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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

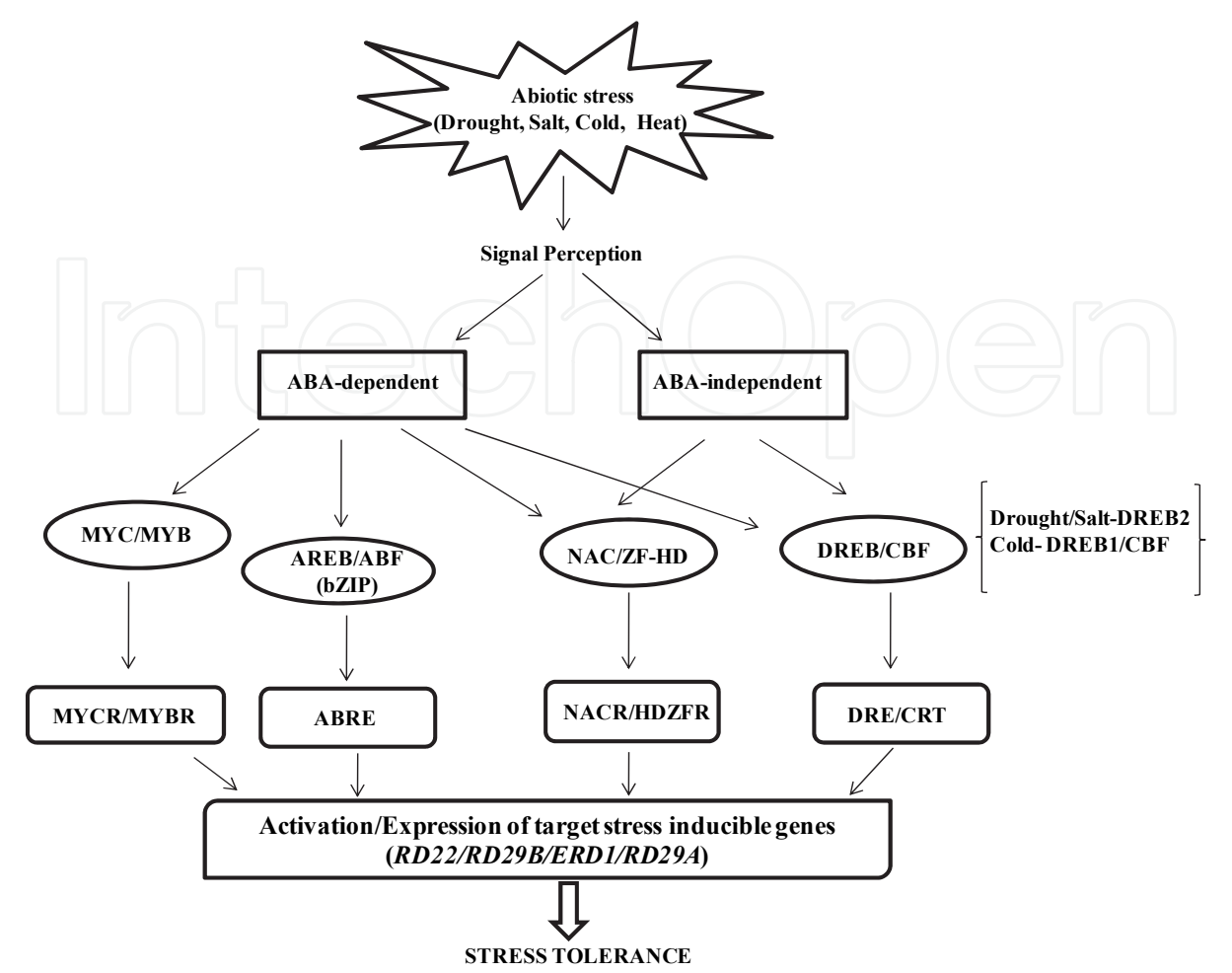


Fig. 1. A schematic representation of transcriptional regulatory networks of *cis*-acting elements and transcription factors involved in abiotic-stress-responses. Transcription factors are shown in ellipses; *cis*-acting elements are shown in boxes; and target stress inducible genes are shown in long 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).

