1	*Arabidopsis thaliana*	Yes	Drought	Lu *et al.* 2007
AtNAC055	*Arabidopsis thaliana*	NA	Drought, salt	Tran *et al.* 2004
SNAC1	*Oryza sativa*	NA	Cold, drought, salt	Hu *et al.* 2006
SNAC2	*Oryza sativa*	Yes	Cold, drought, salt	Hu *et al.* 2008
OsNAC6	*Oryza sativa*	Yes	Cold, drought, salt	Nakahsima *et al.* 2007
OsNAC5	*Oryza sativa*	Yes	Cold, drought, salt	Takasaki *et al* 2010
SiNAC	*Setaria italica*	NA	Drought, salt	Puranik *et al.* 2011
TaNAC4	*Triticum aestivum*	NA	Cold, salt	Xia *et al.* 2010
bZIP				
GmbZIP1	*Glycine max*	Yes	Drought	Gao *et al.* 2011
OsbZIP23	*Oryza sativa*	Yes	Drought, salt, PEG	Xiang *et al.* 2008
OsABF1	*Oryza sativa*	Yes	Drought, salt, oxidative stress	Hossain *et al.* 2010
OsABF2	*Oryza sativa*	Yes	Drought, salt, oxidative stress	Hossain *et al.* 2010
OsbZIP72	*Oryza sativa*	Yes	Drought	Lu *et al.* 2009
OsAREB1	*Oryza sativa*	Yes	Drought, heat	Jin *et al.* 2010
Ptr ABF	*Poncirus trifoliata*	Yes	Drought, cold	Huang *et al.* 2010
SlAREB	*Solanum lycopersicum*	Yes	Drought, salt	Hsieh *et al.* 2010
MYC/MYB				
AtMYC2	*Arabidopsis thaliana*	Yes	Drought, salt, cold	Abe *et al.* 2003
AtMYB2	*Arabidopsis thaliana*	Yes	Drought, salt	Abe *et al.* 2003
AtMYB4	*Arabidopsis thaliana*	Yes	Salt	Yanhui *et al.* 2006
AtMYB6	*Arabidopsis thaliana*	Yes	Salt	Yanhui *et al.* 2006
AtMYB7	*Arabidopsis thaliana*	Yes	Salt	Yanhui *et al.* 2006
AtMYB44	*Arabidopsis thaliana*	Yes	Salt	Yanhui *et al.* 2006
AtMYB41	*Arabidopsis thaliana*	Yes	Drought, salt	Lippold *et al.* 2009
AtMYB73	*Arabidopsis thaliana*	Yes	Salt	Yanhui *et al.* 2006
MYB15	*Arabidopsis thaliana*	Yes	Drought, salt, cold	Ding *et al.* 2009
GmMYB76	*Glycine max*	No	Salt	Liao *et al.* 2008b
GmMYB92	*Glycine max*	No	Cold, salt	Liao *et al.* 2008b
GmMYB177	*Glycine max*	No	Drought, salt	Liao *et al.* 2008b
OsMYB3R-2	*Oryza sativa*	NA	Drought, salt, cold	Dai *et al.* 2007

Table 4 Overexpression of stress responsive TFs in plants provide tolerance towards various abiotic stresses. Only representative examples have been shown in the table.