Family	Gene	ABA response	Inducible by	Species	cis-element	References
bZIP	ABF1	Yes	Cold	<i>Arabidopsis thaliana</i>	ABREs (CACGTGGC/CGCGTGGC)	Choi et al., 2000
	ABF2	Yes	Salt, Drought	<i>Arabidopsis thaliana</i>	ABREs	Choi et al., 2000
	ABF3	Yes	Salt	<i>Arabidopsis thaliana</i>	ABREs	Choi et al., 2000
	ABF4	Yes	Drought, Salt, Cold	<i>Arabidopsis thaliana</i>	ABREs	Choi et al., 2000
	GmbZIP44	Yes	Drought, Salt	<i>Glycine max</i>	GLM (GTGAGTCAT)	Liao et al., 2008a
	GmbZIP62	Yes	Cold, Drought, Salt	<i>Glycine max</i>	ABRE (CCACGTGG)	Liao et al., 2008a
	GmbZIP78	Yes	Drought, Salt	<i>Glycine max</i>	PB-like (TGAAA)	Liao et al., 2008a
	GmbZIP132	Yes	Cold, Drought, Salt	<i>Glycine max</i>	GCN4-like motif (GTGAGTCAT)	Liao et al., 2008b
	Wlip19	Yes	Cold, Drought	<i>Triticum aestivum</i>	NA	Kobayashi et al., 2008
	OsABI5	Yes	Salt	<i>Oryza sativa</i>	G-box element (CACGTG)	Zou et al., 2008