Gene	**Source**	**Transgenic plant**	**Promoter**	**Abiotic stress tolerance**	**Reference**
DREB/CBF					
DREB1A	*Arabidopsis thaliana*	*Oryza sativa*	*Ubi*	Drought and salt	Oh *et al.* 2005
DREB1A	*A. thaliana*	*Triticum aestivum*	*RD29A*	Drought	Pellegrineschi *et al.* 2004
DREB1A	*A. thaliana*	*Arachis hypogaea*	*RD29A*	Drought and oxidative	Bhatnagar-Mathur *et al.* 2009
DREB1A	*A. thaliana*	*Solanum lycopersicum*	*CaMV35S*	Cold and oxidative	Hsieh *et al.* 2002b
DREB1A	*A. thaliana*	*Dendranthema vestitum*	*CaMV35S / RD29A*	Drought, salt and cold	Hong *et al.* 2006a, 2006b, 2006c
DREB1A	*A. thaliana*	*Dendranthema vestitum*	*CaMV35S*	Heat	Hong *et al.* 2009
DREB1A	*A. thaliana*	*Nicotiana tabacum*	*CaMV35S / RD29A*	Drought and cold	Kasuga *et al.* 2004
CBF1	*A. thaliana*	*Solanum tuberosum*	*CaMV35S*	Cold	Pino *et al.* 2008
HRD	*A. thaliana*	*Oryza sativa*	*CaMV35S*	Drought	Karaba *et al.* 2007
HRD	*A. thaliana*	*Trifolium alexandrinum*	*CaMV35S*	Drought and salt	Abogadallah *et al.* 2011
CBF1	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Cold	Jaglo-Ottosen *et al.* 1998
DREB1A / DREB2A	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought and cold	Liu *et al.* 1998
CBF3	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Cold	Gilmour *et al.* 2000
CBF4	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Cold and drought	Haake *et al.* 2002
DREB2A	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought	Sakuma *et al.* 2006
CBF1	*A. thaliana*	*Brassica napus*	*CaMV35S*	Cold	Jaglo-Ottosen *et al.* 2001
DREB1A	*A. thaliana*	*Solanum tuberosum*	*RD29A*	Salt	Celebi-Toprak *et al.* 2005
DREB1A	*A. thaliana*	*Solanum tuberosum*	*RD29A*	Salt	Behnam *et al.* 2006
DREB1A	*A. thaliana*	*Solanum tuberosum*	*RD29A*	Cold	Behnam *et al.* 2007
CBF1-3	*A. thaliana*	*Solanum tuberosum*	*CaMV35S / RD29A*	Cold	Pino *et al.* 2007
DREB1A	*A. thaliana*	Tall fescue	*RD29A*	Drought	Zhao *et al.* 2007
DREB1B	*Brassica juncea*	*Nicotiana tabacum*	*CaMV35S*	Drought and salt	Cong *et al.* 2008
CBF5 / CBF17	*Brassica napus*	*Brassica napus*	*CaMV35S*	Cold	Savitch *et al.* 2005
DREB	*Caragana korshinskii*	*Nicotiana tabacum*	*CaMV35*	Salt and osmotic	Wang *et al.* 2011
CAP2	*Cicer arietinum*	*Nicotiana tabacum*	*CaMV35S*	Drought and salt	Shukla *et al.* 2006
DREB1	*Glycine max*	*Medicago sativa*	*RD29A*	Salt	Jin *et al.* 2010
DREB2	*G. max*	*Arabidopsis thaliana*	*CaMV35S / RD29A*	Salt, drought and cold	Chen *et al.* 2007
DREB2	*G. max*	*Nicotiana tabacum*	*CaMV35S*	Drought	Chen *et al.* 2007
DREB	*Gossypium hirsutum*	*Triticum aestivum*	*Ubi/RD29A*	Drought, salt and cold	Gao *et al.* 2009
DREB1	*G. hirsutum*	*Nicotiana tabacum*	*CaMV35S*	Freezing	Shan *et al.* 2007
DREB1C	*Medicago truncatula*	*Medicago truncatula* and *Hibiscus rosa-sinensis*	*RD29A*	Cold	Chen *et al.* 2010
DREB1	*Oryza sativa*	*Oryza sativa*	*CaMV35S*	Drought, salt and cold	Ito *et al.* 2006
DREB1A	*O. sativa*	*Arabidopsis thaliana*	*CaMV35S*	Cold and salt	Dobouzet *et al.* 2003
DREB1B	*O. sativa*	*Arabidopsis thaliana*	*CaMV35S*	Cold and heat	Qin *et al.* 2007
DREB2B	*O. sativa*	*Arabidopsis thaliana*	*Ubi*	Drought and heat	Matsukura *et al.* 2010
DREB2A	*Pennisetum glaucum*	*Nicotiana tabacum*	*CaMV35S*	Salt and osmotic	Agarwal *et al.* 2010
EREBP1	*Solanum tuberosum*	*Solanum tuberosum*	*CaMV35S*	Cold and salt	Lee *et al.* 2007
NAC					
NAC019	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought	Tran *et al.* 2004
NAC055	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought	Tran *et al.* 2004
NAC072	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought	Tran *et al.* 2004
NAC2	*Arachis hypogaea*	*Arabidopsis thaliana*	*CaMV35S*	Drought and salt	Liu *et al.* 2011
NAC2	*O. sativa*	*Oryza sativa*	*Ubi*	Cold, salt and drought	Hu *et al.* 2008
NAC063	*O. sativa*	*Arabidopsis thaliana*	*CaMV35S*	Salt tolerance	Yokotani *et al.* 2009
NAC6	*O. sativa*	*Oryza sativa*	*CaMV35S*	Dehydration and salt	Nakashima *et al.* 2007
NAC1	*O. sativa*	*Oryza sativa*	*CaMV35S*	Salt and drought	Hu *et al.* 2006
NAC10	*O. sativa*	*Oryza sativa*	*GOS2/RCc3*	Drought, salt and heat	Jeong *et al.* 2010
NAC69	*Triticum aestivum*	*Triticum aestivum*	*Hvdhn4s*	Dehydration	Xue *et al.* 2011
NAC2	*T. aestivum*	*Arabidopsis thaliana*	*CaMV35S*	Drought and salt	Mao *et al.* 2012
bZIP					
ABF2	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought and salt	Kim 2004
ABF3	*A. thaliana*	*Lactuca sativa*	*CaMV35S*	Drought	Vanjildorj *et al.* 2005
AtbZIP24	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Salt	Yang *et al.* 2009
bZIP17	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Salt	Liu *et al.* 2008
ABF3	*A. thaliana*	*Arabidopsis thaliana* and *Oryza sativa*	*CaMV35S*	Drought	Kang *et al.* 2002; Oh *et al.* 2005
bZIP1	*Capsicum annum*	*Arabidopsis thaliana*	*CaMV35S*	Drought and salt	Lee 2006
bZIP	*Lycopersicum esulentum*	*Nicotiana tabacum*	*CaMV35S*	Drought and salt	Seong 2008
bZIP23	*Oryza sativa*	*Oryza sativa*	*Ubi*	Drought and salt	Xiang *et al.* 2008
bZIP72	*O. sativa*	*Oryza sativa*	*CaMV35S*	Drought	Lu *et al.* 2009
ABF	*Poncirus trifoliata*	*Nicotiana tabacum*	*CaMV35S*	Dehydration and drought	Huang *et al.* 2010
bZIP	*Tamarix hispida*	*Nicotiana tabacum*	*CaMV35S*	Salt	Wang *et al.* 2010
MYC/MYB					
MYC2	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Osmotic	Abe *et al.* 2003
MYB2	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Osmotic	Abe *et al.* 2003
MYB15	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought and Salt	Ding *et al.* 2009
MYB44	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Drought	Jung *et al.* 2008

Table 4 (Cont.)

Gene	Source	Transgenic plant	Promoter	Abiotic stress tolerance	Reference
MYC/MYB (Cont.)					
MYB41	*A. thaliana*	*Arabidopsis thaliana*	*CaMV35S*	Osmotic	Lippold *et al.* 2009
MYB3R-2	*Oryza sativa*	*Arabidopsis thaliana*	*CaMV35S*	Salt, cold and drought	Dai *et al.* 2007
MYB4	*O. sativa*	*Arabidopsis thaliana*	*CaMV35S*	Freezing	Vannini *et al.* 2004
MYB4	*O. sativa*	*Arabidopsis thaliana*	*CaMV35S*	Drought	Mattana *et al.* 2005
MYB4	*O. sativa*	*Lycopersicum esulentum*	*CaMV35S / COR15*	Drought	Vannini *et al.* 2007

along with drought and salt stress (Cong *et al.* 2008). In rice, cold stress induced expression of *OsDREB1A* and *OsDREB1B* has been reported, while exposure to salt and dehydration stress could induce expression of *OsDREB2A* (Dubouzet *et al.* 2003). Similarly, ABA, mannitol and cold treatments had negligible effect on expression of DREB2C (Lee *et al.* 2010). Recently, a new member of the DREB family - *OsDREB1F* has been reported from rice, which is induced in response to salt, drought and cold stress (Wang *et al.* 2008). Various DREB homologs, e.g. *GmDREBa*, *GmDREBb* and *GmDREBc* from *Glycine max*, were induced by salt, drought and cold stress (Li *et al.* 2005). A homolog of *DREB2*-type gene found in wheat was found to be induced in response to cold, while dehydration and salt stress had small effect on its expression (Shen *et al.* 2003a). The expression of several DREB homologs i.e. *FaDREB1* (*Festuca arundinacea*), *DREB1* (*Aloe vera*) and *DmDREBa* and *DmDREBb* [Chrysanthemum (*Dendronthema*×*moriforlium*)] were induced by cold stress (Tang *et al.* 2005; Wang and He 2007; Yang *et al.* 2009).

TRANSGENIC PLANTS OVER EXPRESSING DREB/CBF TRANSCRIPTION FACTOR CONFERS ABIOTIC STRESS TOLERANCE

Various model and crop plants have been engineered using DREB transcription factor to provide stress tolerance under unfavourable environmental conditions. Over expression of AtDREB1A under a constitutive promoter conferred enhanced freezing and dehydration tolerance in transgenic *Arabidopsis* (Liu *et al.* 1998) and tobacco (Kasuga *et al.* 2004) plants respectively. DREB1A/CBF3 overexpressing transgenic plant accumulated proline and various sugars under non-stress conditions (Gilmour *et al.* 2000). However, transgenic *Arabidopsis* and tobacco plants showed stunted growth under non-stressed conditions. Detailed analysis of these plants revealed that overexpression of AtDREB1A under constitutive promoter upregulated 12 stress-related genes in plants that showed two-fold higher expression than in control plants. Among these, six genes were known to be stress-related, while the other six were found to have sequence similarities with cold acclimatization proteins (Liu *et al.* 1998). Likewise, in case of 35S::OsDREB1A transgenic *Arabidopsis*, six genes showed two-fold expression compared to that in control plants (Dubouzet *et al.* 2003; Liu *et al.* 1998; Ito *et al.* 2006). In contrast, when AtDREB1A was expressed under stress inducible RD29A promoter instead of constitutive promoter (CaMV 35S), negative effects on plant growth in transgenic *Arabidopsis* and tobacco were diminished under stress condition (Kasuga *et al.* 2004; Liu *et al.* 1998). Similarly, the *RD29A:DREB1A/CBF3* transgenic wheat showed improved drought stress tolerance (Pellegrineschi *et al.* 2004).