Family	Gene	ABA response	Inducible by	Species	cis-element	References
	ZmbZIP17	Yes	Drought, Heat, Salt	<i>Zea mays</i>	NA	Jia et al., 2009c
	OsbZIP23	Yes	Drought, Salt, PEG	<i>Oryza sativa</i>	NA	Xiang et al., 2008
	OsAREB1	Yes	Drought, Heat	<i>Oryza sativa</i>	ABRE cis-element (ACGTGCC)	Jin et al. 2010
MYC	AtMYC2	Yes	Drought, Salt, Cold	<i>Arabidopsis thaliana</i>	CACATG	Abe et al., 2003
MYB	AtMYB2	Yes	Drought, Salt	<i>Arabidopsis thaliana</i>	TGGTTAG	Abe et al., 2003
	AtMYB4	Yes	Salt, Ethylene, JA, SA	<i>Arabidopsis thaliana</i>	NA	Yanhui et al., 2006
	AtMYB6	Yes	Salt, Ethylene, JA, SA	<i>Arabidopsis thaliana</i>	NA	Yanhui et al., 2006
	AtMYB7	Yes	Salt, Ethylene, JA, SA	<i>Arabidopsis thaliana</i>	NA	Yanhui et al., 2006
	AtMYB44	Yes	Salt, Ethylene, JA, SA	<i>Arabidopsis thaliana</i>	NA	Yanhui et al., 2006
	AtMYB73	Yes	Salt, Ethylene, JA, SA	<i>Arabidopsis thaliana</i>	NA	Yanhui et al., 2006
	MYB15	Yes	Drought, Salt, Cold	<i>Arabidopsis thaliana</i>	Type IIG Myb recognition sites	Agarwal et al., 2006; Ding et al., 2009
	GmMYB76	No	Salt	<i>Glycine max</i>	MBSI (TATAACGGTTTTT)	Liao et al., 2008c
	GmMYB92	No	Cold, Salt	<i>Glycine max</i>	MBSI, MRE4 (TCTCACCTACC)	Liao et al., 2008c
	GmMYB177	No	Drought, Salt	<i>Glycine max</i>	MBSI	Liao et al., 2008c
CBF/DREB	OsMYB3R-2	NA	Drought, Salt, Cold	<i>Oryza sativa</i>	NA	Dai et al., 2007
	DREB1A	No	Cold	<i>Arabidopsis thaliana</i>	DRE sequence (TACCGACAT)	Liu et al., 1998
	DREB2A	No	Drought, Salt	<i>Arabidopsis thaliana</i>	DRE sequence	Liu et al., 1998
	DREB2C	No	Salt, Mannitol, Cold	<i>Arabidopsis thaliana</i>	C-repeat/DRE	Lee et al., 2010
	CBF1	No	Cold	<i>Arabidopsis thaliana</i>	DRE/CRT	Gilmour et al., 1998
	CBF2	NA	Cold	<i>Arabidopsis thaliana</i>	DRE/CRT	Gilmour et al., 1998
	CBF3	NA	Cold	<i>Arabidopsis thaliana</i>	DRE/CRT	Gilmour et al., 1998
	CBF4	Yes	Drought	<i>Arabidopsis thaliana</i>	NA	Haake et al., 2002
	OsDREB1A	No	Cold, Salt, Wounding	<i>Oryza sativa</i>	GCCGAC	Dubouzet et al., 2003
	OsDREB1B	No	Cold	<i>Oryza sativa</i>	DRE/CRT	Dubouzet et al., 2003
	OsDREB1C	Yes	Drought, Salt, Cold, Wound	<i>Oryza sativa</i>	DRE/CRT	Dubouzet et al., 2003
	OsDREB1D	No	None	<i>Oryza sativa</i>	DRE/CRT	Dubouzet et al., 2003
	OsDREB1F	No	Drought, Salt, Cold	<i>Oryza sativa</i>	DRE/CRT	Wang et al., 2008
	OsDREB2A	No	Drought, Salt, faintly to Cold	<i>Oryza sativa</i>	DRE/CRT	Dubouzet et al., 2003
	OsDREB2B	No	Heat, Cold	<i>Oryza sativa</i>	DRE/CRT	Matsukura et al., 2010
	OsDREB2C	No	None	<i>Oryza sativa</i>	DRE/CRT	Matsukura et al., 2010
	OsDREB2E	No	None	<i>Oryza sativa</i>	DRE/CRT	Matsukura et al., 2010
	TaDREB1	No	Cold, Drought	<i>Triticum aestivum</i>	DRE sequence (TACCGACAT)	Shen et al., 2003a
	WDREB2	Yes	Drought, Salt, Cold	<i>Triticum aestivum</i>	NA	Egawa et al., 2006
	HvDRF1	Yes	Drought, Salt	<i>Hordeum vulgare</i>	T(T/A)ACCGCCTT)	Xue and Loveridge, 2004
	HvDREB1	No	Drought, Salt, Cold	<i>Hordeum vulgare</i>	DRE/CRT elements	Xu et al., 2009
	ZmDREB2A	No	Drought, Salt, Cold, Heat	<i>Zea mays</i>	DRE sequence	Qin et al., 2007
	PgDREB2A	No	Drought, Salt, Cold	<i>Pennisetum glaucum</i>	(DRE) ACCGAC	Agarwal et al., 2007
	SbDREB2	NA	Drought	<i>Sorghum bicolor</i>	NA	Bihani et al., 2011
	SiDREB2	No	Drought, Salt	<i>Setaria italica</i>	NA	Lata et al., 2011
	CaDREB-LP1	No	Drought, Salt, Wounding	<i>Capsicum annum</i>	NA	Hong and Kim, 2005
	AhDREB1	NA	Salt	<i>Artiplex hortensis</i>	DRE sequence	Shen et al., 2003b
	GmDREBa	No	Cold, Drought, Salt	<i>Glycine max</i>	DRE sequence	Li et al., 2005
	GmDREBb	Yes	Cold, Drought, Salt	<i>Glycine max</i>	DRE sequence	Li et al., 2005
	GmDREBc	No	Drought, Salt	<i>Glycine max</i>	DRE sequence	Li et al., 2005
	GmDREB2	No	Drought, Salt	<i>Glycine max</i>	DRE sequence	Chen et al., 2007
	DmDREBa	Yes	Cold	<i>Dendronthema x moriflorium</i>	DRE sequence	Yang et al., 2009