In literature, there are only a few reports of transgenic plants for DREB2 genes. Liu *et al.* (1998) first reported AtDREB2A expression in *Arabidopsis*, but they did not notice any stress tolerance in transgenic *Arabidopsis*. A post-translational modification by deleting a portion of the protein between the 135th and 165th amino acid of AtDREB2A is important for its proper functioning, which leads to up-regulation of downstream genes in transgenic *Arabidopsis* (Sakuma *et al.* 2006). Tobacco has been broadly studied for DREB expression under various abiotic stresses. Chen *et al.* (2007) transformed tobacco with GmDREB2 under CaMV 35S promoter. The resultant transgenic tobacco plants showed increased drought tolerance and accumulated 4.5-fold higher proline content. Interestingly, in this case, the constitutive expression did not induce phenotypic abnormalities as previously reported in several plants with constitutive expression of DREB genes. Agarwal *et al.* (2010) reported enhanced osmotic stress tolerance in transgenic tobacco transformed with PgDREB2A from *Pennisetum glaucum*. Due to overexpression of PgDREB2A, transgenic tobacco plants showed 4-fold higher germination as compared to wild type under 200 mM NaCl. In addition to this, transgenic plants exhibited better plant growth in terms of leaf area, root number, root length and fresh weight compared to wild type under both stress conditions. Constitutive expression of AtCBF1 in *Arabidopsis* (Jaglo-Ottosen *et al.* 1998) conferred freezing stress tolerance, while in transgenic tomato, the AtCBF1 expression showed tolerance to drought (Hsieh *et al.* 2002a). Transgenic *Arabidopsis* plants that expressed AtCBF3 showed freezing tolerance, while overexpression of AtCBF4 conferred freezing and dehydration tolerance. Likewise, transgenic *Arabidopsis* plant that expressed GmDREB2 under both constitutive and stress inducible promoters showed drought and salt stress tolerance (Chen *et al.* 2007). Transgenic plants showed high root/shoot ratio that resulted in enhanced water uptake under dehydration conditions. Expression of several CBF-type genes in transgenic canola resulted in freezing tolerance and high photosynthetic activity (Savitch *et al.* 2005). Transgenic *Chrysanthemum* with expression of AtDREB1A showed drought and salt tolerance and accumulated higher proline content and ROS scavenging enzymes activity (Hong *et al.* 2006a, 2006b, 2006c). In this way, various DREBs for different organisms were isolated and transformed under constitutive or stress inducible promoters in rice (*Oryza sativa*) (Oh *et al.* 2005; Ito *et al.* 2006), potato (*Solanum tuberosum*) (Lee *et al.* 2007), tall fescue (*Festuca arundinacea*) (Zhao *et al.* 2007) as well as in wheat (*Triticum aestivum*) (Wang *et al.* 2006). These plants exhibited enhanced stress tolerance by accumulation of proline, LEA protein, soluble sugars as well as enhanced activity of different ROS scavenging enzymes. Genes expressed under constitutive promoter showed growth retardation that can be eliminated by stress inducible promoters like RD29A. From these studies, it can be concluded that DREBs play important role in abiotic stress responses and tolerance in plants.

NAC regulon

The first NAC transcription factor was described fifteen years ago by Souer *et al.* (1996). Now, genomes of a number of plant species have been fully sequenced, revealing the NAC gene family to code for one of the largest families of transcription factors in plants (Shen *et al.* 2009). NAC (NAM, ATAF1/2 and CUC2) domain proteins comprised one of the largest plant-specific TF family represented by ~105 genes in *Arabidopsis* (Ooka *et al.* 2003), ~140 genes in rice (Fang *et al.* 2008) and ~101 genes in soybean genome (Pinheiro *et al.* 2009). Ooka *et al.* (2003) classified the NAC proteins into 18 sub-groups in *Arabidopsis* and *Oryza sativa*, based on their amino acid sequence similarities. NAC proteins are plant-specific transcription factors and more than 100 NAC genes have been identified in *Arabidopsis* and *Oryza sativa* to date. Shen *et al.* (2009)

carried out a genome wide bioinformatics survey on plant NAC domain TFs and identified a total of 1232 NAC proteins from 11 different plant species including 148 NAC TFs from *Populus*.

A NAC transcription factor has the conserved NAC domain in the N-terminal (Ooka *et al.* 2003) as well as a more variable, transcriptional activation or repression region in the C-terminal (Hao *et al.* 2010). NAC domain at the N-terminus, which comprises nearly 160 amino acid residues that are divided into five subdomains (A-E) (Ooka *et al.* 2003). The C-terminal region of NAC proteins, usually containing the transcriptional activation domain, is highly diversified both in length and sequence (Ooka *et al.* 2003). The NAC domain was identified based on consensus sequences from *Petunia* NAM and *Arabidopsis* ATAF1/2 and CUC2 proteins (Aida *et al.* 1997). NAC sub domains D and E are required for DNA-binding ability, while the C-terminal region can function as a transcriptional activation domain (Xie *et al*. 2000; Duval *et al*. 2002). Thirteen *Arabidopsis* and six rice NAC transcription factors have been shown to contain α-helical transmembrane motif in the far C-terminal region, which anchors the NAC protein to intracellular membranes rendering them inert.