Family	Gene	ABA response	Inducible by	Species	cis-element	References
	DmDREBb	Yes	Cold	<i>Dendronthema x moriforlium</i>	DRE sequence	Yang et al., 2009
	PNDREB1	No	Drought, Cold	<i>Arachis hypogea</i>	DRE sequence	Mei et al., 2009
	CAP2	Yes	Drought, Salt, Auxin	<i>Cicer arietinum</i>	C-repeat/DRE (TACCGACAT)	Shukla et al., 2006
	DvDREB2A	Yes	Drought, Heat, Cold	<i>Dendrathema</i>	DRE sequence (TACCGACAT)	Liu et al., 2008
	SbDREB2A	NA	Drought, Salt, Heat	<i>Salicornia brachiata</i>	DREs (ACCGAC and GCCGAC)	Gupta et al., 2010
NAC	ATAF1		Drought	<i>Arabidopsis thaliana</i>	NA	Lu et al., 2007
	AtNAC2		Salt	<i>Arabidopsis thaliana</i>	NA	He et al., 2005
	AtNAC019		Drought, Salt	<i>Arabidopsis thaliana</i>	CATGTG motif	Tran et al., 2004
	AtNAC055		Drought, Salt	<i>Arabidopsis thaliana</i>	CATGTG motif	Tran et al., 2004
	AtNAC072		Drought, Salt	<i>Arabidopsis thaliana</i>	CATGTG motif	Tran et al., 2004
	OsNAC6		Cold, Drought, Salt	<i>Oryza sativa</i>	NA	Nakahsima et al., 2007
	SNAC1		Cold, Drought, Salt	<i>Oryza sativa</i>	NAC recognition sequence	Hu et al., 2006
	SNAC2		Cold, Drought, Salt	<i>Oryza sativa</i>	NAC recognition sequence	Hu et al., 2008
	CarNAC5		Drought, Heat	<i>Cicer arietinum</i>	NA	Peng et al., 2009
	TaNAC4		Cold, Salt, Wounding, Ethylene, MeJA	<i>Triticum aestivum</i>	NA	Xia et al., 2010
	GhNAC2		Cold, Drought	<i>Gossypium hirsutum</i>	NA	Meng et al., 2009
	GhNAC3		Cold	<i>Gossypium hirsutum</i>	NA	Meng et al., 2009
	GhNAC4		Cold, Drought, Salt	<i>Gossypium hirsutum</i>	NA	Meng et al., 2009
	GhNAC5		Cold, Drought	<i>Gossypium hirsutum</i>	NA	Meng et al., 2009
	GhNAC6		Cold, Drought, Salt	<i>Gossypium hirsutum</i>	NA	Meng et al., 2009
	SiNAC		Drought, Salt, Ethephone, MeJA	<i>Setaria italica</i>	NA	Puranik et al., 2011
WRKY	OsWRKY45			<i>Oryza sativa</i>	NA	Qiu and Yu, 2009
	GmWRKY21			<i>Glycine max</i>	W-box (TTGAC)	Zhou et al., 2008
	GmWRKY54			<i>Glycine max</i>	W-box	Zhou et al., 2008
	GmWRKY13			<i>Glycine max</i>	W-box	Zhou et al., 2008
	NbWRKY			<i>Nicotiana benthamiana</i>	NA	Archana et al., 2009
ZFP	ZPT2-3			<i>Petunia sp.</i>	NA	Sugano et al., 2003
	OSISAP1			<i>Oryza sativa</i>	NA	Mukhopadhyay et al., 2004
	CaZF			<i>Cicer arietinum</i>	EP1S (TGACAGTGICA)	Jain et al., 2009

Table 1. Response of transcription factors to various stresses.