NAC proteins play important roles in plant growth, development and hormone signaling (Olsen *et al.* 2005), stress responses (Lu *et al.* 2007) such as drought, salinity and cold shock (Hu *et al*. 2006; Wang *et al.* 2009).

TRANSGENIC PLANTS OVER EXPRESSING NAC TRANSCRIPTION FACTORS CONFERS ABIOTIC STRESS TOLERANCE

Transgenic over expression of diverse NAC factors in species ranging from *A. thaliana* to wheat (Xia *et al.* 2010; Yang *et al.* 2011) show improved drought and salt tolerance. Recently, a NAC gene *SNAC1* (stress-responsive NAC1) was isolated and characterized in rice. *SNAC1*was induced by drought and salinity predominantly in guard cells. *SNAC1* over-expressing transgenic rice plants showed significantly improved drought resistance under field conditions and strong tolerance to salt stress (Hu *et al.* 2006). The cDNA encoding a NAC protein was first reported as the *RESPONSIVE TO DEHYDRATION 26* (*RD26*) gene in *Arabidopsis* (Yamaguchi-Shinozaki *et al.* 1992). *Arabidopsis RD26* encodes a NAC protein and is induced not only by dehydration but also by ABA. Transgenic *Arabidopsis* plants overexpressing *RD26* were highly sensitive to ABA, whereas *RD26*-repressed plants were insensitive (Fujita *et al.* 2004). *OsNAC6* expression was induced by cold, drought, high salinity and ABA. OsNAC6 showed high sequence similarity to the *Arabidopsis* stress-related NAC proteins – ANAC019, ANAC055 and ANAC072 (RD26) (Ooka *et al.* 2003). Ohnishi *et al.* (2005) also reported that *OsNAC6* was induced by cold, high salinity, drought, and ABA. Nakashima *et al.* (2007) showed that many abiotic and biotic stress-responsive genes were upregulated in *OsNAC6*-overexpressing rice plants, and that the transgenic lines were tolerant to dehydration and high salinity. Expression analysis revealed that ONAC045 was induced by drought, high salt, low temperature stresses and abscisic acid (ABA) treatment in leaves and roots. In *Brassica napus*, nine NACs were reported to be differently regulated by biotic and abiotic stresses (Hegedus *et al.* 2003). Three *Arabidopsis* NAC genes, ANAC019, ANAC055 and ANAC072 were shown to bind to the promoter region of ERD1, which was characterized as a stress-responsive gene (Tran *et al.* 2004). Over expression of another NAC gene OsNAC6/SNAC2 in rice resulted in enhanced tolerance to drought, salt and cold during seedling development (Hu *et al.* 2008). Transgenic rice plants over expressing ONAC045 showed enhanced drought and salt tolerance, indicating that ONAC045 played an important role in abiotic stress response and may serve as a potential target for engineering stress tolerant rice. In rice, ONAC5 and ONAC6 transcripts are induced by ABA, drought, and salt stress (Takasaki *et al.* 2010). ONAC5 and ONAC6 activate stress-inducible genes such as OsLEA3 by direct binding to the promoter and they interact *in vitro* suggesting functional dimerization of these TFs (Takasaki *et al.* 2010). Over expression of SNAC1 enhanced salt and drought tolerance in transgenic rice and OsNAC10 improved drought tolerance and grain yield (Hu *et al.* 2006; Jeong *et al.* 2010). OsNAC10-regulated target genes mainly included protein kinases and TFs (AP2, WRKY, LRR, NAC and Zn-finger types) as well as the stress-responsive genes such as cytochrome P450 and the potassium transporter HAK5 (Jeong *et al.* 2010). In *Brassica napus*, nine members of the NAC (BnNAC) were identified for their differential expression after feeding with flea beetle and treatment of cold temperature (Hegedus *et al.* 2003). In *Arabidopsis*, Tran *et al.* (2004) and Fujita *et al.* (2004) reported that three NAC genes ANAC019, ANAC055 and ANAC072 were induced by drought, salinity and/or low temperature and the transgenic *Arabidopsis* plants over-expressing these genes showed improved stress tolerance compared to the wild type. Furthermore, proteins of these genes can bind to the promoter sequences with CATGTG motif (Tran *et al.* 2004). Another stress-related *Arabidopsis* NAC gene is AtNAC2 that can be induced by high salinity, abscisic acid (ABA), aminocyclopropane carboxylic acid (ACC), and naphthalene acetic acid (NAA) has been predicted to be a downstream gene in the ethylene and auxin signal pathways (He *et al.* 2005). Over-expression of AtNAC2 resulted in alteration of lateral root development and enhanced salt tolerance (He *et al.* 2005). Another stress-responsive NAC gene OsNAC6, which is a member of ATAF subfamily (Ooka *et al.* 2003) has been reported for its induction by abiotic stresses and jasmonic acid treatment (Ohnishi *et al.* 2005) and overexpression of this gene in rice resulted in enhanced tolerance to dehydration stresses (Nakashima *et al.* 2007). The SNAC1-overexpressing rice plants also showed improved salt tolerance, further emphasizing the usefulness of this gene in stress tolerance. S*NAC1* over-expressing transgenic rice plants showed significantly improved drought tolerance under field conditions and strong tolerance to salt stress (Hu *et al.* 2006).

TRANSCRIPTION FACTORS INVOLVED IN ABA-DEPENDENT PATHWAY

AREB/ABF (bZIP) regulon

bZIP transcription factors are a class of transcription factors, which are highly conserved and are extensively present in animals, microorganisms, higher plants, green algae, moss and fern. In addition to this, bZIP TFs could also be detected in other organisms such as mammal (*Mus musculus*), non-mammal (*Gallus gallus*), insect (*Drosophila melanogaster*), nematode (*Caenorhabditis elegans*), echinoderms (*Strongylocentrotus purpuratus*), urochordata (*Ciona intestinalis*), yeast (*Saccharomyces cerevisiae*), pathogen (*Ustilago maydis*), protozoa (*Dictyostelium discoideum* and *Leishmania braziliensis*), bacteria (*Bacillus licheniformis* and *Polaribacter dokdonensis*) and archaea (*Hyperthermus butylicus*) and so on. Many plant transcription factors, such as O2 of maize, PosF21 of *Arabidopsis*, HBP-1 of wheat and rice belong to this group.

The bZIP TFs are characterized by a 40 to 80 amino-acid-long conserved domain (bZIP domain) (Wingender *et al.* 2001). Plant bZIP proteins preferentially bind to DNA sequences with an ACGT core. Binding specificity is regulated by flanking nucleotides. Plant bZIPs preferentially bind to the A-box (TACGTA), C-box (GACGTC) and G-box (CACGTG).

The common features of bZIP transcription factors include (Lee *et al.* 2006):

1. A basic region specifically and directly binding to DNA
2. A leucine-zipper for dimerization adjacent to the basic region
3. An acidic activation domain in N-terminus binding to DNA in dimerized forms

Apart from the bZIP domain, bZIPs also contain other conserved domains that may function as transcriptional activators, including proline-rich, glutamine-rich and acidic domains (Liao *et al.* 2008a).

Initially, plant bZIP proteins were classified into five families on the basis of similarities of their bZIP domain (Vettore *et al.* 1998). Later, Correa *et al.* (2008) identified 13 groups of bZIP homologues in angiosperms that represent 34 Possible Groups of Orthologues (PoGOs). The 34 PoGOs may correspond to the complete set of ancestral angiosperm bZIP genes that participated in the diversification of flowering plants. *Arabidopsis thaliana* genome sequence indicated the presence 75 to 77 bZIP proteins representing members of ten groups of homologues on sequence similarity of the basic region (Jakoby *et al.* 2002). Apart from *Arabidopsis*, an additional one group have been identified by Nijhawan *et al.* (2008) in rice and three groups by Correa *et al.* (2008) in multiple green plants indicating a unified classification of angiosperm bZIP genes. The groups were named with letters referring to some of their prominent members (A for ABF/AREB/ABI5, C for CPRF2-like, G for GBF, H for HY5), to protein size (B for big and S for small), or alphabetical. Seven members of group A have been studied (*AtbZIP39/ABI5*, *AtbZIP36/ABF2/AREB1*, *AtbZIP38/ABF4/AREB2*, *AtbZIP66/AREB3*, *AtbZIP40/GBF4*, *AtbZIP35/ABF1* and *AtbZIP37/ABF3*). *Arabidopsis* has about four times as many *bZIP* genes as yeast, worm and human (Meshi and Iwabuchi 1995). bZIP distribution in few plant species shown in **Fig. 3** using PlantTFDB-V2.0. Wang *et al.* (2011) reported that *Sorghum* genome encodes at least 92 bZIP transcription factors. A total of 101, 99, 216, 45 and 108 putative bZIP genes have been detected in *Arabidopsis*, rice, maize, wheat and soybean respectively (PlantTFDB-V2.0; SoyTFKB-2.0). Similarly, about 100 putative bZIP sequences were predicted in the rice genome and classified into 10 sub families (Guo *et al.* 2005).

Generally, bZIP TFs play important roles in various physiological and developmental processes like organ and tissue differentiation (Shen *et al.* 2007), unfolded protein response (Liu *et al.* 2007), plant senescence (Lee *et al.* 2006) etc. On the other hand, accumulated data show that bZIP TFs have also been regarded as important regulators in response to various abiotic stresses and signaling such as salt and freezing stress (Liao *et al.* 2008b), methyl viologen-mediated oxidative stress (Lee *et al.* 2006).