Family	Gene	Transgenic Plants	Stress Tolerance	References
bZIP	ABF2	Arabidopsis	Drought	Kim et al., 2004
	ABF3	Arabidopsis	Drought	Kang et al., 2002
	ABF4	Arabidopsis	Drought	Kang et al., 2002
	GmbZIP44	Arabidopsis	Salinity, Freezing	Liao et al., 2008a
	GmbZIP62	Arabidopsis	Salinity, Freezing	Liao et al., 2008a
	GmbZIP78	Arabidopsis	Salinity, Freezing	Liao et al., 2008a
	GmbZIP132	Arabidopsis	Salinity	Liao et al., 2008b
	AtbZIP60	Arabidopsis	Salinity	Fujita et al., 2007
	Wlip19	Tobacco	Freezing	Kobayashi et al., 2008
	OsABI5	Rice	Salinity	Zou et al., 2008

Family	Gene	Transgenic Plants	Stress Tolerance	References
	OsZIP23	Rice	Drought, Salinity	Xiang et al., 2008
	OsAREB1	Rice	Drought, Heat	Jin et al. 2010
bHLH	AtMYC2	Arabidopsis	Osmotic stress	Abe et al., 2003
MYB	AtMYB2	Arabidopsis	Osmotic stress	Abe et al., 2003
	MYB15	Arabidopsis	Drought, Salinity	Ding et al., 2009
	OsMYB3R-2	Arabidopsis	Drought, Salinity, Cold	Dai et al., 2007
	OsMYB4	Arabidopsis	Freezing	Vannini et al., 2004
	OsMYB4	Arabidopsis	Drought	Mattana et al. 2005
	OsMYB4	Tomato	Drought	Vannini et al., 2007
CBF/DREB	AtDREB1A	Arabidopsis	Drought	Liu et al., 1998
	AtDREB1A	Tobacco	Freezing, Drought	Kasuga et al., 2004
	AtDREB1A	Wheat	Drought	Pellegrineschi et al., 2004
	AtDREB1A	Rice	Drought, Salinity	Oh et al., 2005
	AtDREB1A	Potato	Salinity	Behnam et al., 2006
	AtDREB1A	Peanut	Drought	Bhatnagar-Mathur et al., 2006
	AtDREB2A-CA	Arabidopsis	Drought	Sakuma et al., 2006
	AtCBF1	Arabidopsis	Salinity	Jaglo-Ottosen et al.,1998
	AtCBF2	Tomato	Freezing	Hsieh et al., 2002
	AtCBF3	Arabidopsis	Freezing	Gilmour et al., 2000
	AtCBF4	Arabidopsis	Freezing	Haake et al., 2002
	BNCBF5	Brassica napus	Freezing	Savitch et al., 2005
	BNCBF17	Brassica napus	Freezing	Savitch et al., 2005
	AtDREB2C	Arabidopsis	Thermotolerance	Lim et al., 2007
	OsDREB1A	Arabidopsis	Drought, Salinity, Freezing	Dubouzet et al., 2003
	OsDREB2B	Arabidopsis	Drought, Thermotolerance	Matsukura et al., 2010
	OsDREB1F	Rice, Arabidopsis	Drought, Salinity, Freezing	Wang et al., 2008
	OsDREB1G	Rice	Drought	Chen et al., 2008
	ZmDREB2A	Arabidopsis	Drought, Thermotolerance	Qin et al., 2007
	PgDREB2A	Tobacco	Hyperionic, Hyperosmotic	Agarwal et al., 2010
	AhDREB1	Tobacco	Drought, Salinity	Shen et al., 2003b
	LeCBF1	Arabidopsis	Freezing	Zhang et al., 2004
	GhDREB1	Tobacco	Freezing	Shan et al., 2007
	CAP2	Tobacco	Drought, Salinity	Shukla et al., 2006