TRANSGENIC PLANTS OVEREXPRESSING bZIP TRANSCRIPTION FACTORS CONFERS ABIOTIC STRESS TOLERANCE

The role of bZIP TFs in drought, high salinity and cold stresses has been established in *Arabidopsis* (Kim *et al.* 2004), rice (Lu *et al.* 2009) tomato (Hsieh *et al.* 2010), soybean (Liao *et al.* 2008c) and pepper (Lee *et al.* 2006). Several cold induced bZIP factors have been reported such as LIP15 from maize (Kusano *et al.* 1995), LIPl9 from rice (Aguan *et al.* 1993) and TBZI7 from tobacco (Kusano *et al.* 1998). In addition, the mlip15 factor has been shown to bind to the maize *Adhl* gene promoter, which is also induced by low temperature. One class of bZIP proteins that is linked to stress responses comprises the TGA/*octopine synthase* (*ocs*)-element-binding factor (OBF) proteins. These bind to the *activation sequence-1* (*as-1*)/*ocs* element, which regulate the expression of some stress-responsive genes such as the *PR-1* and *GLUTATHIONE S-TRANSFERASE6* (*GST6*) genes (Chen and Singh 1999). In *Arabidopsis*, there are seven members of the TGA/OBF family, which play important roles in plant defense, xenobiotic stress responses and development. Most of ABRE binding bZIPs belong to group A, in which the expression of several members could be strongly induced by ABA and abiotic stresses (Jakoby *et al.* 2002; Hu *et al.* 2006; Lu *et al.* 2009). *Arabidopsis* plants that overexpress either ABF3 or ABF4 proteins have ABA hypersensitivity and other ABA-associated phenotypes, have altered expression of ABA/stress regulated genes and exhibit reduced transpiration and enhanced drought tolerance (Kang *et al.* 2002). A bZIP transcription factor from maize designated as ABP9 (ABRE binding protein 9) has been identified, which specifically binds to ABRE2 motif. Transgenic *Arabidopsis* plants constitutively overexpressing *ABP9* showed improved photosynthetic capacity of plants under both stresses (drought and heat stresses) by regulating the photosynthetic pigment composition, elevating carbon-use efficiency and increasing ABA contents. In contrast, transgenic plants of antisense *OsABI5* exhibited increased tolerance to salt and PEG treatment (Zou *et al.* 2008) suggesting its negative regulatory role in stress tolerance. Recently, overexpression of *OsbZIP23* in transgenic rice showed positive role that can regulate the expression of a wide spectrum of stress related genes (up- or down-regulation) in response to abiotic stresses (drought, salinity) through an ABA dependent pathway (Xiang *et al.* 2008). Similarly, alteration of *OsbZIP23* expression can change the expression levels of more than 1000 genes and as a matter of fact, many of these genes are involved in stress responses or tolerance. Another bZIP TF (ThbZIP1) gene was cloned from *T. hispida* and its expression was found to be differentially regulated by various abiotic stresses (Wang *et al.* 2010). Nijhawan *et al.* (2008) reported 37 drought/salinity/cold-regulated *bZIP* genes in rice. The ZmbZIP72 gene expressed differentially in various organs of maize plants and was induced by abscisic acid, high salinity and drought treatment in seedlings. In rice, OsbZIP72 was reported to function as a positive regulator in ABA signal transduction and the seedlings overexpressing OsbZIP72 showed an increased drought tolerance (Lu *et al.* 2009). In rice, overexpression of OsbZIP23, OsbZIP72 and OsAREB1 conferred abscisic acid (ABA) sensitivity and drought tolerance (Xiang *et al.* 2008; Lu *et al.* 2009; Jin *et al.* 2010). The constitutive overexpression of ABF3 in *Arabidopsis* and rice also results in enhanced drought tolerance (Kang *et al.* 2002; Oh *et al.* 2005). Moreover, in rice, overexpression of the positive regulators of ABA signaling, OsbZIP23 and OsbZIP72, enhances abiotic stress tolerance (Xiang *et al.* 2008) and mutants of *OsABF1* are more sensitive to drought and salinity (Hossain *et al.* 2010). The bZIP transcription factor OsABF1 (*Oryza sativa* ABA responsive element binding factor 1) is an ABA responsive element binding factor that enhances abiotic stress signaling in rice. Several members of bZIP family in rice have been identified for their functions potentially related to biotic or abiotic stress response or signaling. For example, *LIP19* is induced by low temperature and may function as a molecular switch in cold signalling in rice (Shimizu *et al.* 2005). *OsBZ8*, another bZIP gene of the family, is rapidly induced by ABA and shows stronger expression in salt-tolerant cultivars than in salt-sensitive cultivars (Mukherjee *et al.* 2006). Zou *et al.* (2008) reported *OsABI5* encodes a protein that can bind to ABRE (G-box) and was suggested to be involved in ABA signal transduction and stress responses.

MYC/MYB regulon

The MYC/MYB families of proteins are diverse in nature and have been reported in both plants and animals and perform multiple functions. Members of this family were first identified in the regulation of anthocyanin biosynthesis (Goodrich *et al.* 1992). Both MYC/MYB transcription factors participate in the ABA-dependent pathway and up regulate various abiotic stress responsive genes. The DNA-binding domain of plant MYB proteins usually consist of two imperfect repeats of about 50 residues (R2, R3), whereas it contains three repeats (R1, R2 and R3) in animals. However, OsMYB3R-2 with three repeats was reported in rice (Dai *et al.* 2007). Different MYB proteins bind to different *cis*-elements present on their target gene's promoter. Mammalian MYBs such as C-MYB, A-MYB, and B-MYB bind to the cognate site T/CAACG/TGA/C/TA/C/T (MBSI). While several plants MYB proteins that bind to

MBSI will also bind to a second site, TAACTAAC (MBSII) (Romero *et al.* 1998). Since, MYC/MYB TF is ABA-dependent; it accumulates only after ABA accumulation. Chen *et al.* (2006) reported that *AtMYB4* (At1g22640), *AtMYB6* (At4g09460), *AtMYB7* (At2g16720), *AtMYB44* (At5g67300), *AtMYB73* (At4g37260), *AtMYB77* (At3g50060), and *AtMYBCDC5* (At1g09770) were found to be constitutively expressed in all organs and during all stress treatments (Chen *et al.* 2006). Two important MYC/MYB transcription factors AtMYC2 and AtMYB2 proteins bind to CACATG and TGGTTAG *cis*-acting elements, respectively, of the RD22 promoter of *Arabidopsis* and cooperatively activate this promoter (Abe *et al.* 1997).

TRANSGENIC PLANTS OVEREXPRESSING MYC/MYB TRANSCRIPTION FACTORS CONFERS ABIOTIC STRESS TOLERANCE

Overexpression of *AtMYC2* and *AtMYB2* and *AtMYC2* plus *AtMYB2* under constitutive promoter (CMV 35 S) in *Arabidopsis* induced ABA responsive stress genes. The transgenic plants showed an ABA-hypersensitive phenotype and increased osmotic stress tolerance (Abe *et al.* 2003). Overexpression of *MYB15* results in improved drought and salt tolerance in *Arabidopsis* (Ding *et al.* 2009). 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 *StMYB1R-1* transgene in potato plants improved plant tolerance to drought stress while having no significant effects on other agricultural traits (Shin *et al.* 2011).

CONCLUSION AND FUTURE PROSPECTIVE

The fact that World population is increasing exponentially but our food production is not increasing with this pace is worrying one and all. It is estimated that in 2050, world population will cross 9 billion (Godfray *et al.* 2010). Along with this, our arable land is decreasing day by day due to increasing severity of soil destruction by environmental conditions (Golldack *et al.* 2011). Abiotic stresses such as dehydration, high salinity, cold and heat are the major stresses, which affect plants metabolic and physiological process leading to heavy loss in crop yield. Although, conventional breeding has been very helpful in developing stress tolerant varieties of crop plants but it has its own limitations. In this context, transgenic technology can be an important alternative approach for enhancing stress tolerance in plants. In response to abiotic stresses, various categories of signaling molecules, functional proteins and regulatory proteins have been identified, which play an important role in plant tolerance toward these stresses. Since, abiotic stress is a complex phenomenon; genetic engineering of plants with regulatory protein like transcription factor can be a strong approach for enhancing plant tolerance to abiotic stresses, thus increasing the crop productivity. Various attempts have made to augment plant stress tolerance by overexpressing various kinds of functional proteins such as enzymes for the synthesis of osmoprotectants and ion transporters (Zhang *et al.* 2004). But, engineering of single enzymes is not sufficient, because multiple stress responses are necessary for plants to endure severe stress conditions. In plants, it is possible for a single transcription factor to control the expression of many target genes through the specific binding of the transcription factor to *cis* acting elements in the promoters of their respective target genes. In this regard, role of several transcription factors related to the plant response to abiotic stress has been elucidated and many of these factors have already been shown to be effective for engineering abiotic stress tolerance in model plants like tobacco or *Arabidopsis*. With this viewpoint, TFs such as CBF/DREB, bZIP and NAC transcription factors needs special attention, which have their unique significance due to their involvement in multiple stress responsive pathways. A number of transgenic plants have been generated using these TFs genes to improve abiotic stress tolerance, including drought, salt and cold (Saibo *et al.* 2009; Hussain *et al.* 2011). Therefore, to obtain a fruitful transgenic crop having economic values, it is essential to identify and functionally characterize new TFs genes and raise stable transgenic plants. A deeper understanding of the transcription factors regulating these genes, the products of the major stress responsive genes and cross talk between different signaling components should remain an area of intense research activity in future. It is desirable that appropriate stress inducible promoters should drive the stress genes as well as transcription factors, which will minimize their expression under a non-stress condition thereby reducing yield penalty.

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