Family	Gene	Transgenic Plants	Stress Tolerance	References
	PeDREB2	Tobacco	Salinity	Chen et al., 2009
	HvDREB1	Arabidopsis	Salinity	Xu et al., 2009
NAC	AtNAC2	Arabidopsis	Drought	Tran et al., 2004
	AtNAC019	Arabidopsis	Drought	Tran et al., 2004
	AtNAC055	Arabidopsis	Drought	Tran et al., 2004
	SNAC1	Rice	Drought, Salinity	Hu et al., 2006
	OsNAC6	Rice	Drought, Salinity	Nakashima et al., 2007
	ONAC045	Rice	Drought, Salinity	Zheng et al., 2009
ERF	SodERF3	Tobacco	Drought, Salinity	Trujillo et al., 2008
	GmERF3	Tobacco	Drought, Salinity	Zhang et al., 2009
WRKY	OsWRKY89	Rice	UV irradiation	Wang et al., 2007
	OsWRKY45	Arabidopsis	Drought, Salinity	Qiu and Yu, 2009
	GmWRKY21	Arabidopsis	Freezing	Zhou et al., 2008
	GmWRKY54	Arabidopsis	Drought, Salinity	Zhou et al., 2008
ZFP	Alfin1	Alfalfa	Salinity	Winicov and Bastola, 1999
	SCOF-1	Tobacco	Freezing	Kim et al., 2001
	ZPT2-3	Petunia	Drought	Sugano et al. 2003
	OSISAP1	Tobacco	Drought, Salinity, Freezing	Mukhopadhyay et al., 2004
	OSISAP2	Onion	Salinity	Xu and Que, 2007
	Zat12	Arabidopsis	Oxidative, Light Stress	Davletova et al., 2005
	Zat7	Arabidopsis	Salinity	Ciftci-Yilmaz et al., 2007
	CaZF	Tobacco	Salinity	Jain et al., 2009
Others	HARDY	Rice	Drought, Salinity	Karaba et al., 2007

Table 2. Stress response of overexpressing transcription factors in transgenic plants.

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-

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, C1, 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 (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 *AtMYBCDC5* (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 *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).

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 *OsDREB1B* 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/CBF1* or *DREB1A/CBF3* show strong tolerance to freezing, drought, and high salinity stresses implying that *DREBs/CBFs* affect multiple genes (Jaglo-Ottosen et al., 1998; Liu et al., 1998; Kasuga et al., 1999). *DREB1A/CBF3* 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/CBF3* wheat transgeneic showed improved drought stress tolerance (Pellegrineschi et al., 2004). Likewise, the constitutively overexpressing *CBF3/DREB1A* and *ABF3* 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 (*UGS5*) 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). *OSISAP1* 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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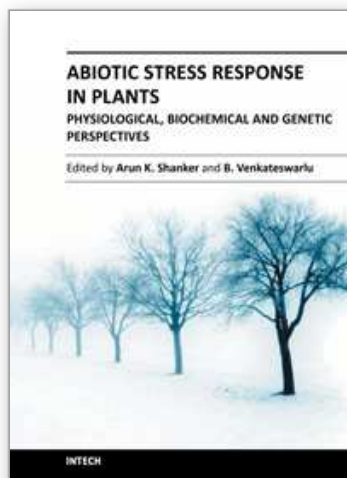
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Plants, unlike animals, are sessile. This demands that adverse changes in their environment are quickly recognized, distinguished and responded to with suitable reactions. Drought, heat, cold and salinity are among the major abiotic stresses that adversely affect plant growth and productivity. In general, abiotic stress often causes a series of morphological, physiological, biochemical and molecular changes that unfavorably affect plant growth, development and productivity. Drought, salinity, extreme temperatures (cold and heat) and oxidative stress are often interrelated; these conditions singularly or in combination induce cellular damage. To cope with abiotic stresses, of paramount significance is to understand plant responses to abiotic stresses that disturb the homeostatic equilibrium at cellular and molecular level in order to identify a common mechanism for multiple stress tolerance. This multi authored edited compilation attempts to put forth an all-inclusive biochemical and molecular picture in a systems approach wherein mechanism and adaptation aspects of abiotic stress are dealt with. The chief objective of the book hence is to deliver state of the art information for comprehending the effects of abiotic stress in plants at the cellular level.

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